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Abstract

Group-living animals, humans included, produce vocalizations like screams, growls, laughs, and victory calls. Accurately decoding such emotional vocalizations serves both individual and group functioning, suggesting that (i) vocalizations from in-group members may be privileged, in terms of speed and accuracy of processing, and (ii) such processing may depend on evolutionary ancient neural circuitries that sustain and enable cooperation with and protection of the in-group against outside threat. Here, we examined this possibility and focused on the neuropeptide oxytocin. Dutch participants self-administered oxytocin or placebo (double-blind, placebo-controlled study design) and responded to emotional vocalizations produced by cultural in-group members (Native Dutch) and cultural out-group members (Namibian Himba). In-group vocalizations were recognized faster and more accurately than out-group vocalizations, and oxytocin enhanced accurate decoding of specific vocalizations from one's cultural out-group—triumph and anger. We discuss possible explanations and suggest avenues for new research.

Keywords

emotions, group living, communication, hormones, evolution

In many group-living species, vocalizations such as screams, growls, and laughs communicate emotional states to conspecifics. Such signals can trigger receivers' tendencies toward social approach and affiliation or toward vigilance and protective defense. For example, laughter and sobs of grief both encourage closely coordinated, intimate interactions (Burgdorf et al., 2008; De Marco, Cozzolino, Dessi-Fulgheri, & Thierry, 2011), while screams of fear and victory calls may signal threat and trigger vigilance in the listener (Mouterde et al., 2012; Murphy, Lea, & Zuberbuhler, 2013). Thus, similar to other forms of nonverbal emotional communication, such as facial expressions and bodily postures, emotional vocalizations can induce or strengthen affiliation and approach or potentiate vigilance and avoidance (De Gelder et al., 2010; Frijda, 1986; Van Kleef, De Dreu, & Manstead, 2010).

In contrast to many other forms of emotional communication however, vocalizations do not require bodily agility or visual acuity. Furthermore, with emotional vocalizations being used by a broad variety of species, including dogs, dolphins, mice, rats, sheep, elephants, and nonhuman primates (Davis, Parr, & Gouzoules, 2003; Gurski, Davis, & Scott, 1980), emotional vocalizations are partly preserved across phylogenetic groups and may serve basic functions in group-living species (Belin et al., 2008; Darwin, 1872; Davila Ross, Owren, & Zimmermann, 2009; Marler & Mitani, 1988; Scheumann, Hasting, Kotz, & Zimmermann, 2014). Indeed, in humans, some types of emotional vocalizations are present from the very beginning of life (Blasi et al., 2011; DeCasper & Fifer, 1980), are processed very rapidly (Sauter & Eimer, 2010), and are cross-culturally consistent (Sauter, Eisner, Ekman, & Scott, 2010).

Although the accurate assessment of, and responding to, emotional vocalizations is well documented and understood (Bestelmeyer, Maurage, Rouger, Latinus, & Belin, 2014; Laukka et al., 2013; Pell et al., 2015), its neuroendocrine underpinnings remain elusive. Here, we fill this void by exploring perceptual assessments of emotional vocalizations as a function of oxytocin—a nine-amino acid peptide hormone that is synthesized primarily in the paraventricular and supraoptic nuclei of the hypothalamus and the posterior pituitary (Bos, Panksepp, Bluthe, & Van Honk, 2012; Carter, 2014; Donaldson & Young, 2008; Ludwig & Leng, 2006; Meyer-Lindenberg, Domes, Kirsch, & Heinrichs, 2011). We ask three main questions: (1) Does oxytocin influence the accurate assessment of

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emotion vocalizations in human subjects? (2) Is such possible influence moderated by the source of the vocalizations—whether the vocalizations were produced by members of a culturally familiar in-group or a culturally unfamiliar out-group? and (3) Is such possible influence moderated by the type of emotion that is being vocalized?

Oxytocin and Social Cognitive Processes

In both human and nonhuman animals, oxytocin is released and elevated during intimate social interactions such as birth and lactation, pair-bond formation, and interpersonal contact between parents and their offspring, close friends, and sharing among group members (e.g., Carter, 2014; Seltzer, Ziegler, & Pollak, 2010; Wittig et al., 2014). Upon its release from neuronal soma, axons, and dendrites, oxytocin flows through neural tissue by a process termed volume transmission, allowing the oxytocin molecule to quickly affect social–emotional functions in the brain (Carter, 2014; Domes et al., 2010; Donaldson & Young, 2008; Ludwig & Leng, 2006; Meyer-Lindenberg et al., 2011). Accumulating evidence suggests that in humans, oxytocin acts on the mesocorticolimbic circuitry promoting (affiliative) approach, especially when (social) stimuli have positive valence, and on the cortico-amygdala circuitry reducing withdrawal from (social) threat (thus permitting alternative responses to danger and threat than fight or flight; De Dreu & Kret, 2016; Harari-Dahan & Bernstein, 2014; Kemp & Guastella, 2011). Thus, oxytocin promotes the formation and maintenance of social bonds (e.g., Rilling & Young, 2014) and enables positive parent–offspring interactions such as play and caring (Feldman et al., 2010), as well as aggressive responding to danger, especially threat to offspring (so-called maternal defense; Bosch, Meddle, Beiderbeck, Douglas, & Neumann, 2005; De Dreu et al., 2010; De Dreu, Shalvi, Greer, Van Kleef, & Handgraaf, 2012).

Because of its involvement in group life, oxytocin may also have a functional role in decoding emotional vocalizations. Indeed, decoding emotional conspecific sounds recruits the auditory cortex along with the evolutionary ancient amygdalar-hippocampal circuitry (Blasi et al., 2011; Fecteau, Belin, Joanette, & Armory, 2007). This amygdalar-hippocampal circuitry is among the premier targets of hypothalamic oxytocin. Furthermore, Marlin, Miltre, D'amour, Chao, and Froemke (2015) recently showed that oxytocin enabled female mice to find and retrieve their pups based on the ultrasonic sounds that these pups emitted. Maternal pup retrieval relies on the (left) auditory cortex, an area dense in oxytocin receptors. Oxytocin in this region accelerated retrieval behavior, suggesting that oxytocin sensitizes the auditory cortex to acoustic social stimuli, such as vocalizations from isolated pups.

Two issues relating to oxytocin's role in the perception of acoustic social stimuli, such as emotional vocalizations, are addressed here. First, the study by Marlin, et al. (2015) considered vocalized cues from the mother's own offspring, to which she is attuned and familiar. One question is whether and how oxytocin in humans affects the processing of vocalizations from close others. We know that humans are better in assessing vocalizations produced by members of their own cultural group as compared to vocalizations from individuals belonging to distinct cultural groups (Sauter et al., 2010). Thus, for assessing emotional vocalizations, oxytocin may interact with cultural group membership, although the precise form of such an interaction is difficult to anticipate. On the one hand, distinguishing between cultural in-group and out-group manifests itself in a bias favoring emotional vocalizations from the cultural in-group. On the other hand, however, such stronger distinction may show up in enhanced attention to the features and characteristics of the cultural out-groups.

The second issue addressed here concerns the type of emotional vocalization. Marlin and colleagues (2015) focused on one particular type of vocalization—distress calls by pups isolated from their mother. Humans and other group-living animals vocalize a range of emotional states (Sauter et al., 2010). Here, we explored whether and how oxytocin affects the accurate decoding of emotional vocalizations of pleasure, amusement, relief, sadness, anger, disgust, fear, and triumph from cultural in-group and out-group members. These vocalizations were developed by and extensively tested in Sauter, Eisner, Ekman, and Scott (2010), who demonstrated accurate recognition by naive listeners. Importantly, these stimuli have been validated by listeners from the cultural groups, in which they were produced, ensuring that they represent recognizable signals of the intended emotions. Finally, this set includes a range of positive and negative emotions, allowing for fine-grained analysis of accuracy in decoding emotional vocalizations, and allowed us to explore possible interactions between specific emotion vocalizations, cultural group, and oxytocin. Expecting such interactions is not unrealistic, given that previous studies have found that intranasal administration of oxytocin in humans sometimes facilitates and sometimes impedes emotion recognition of and responding to facial displays of pleasure, anger, fear, and sadness (e.g., Bos et al., 2012; Ebitz, Watson, & Platt, 2013; Shahrestani, Kemp & Guastella, 2013; Van IJzendoorn & Bakermans-Kranenburg, 2012).

Method and Materials

Participants and Ethics

Male and female participants were recruited via an online system at the University of Amsterdam and offered a monetary reward of €10 for participating in a study on the effects of medication on test scores and decision-making. The experiment was approved by the Ethics Committee of the University of Amsterdam (file AO-749) and adhered to the Helsinki Protocol.

Statistical power. As this is the first study on decoding of acoustic stimuli as a function of oxytocin, power analyses and required sample size were determined as follows. First, our earlier work on effects of oxytocin on in-group favoritism (using the Implicit Association Test; De Dreu, Greer, Van

Kleef, Shalvi, & Handgraaf, 2011) provided an η^2 input of .083 into G-Power, which gave an required sample size of 89 (given $\alpha = .05$ and $\beta = .80$). We decided to recruit more because the estimated sample size was based on studies using males only. Second, Sauter et al. (2010) provided η^2 input into G-power to reliably detect effects for cultural group membership (collapsed across vocalizations) with an estimated sample size of 36 (given $\alpha = .05$ and $\beta = .80$). Accordingly, our sample of $N = 121$, with 25 (27) males and 35 (34) females in the oxytocin (placebo) condition, provides for a well-powered design.

Exclusion criteria. Potential participants filled out an online medical screening questionnaire and were invited only if their medical screening did not indicate any of the following: significant medical or psychiatric illness, medication, smoking more than five cigarettes per day, drug or alcohol abuse, and, in case of female participants (uncertainty about), pregnancy. Prior to the experiment, participants received information about the study and provided written informed consent. Upon completion of the experiment, participants received compensation and a written debriefing.

Substance Administration

Participants were instructed to refrain from smoking or drinking (except water) for 2 hr before the experiment. Experimental sessions took place between noon and 5 p.m. and lasted for approximately 1.5 hr. Participants were seated in individual, soundproof cubicles, and were randomly assigned to the oxytocin or placebo group (double-blind, placebo-controlled between-subjects design). Participants self-administered a single intranasal dose of 24 international unit (IU) oxytocin (Syntocinon Spray, Novartis, Basel, Switzerland; 3 puffs per nostril, each with 4 IU oxytocin) or placebo, 30 min before the start of the experimental tasks. To avoid any subjective (e.g., olfactory) effects other than those caused by oxytocin, the placebo contained all the active ingredients except for the neuropeptide and was delivered in the same bottles as the oxytocin spray (De Dreu et al., 2010; De Dreu et al., 2011).

Procedure, Experimental Tasks, and Measures

Following self-administration, the experimenter unlocked the participant's computer and left. Adhering to common practice in studies on oxytocin, participants worked on unrelated tests for 30 min, allowing the neural effects of intranasal oxytocin to peak (Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008; De Dreu et al., 2011; Kirsch et al., 2005). The test batteries included a 60-item personality measure, a 42-item measure of need for closure, a 15-item measure of social dominance orientation, and a 24-item measure of social value orientation. The order in which questionnaires were presented varied randomly between subjects. After 30 min, and regardless whether subjects had finished the measures, the computer switched to instructions for the main task. Questionnaire data were thus incomplete and not analyzed.

For the main task, participants were asked to put on headphones and were asked to classify vocalizations into one of eight possible emotions in a forced-choice task. They performed 192 randomly ordered trials (96 stimuli played in two runs: half in-group, half male; all emotions equally represented; Figure 1). In-group emotional vocalizations were adopted from previously validated Dutch stimuli (hearing sounds from Sauter, 2013). The out-group emotional vocalizations were taken from a validated set of Namibian stimuli (Sauter et al., 2010). Recordings were somewhat noisier for out-group vocalizations due to differences in recording conditions (see also Discussion and Conclusions).

Target stimuli were pleasure, amusement, relief, sadness, anger, disgust, fear, and triumph (Sauter, 2013; Sauter et al., 2010). Sauter et al. also included vocalizations of surprise, but these were not included here because surprise has, unlike the other emotions in this set, been conceptualized as a preaffective state (see Noordewier & Breugelmans, 2013). On each trial, the emotion that participants inferred, and decision latency, were recorded. Responses were coded as (in)accurate when they (did not) matched the emotion expressed in that vocalization, determined by the intended emotion of the sender. Because eight response options were given (pleasure, sadness, fear, anger, disgust, triumph, amusement, and relief), the baseline probability of being accurate was 12.5%. All categories of emotional vocalizations were accurately recognized above chance level.

Results

Data Analytic Approach

Inspection of the raw data revealed five extreme subjects that were classified as outliers (3 standard error [*SE*] $\pm$ mean accuracy and 3 *SE* $\pm$ mean response latency). Because removing these subjects had no substantive effects, we analyzed the full sample. The perception of emotional vocalizations was measured using recognition accuracy (coded as a binary variable: 0 = *incorrect*; 1 = *correct*) and response latencies. A binary distribution function, implemented in the generalized mixed multilevel model (GMML) in SPSS, was used for the accuracy data (see Appendix for computing scripts; also see http://www.ibm.com/support/knowledgecenter/SSLVMB_21.0.0/com.ibm.spss.statistics.help/alg_glmm_testing_df.htm for more detail about the computation of degrees of freedom underlying the inferential statistics of GMML).

To account for skewness in the reaction time data, we employed a γ distribution with a log link. Both accuracy and response latency data were thus analyzed using GMMLs with a random intercept for each subject and as fixed factors (interactions among) stimulus group (in-group/out-group), emotional vocalization (pleasure, sadness, fear, anger, disgust, triumph, amusement, and relief), and treatment (oxytocin/placebo). This approach is statistically more powerful, as it takes individual differences in intercept into account (as a random

Figure 1. Example of experimental setup (top) and sound stimulus (bottom).

effects variable), controls for interdependence and autocorrelations between trials, and permits the analysis of binary or skewed dependent variables. Thus, by nesting trials within individuals, we account for nonindependence across trials within individuals.

The two repetitions of each emotional vocalization were not modeled, as the nonindependence was deemed low due to the large number of trials and 48 different stimuli (in several ways, we tested whether trial was a random factor or not: for trial as random factor with ''participant'' as subject specification, $p = .790$; and for trial as random factor without any subject specification, $p = .325$). We further note that an alternative approach is to average responses across trials with the same emotional vocalization and analyze mean accuracy in standard analysis of variance (ANOVA) designs. This analysis produces similar results and permits identical conclusions.

Our study is among the few in which intranasal oxytocin was given to male and female subjects. Although we had no a priori expectations about possible gender effects, we decided to include main effects of gender, and its two-way interactions with emotion vocalization, group, and treatment. Higher order interactions were omitted because the number of males and females differed, rendering possible interpretation problematic.

Accuracy in Decoding Emotional Vocalizations

Accuracy in decoding emotional vocalizations was analyzed first. The overall model estimate was significant, $F(48, 23152) = 98.621$, $p \leq .0001$. Main effects for group, $F(1, 23152) = 1{,}353.722$, $p \leq .0001$, and emotion, $F(7, 23152) = 376.602$, $p \leq .0001$, were qualified by two-way interactions among

Table 1. Accuracy in Decoding Emotional Vocalizations From Cultural In-Group Members (Dutch) and Out-Group Members (Namibian Himba).

	Cultural In-Group		Cultural Out-Group				
Vocalization	M^a	SE^b	M	SE	t^c	$p \leq$	95% CI [LL, UL]
Triumph	.435	.013	.311	.012	6.915	.001	[.088, .158]
Amusement	.928	.007	.929	.006	−0.072	.943	[−.020, .020]
Anger	.623	.013	.271	.012	20.389	.001	[.318, .386]
Sadness	.677	.012	.511	.013	9.240	.001	[.131, 0.202]
Pleasure	.826	.009	.426	.013	24.428	.001	[.368, .432]
Disgust	.961	.005	.795	.011	14.161	.001	[.143, .189]
Fear	.640	.013	.389	.013	13.987	.001	[.216, .287]
Relief	.935	.007	.442	.013	33.786	.001	[.464, .521]

Note. CI = confidence interval; LL = lower limit; UL = upper limit.
[a]Numbers reflect proportion accurate (range 0.0–1.0; with chance-level accuracy = 0.125). [b]SE = standard error. [c]Values are based on paired sample t-tests.

Table 2. Accuracy in Decoding Emotional Vocalizations Following Intranasal Oxytocin or Placebo.

	Oxytocin		Placebo				
Vocalization	M^a	SE^b	M	SE	t^c	$p \leq$	95% CI [LL, UL]
Triumph	.395	.013	.349	(.013)	2.560	.011	[.012, .082]
Amusement	.947	.007	.906	(.006)	4.441	.001	[.024, .061]
Anger	.467	.013	.423	(.013)	2.386	.017	[.008, .019]
Sadness	.618	.012	.567	(.013)	2.771	.006	[.015, .086]
Pleasure	.611	.013	.641	(.012)	−1.665	.096	[−.065, .005]
Disgust	.883	.009	.873	(.008)	0.778	.437	[.014, .033]
Fear	.509	.014	.521	(.013)	−0.633	.527	[−.048, .025]
Relief	.698	.013	.678	(.012)	1.134	.257	[−.014, .053]

Note. CI = confidence interval; LL = lower limit; UL = upper limit.
[a]Numbers reflect proportion accurate (range 0.0–1.0; with chance-level accuracy = 0.125). [b]SE = standard error. [c]Values are based on paired sample t-tests.

group and emotion, $F(7, 23152) = 73.073$, $p \leq .0001$, and among emotion and treatment, $F(7, 23152) = 3.949$, $p \leq .001$.

The Group × Emotion interaction replicates earlier work in this area (e.g., Sauter et al., 2010) and is revealed in Table 1. As can be seen, all emotional vocalizations except for amusement are more accurately decoded when they are from one's cultural in-group rather than a cultural out-group (for amusement there is no difference in accuracy). The Emotion × Treatment interaction is shown in Table 2. It reveals oxytocin-enhanced (relative to placebo) decoding of mostly approach-oriented vocalizations like triumph, anger, sadness, and amusement (but not pleasure) and no such oxytocin enhancement for more avoidance-related vocalizations like disgust, fear, and, perhaps, relief. We return to this below.

Both two-way interactions were further qualified by a significant Group × Emotion × Treatment interaction, $F(7, 23152) = 3.590$, $p \leq .001$ (when collapsing across trials, a repeated measures ANOVA reveals this three-way interaction at $F(7, 833) = 2.138$, $p = .038$ with observed statistical power at 0.816). Figure 2 shows decoding as a function of group and treatment for each category of emotional vocalization. Because of the current focus on the effects of oxytocin, treatment effects within- (rather than between) cultural groups were estimated using student t-tests.

Several observations can be made. First, with the exception of amusement, $t(120) = 3.702$, $p = .001$, 95% confidence interval (CI) [0.024, 0.077], and relief, $t(120) = 2.181$, $p = .029$, 95% CI [0.003, 0.054], oxytocin did not improve accurate decoding of emotion vocalizations from one's own cultural group. Thus, triumph, anger, disgust, fear, pleasure, and sadness were all equally well decoded by participants receiving oxytocin or placebo. Second, oxytocin reduced accurate decoding of pleasure when it was vocalized by one's cultural out-group, $t(120) = -3.831$, $p = .001$, 95% CI [−0.149, −0.048]. Third, oxytocin enhanced accurate decoding for emotional vocalizations from one's cultural out-group, specifically for amusement, $t(120) = 2.576$, $p = .011$, 95% CI [0.008, 0.0612]), triumph, $t(120) = 2.729$, $p = .006$, 95% CI [0.019, 0.114], anger, $t(120) = 2.281$, $p = .023$, 95% CI [0.007, 0.099], and sadness, $t(120) = 2.057$, $p = .040$, 95% CI [0.003, 0.106].

Taken together, oxytocin improved accuracy for a range of emotional vocalizations produced by out-group members

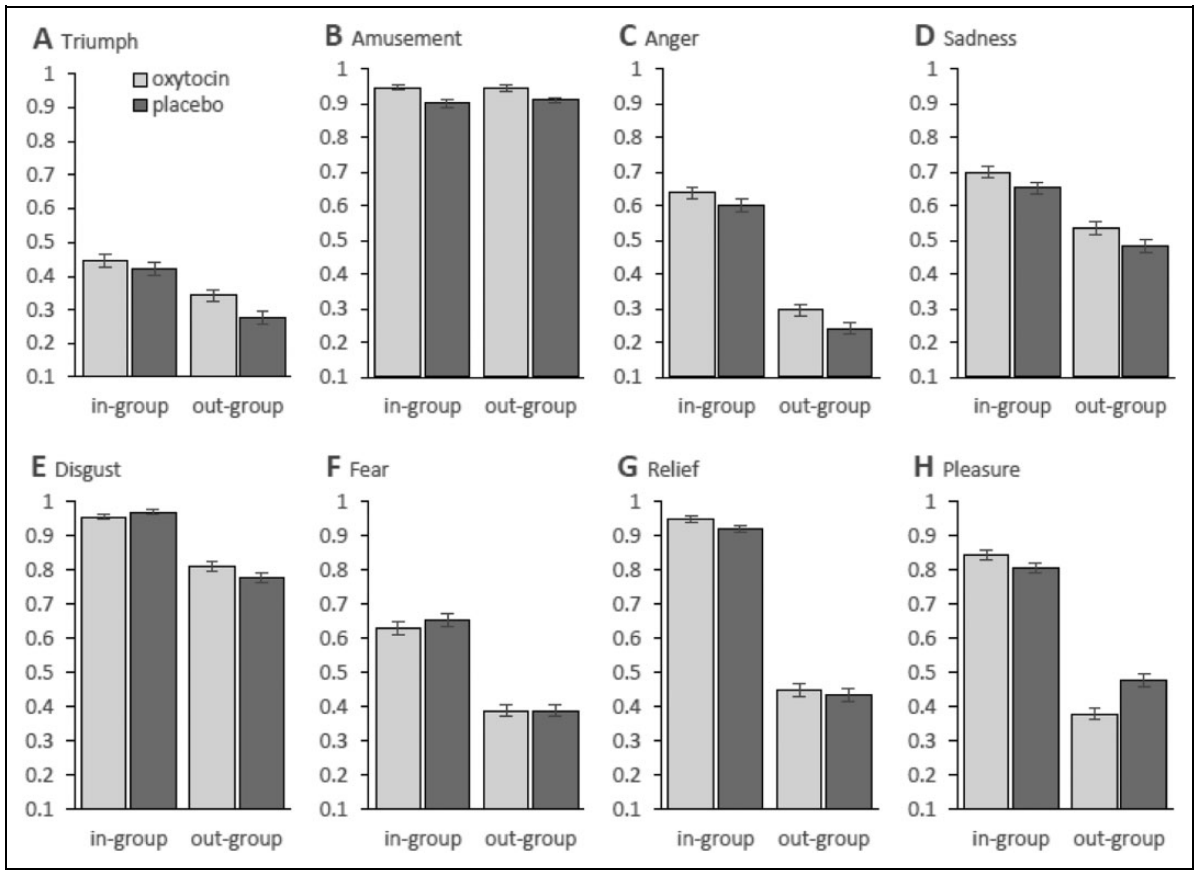

Figure 2. Decoding accuracy (range 0.0–1.0; chance level = 0.125) as a function of oxytocin and sender's cultural group (displayed mean ± SEM); connectors indicate significant contrasts at $p \leq .025$. (A) triumph, (B) amusement, (C) anger, (D) sadness, (E) disgust, (F) fear, (G) relief, and (H) pleasure.

(anger, sadness, triumph) as well as enhancing the recognition of amusement vocalizations from both in- and out-group members. Finally, oxytocin reduced accuracy for the recognition of pleasure vocalizations when produced by out-group members.

Gender. Gender had few effects and did not alter the patterns observed above. Next to a main effect for gender, $F(1, 23152) = 805.917$, $p \leq .0001$, we found two-way interactions between gender and group, $F(1, 23152) = 333.391$, $p \leq .0001$, and between gender and treatment, $F(1, 23152) = 6.515$, $p = .011$. Inspection of the means revealed that females were more accurate than males, especially when decoding emotional vocalizations from their own cultural in-group ($M_{\text{in-group}} = 0.8714$ vs. $M_{\text{in-group}} = 0.6349$), $t(120) = 30.721$, $p \leq .0001$, and somewhat less when decoding vocalizations from cultural out-groups ($M_{\text{out-group}} = 0.5582$ vs. $M_{\text{out-group}} = 0.4603$), $t(120) = 10.589$, $p \leq .001$. Also, females benefited somewhat more from oxytocin ($M_{\text{OT}} = 0.7290$ vs. $M_{\text{PL}} = 0.6988$), $t(120) = 3.593$, $p = .001$, and for males ($M_{\text{OT}} = 0.5534$ vs. $M_{\text{PL}} = 0.5411$), $t(120) = 1.330$, $p = .182$. We note that both interactions involving gender are ordinal rather than disordinal in form. It follows that, with regard to decoding emotional vocalizations, oxytocin does not have sexually dimorphic effects.

Response Latencies for Decoding Emotional Vocalizations

Possibly, oxytocin-enhanced accuracy in decoding is associated with slower responding (i.e., a speed-accuracy trade-off). To examine this, we analyzed (log transformed) response latencies for correct responses. Few effects emerged. We found a main effect of group, $F(1, 23152) = 66.549$, $p \leq .0001$, showing that responses to emotional vocalizations from the cultural in-group were faster than responses to the vocalizations from the cultural out-group ($M_{\text{in-group}} = 3.334$, $SE = .0025$ vs. $M_{\text{out-group}} = 3.438$, $SE = .0023$).

A Group × Emotion interaction, $F(7, 23152) = 39.918$, $p \leq .001$, showed that faster responses to cultural in-group vocalizations were found for all emotions, except for triumph and amusement (which did not differ significantly as a function of cultural group). These effects may be due to differences in materials used in the cultural in-group and out-group trials (see Method). We limit ourselves to noting that treatment was not involved in any of the effects. Because oxytocin did not significantly affect response latencies (all $F(7, 23,152] < 1$, all $ps > .1$), it can be concluded that oxytocin-induced changes in recognition accuracy for emotional vocalizations were not offset by reduced speed of responding.

Gender. Including gender and its two-way interactions with treatment, group, and emotion revealed a main effect for gender, $F(1, 23152) = 342.945$, $p \leq .0001$, and two-way interaction between gender and group, $F(1, 23152) = 84.641$, $p \leq .0001$, and between gender and emotion, $F(1, 23152) = 46.081$, $p \leq .0001$. Inspection of the means revealed that females were faster than males, especially when decoding emotional vocalizations from their cultural in-group ($M_{\text{females}} = 3.29$ vs. $M_{\text{males}} = 3.38$), $t(120) = -18.695$, $p \leq .0001$, and less when decoding vocalizations from their cultural out-group ($M_{\text{females}} = 3.40$ vs. $M_{\text{males}} = 3.43$), $t(120) = -5.747$, $p \leq .001$. The Emotion × Gender interaction revealed that female and male subjects were equally fast in decoding all emotions except sadness, which was decoded faster by female compared to male subjects. However, these effects are not discussed further because none of the contrasts reached statistical significance (all ts < 1.64, ps ≥ .11). Importantly, no interactions between gender and treatment reached significant, all Fs ≤ 1.30 and all ps ≥ .25.

Discussion and Conclusions

Recent work implicated oxytocin in auditory specialization in mice for perceiving emotional vocalizations from their offspring (Marlin, Miltre, D'amour, Chao, & Froemke, 2015). Our study addressed, firstly, whether such oxytocin-enhanced enhancement of auditory social stimuli occurs in humans too and whether it depends on the sender's cultural in-group or out-group membership. The answer is clear: Oxytocin enhances the accurate decoding of emotional vocalizations and the sender's cultural group membership matters. We further asked whether such oxytocin-enhanced specialization is specific for some emotional vocalizations or, alternatively, extends toward emotional vocalizations in general. Here, again our data provide a clear answer—oxytocin-enhanced decoding accuracy is seen for some emotional vocalizations but not for others.

The clarity of these overarching answers notwithstanding, the specific pattern of results was neither anticipated nor straightforward. Across the board, we found oxytocin-enhanced decoding performance for cultural out-groups in four of the eight emotions, and in two, we (also) found enhanced decoding performance for the cultural in-group. Only for pleasure did we see reduced performance for the out-group. In short, these results show that oxytocin enhances accurate decoding of emotional vocalizations from cultural out-groups, more than that it enhances accurate decoding of emotional vocalizations from the cultural in-group.

The four vocalizations from cultural out-groups, for which oxytocin enhanced accurate decoding, differ in valence (e.g., amusement and triumph vs. anger and sadness). It thus follows that oxytocin does not enhance (or reduce) decoding as a simple function of the vocalization's positive or negative valence. At the same time, it can be argued that the emotional vocalizations for which we observed oxytocin-enhanced decoding accuracy (triumph, amusement, anger, sadness) share and signal an approach orientation, whereas those vocalizations for which we saw no effects for oxytocin (relief, disgust, fear) share and signal an avoidance orientation—with disgust and fear being responses to impending threat and relief being a response to adequate avoidance (or resolution) or a threat (see, e.g., Amodio, Shah, Sigelman, Brazy, & Harmon-Jones, 2004; Baas, De Dreu, & Nijstad, 2008, 2011; Carver, 2009; Frijda, 1986; Higgins, 1997; Idson, Liberman, & Higgins, 2000; Mowrer, 1960; Van Kleef et al., 2010).

At the outset, we noted that oxytocin biases biobehavioral approach-avoidance toward approach and away from avoidance (De Dreu & Kret, 2016; Harari-Dahan & Bernstein, 2014; Kemp & Guastella, 2011). Although it may be that one outcome of the oxytocin-biased biobehavioral approach/avoidance system is a specific tuning toward approach-related triggers and signals, sounds included, the observed enhancement occurred only for vocalizations from a cultural out-group. One possibility is that expressions from out-group members were less clear (both acoustically and in terms of emotional meaning), thus requiring more work and mental effort. Indeed, recordings were somewhat noisier for out-group vocalizations due to differences in recording conditions. While this may have contributed to the overall in-group advantage found, earlier work showing that Namibian listeners perform better with the (noisier) Namibian stimuli as compared to (cleaner) English stimuli is inconsistent with such an explanation (Sauter et al., 2010). Furthermore, while we cannot exclude that some out-group vocalizations are decoded better under oxytocin because these were noisier (rather than being from a cultural out-group), it is difficult to see why this would pertain to some out-group vocalizations and not to others.

A second possibility is that recognition in some conditions reached a ceiling and could not further improve. While accuracy was high indeed in some conditions, the ceiling was not reached and unlikely impacted on our key findings with oxytocin. For example, even in the case of amusement, where recognition exceeded 90%, oxytocin still improved recognition. The same holds for triumph, where recognition was rather low at 35% and oxytocin also boosted recognition.

The third possibility, which we prefer, is that oxytocin not only induces a preference for approach-related stimuli but also enhances a more open-minded and holistic processing mode. There is some evidence that, indeed, oxytocin upregulates openness to experience and extroversion (Cardoso, Ellenbogen, & Linnen, 2014) and induces a global as opposed to more detail-focused mind-set (De Dreu et al., 2014). Perhaps individuals with higher levels of oxytocin take a broader perspective and more deeply process signals from members of other cultural groups. While such a proposition is compatible with the current findings, targeted research is needed to verify this possibility.

The proposal that oxytocin permits a broader and more inclusive processing of (approach triggering) information,

emotional vocalizations included, also fits with the established finding that oxytocin upregulates in-group bounded cooperation and empathy and defensive responding to (threatening) outsiders and cultural out-groups (see, e.g., De Dreu et al., 2010; 2011; 2012). Specifically, from a functionalist perspective, it follows that emotional vocalizations are decoded to further individual and group survival and prosperity, for example, to warn others about impending danger and to swiftly respond to such threat or to affiliate with and help others. Possibly, emotional vocalizations from cultural in-groups and out-groups have different meanings and behavioral implications (e.g., Frijda, 1986; Van Kleef et al., 2010). For example, vocalized triumph within one's cultural in-group may trigger affiliative tendencies, whereas vocalized triumph within a cultural outgroup may upregulate vigilance and protective shielding. Likewise, vocalization of sadness from someone within one's own cultural group may elicit stronger affiliation tendencies than sadness vocalizations from a cultural outgroup member.

A considerable number of previous studies have found that intranasal administration of oxytocin in humans sometimes facilitates and sometimes impedes emotion recognition and empathic responding to facial displays of pleasure, anger, fear, and sadness. However, findings are somewhat inconsistent and effect sizes tend to be small (Bos et al., 2012; Ebitz et al., 2013; Shahrestani, et al., 2013; Van IJzendoorn & Bakermans-Kranenburg, 2012). Our findings show that oxytocin modulates the recognition of not only facial expressions of emotion but also emotional vocalizations. Our study is the first to reveal strong moderation by the sender's group membership, with especially approach-triggering vocalizations from cultural out-groups being better decoded under oxytocin than placebo. Although we cannot rule out the possibility that the sender's group membership is important only for emotional vocalizations, our findings may suggest that some of the inconsistencies observed in earlier work on oxytocin and emotion recognition could be accounted for by perceived group membership and social categorization processes (also see Lambert, Declerck, & Boone, 2014; Melchers, Montag, Felten, & Reuter, 2015).

Far from being specific to humans, emotional vocalizations are observed in a broad range of group living animals (Davis et al., 2003; Gurski et al., 1980). Recent work implicates oxytocin in female mice retrieving their pups through enhanced sensitivity to pup (ultrasonic) vocalizations (Marlin et al., 2015). Our results suggest that oxytocin may be functional too when other emotional vocalizations are being emitted and herein lies an important avenue for future research. These findings fit well with the notion that (i) emotional vocalizations are partly preserved across phylogenetic groups, (ii) group-living animals, humans included, are biologically prepared to quickly and accurately identify conspecifics' emotional vocalizations, and (iii) such responding is sustained and facilitated by oxytocin.

Appendix

Computing Scripts for the Generalized Mixed Multilevel Model Analysis of Accuracy

```
GENLINMIXED
/DATA_STRUCTURE SUBJECTS=ID*group*trial
/FIELDS TARGET=accuracy TRIALS=NONE OFFSET=
NONE
/TARGET_OPTIONS REFERENCE=0 DISTRIBU-
TION=BINOMIAL LINK=LOGIT
/FIXED EFFECTS=group emot sex treatment group*emot
group*treatment emot*sex emot*treatment sex*treatment
group*emot*treatment group*sex emot*sex*treatment
USE_INTERCEPT=TRUE
/RANDOM USE_INTERCEPT=TRUE SUBJECTS=ID
COVARIANCE_TYPE=VARIANCE_COMPONENTS
COVARIANCE_TYPE=VARIANCE_COMPONENTS
/BUILD_OPTIONS TARGET_CATEGORY_ORDER=
ASCENDING INPUTS_CATEGORY_ORDER=ASCEN-
DING MAX_ITERATIONS=100 CONFIDENCE_
LEVEL=95 DF_METHOD=RESIDUAL COVB=MODEL
/EMMEANS_OPTIONS SCALE=ORIGINAL PADJUST=
LSD.
```

Authors' Note

C.K.W.D.D., M.E.K., and D.A.S. designed the experiment, coordinated data collection, analyzed the data, and wrote the article.

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