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The role of oxytocin in the facial mimicry of affiliative vs. non-affiliative emotions



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ABSTRACT

The present paper builds upon a growing body of work documenting oxytocin's role in social functioning, to test whether this hormone facilitates spontaneous mimicry of others' emotional expressions. In a double-blind, randomized trial, adult Caucasian males ($n = 145$) received a nasal spray of either oxytocin or placebo before completing a facial mimicry task. Facial expressions were coded using automated face analysis. Oxytocin increased mimicry of facial features of sadness (lips and chin, but not areas around the eyes), an affiliative reaction that facilitates social bonding. Oxytocin also increased mimicry of happiness, but only for individuals who expressed low levels of happiness in response to neutral faces. Overall, participants did not reliably mimic expressions of fear and anger, echoing recent theoretical accounts of emotional mimicry as dependent on the social context. In sum, our findings suggest that oxytocin facilitates emotional mimicry in ways that are conducive to affiliation, pointing to a possible pathway through which oxytocin promotes social bonding.

1. Introduction

In 1906, Lipps already suggested that emotional empathy stems from the motor mimicry of other people's facial movements, which through afferent feedback creates a matching emotional state in the observer. One century and many empirical studies later, this suggestion still holds (see Price and Harmon-Jones, 2015, for a review). Equally well supported is the idea that mimicry is motivated by affiliative goals (Lakin and Chartrand, 2003), and that it promotes both trust (Gueguen et al., 2013) and prosocial behaviour (van Baaren et al., 2004).

What remains unclear, however, are the biological antecedents that support emotional mimicry. We propose that one important factor that is part of this equation is oxytocin. We build upon a growing body of work documenting oxytocin's role in social functioning (reviewed in

MacDonald and MacDonald, 2010) to hypothesise that people with elevated oxytocin should display higher levels of mimicry. We further predict that this facilitating effect will be especially prevalent for emotions that inspire social approach and prosocial behaviour, such as happiness and sadness (Fischer et al., 2012; Goetz et al., 2010).

1.1. Social effects of oxytocin

Oxytocin has been shown to play a critical role in affiliation. It has been linked to physical proximity and social grooming (Feldman et al., 2011) as well as to high levels of emotional empathy, both self-reported and indexed by biological markers (Geng et al., 2018; Hurlmann et al., 2010; Shamay-Tsoory et al., 2013). Oxytocin is further implicated in reciprocal and synchronous social interactions—for example,

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peripheral oxytocin was found to be positively related to the degree of reciprocity between romantic partners, and it distinguished couples who were still together at a six-months follow-up from those who had broken up (Schneiderman et al., 2012). How does oxytocin support such complex social behaviours? It is possible that oxytocin amplifies participants' tendency for automatic motor simulation. If true, this would help explain evidence that oxytocin promotes emotion recognition (for recent meta-analyses see Leppanen et al., 2017; Shahrestani et al., 2013), memory representations of previously seen faces (Rimmele et al., 2009) and rapid conceptual detection of affect from social stimuli (Guastella and MacLeod, 2012).

1.2. Does oxytocin promote mimicry?

Studies investigating the role of oxytocin in non-emotional mimicry have rendered inconclusive results. Whereas one experiment found that oxytocin increased the tendency to simulate other people's finger movements (De Coster et al., 2014), another found no effect of oxytocin on contagious yawning (Gallup and Church, 2015). In fact, oxytocin made participants more likely to try to conceal their yawns. According to the authors, this may indicate the heightened sensitivity to the social stigma attached to public yawning and the reluctance to express signs of boredom that may promote disaffiliation with the experimenter.

For emotional mimicry, to our knowledge there is only one study so far reported in the literature, focusing on mimicry of happiness and anger (Korb et al., 2016). Oxytocin increased Corrugator Supercillii muscle (CS) activity in male adults in response to infants' expressions of anger (but only marginally for adult targets), and a small marginal increase was found for mimicry of infants' (but not adults') expressions of happiness. Although the authors interpreted this as evidence that oxytocin facilitates anger mimicry towards infant targets, CS activity was unspecific and could also have indicated sadness (Blairy et al., 1999) or worry (Peasley-Miklus and Vrana, 2000), opening the possibility that the effect reflected enhanced concern for the distress of a vulnerable other.

Taken together, these previous findings indicate that it may be insufficient to conceive of mimicry as simple perception-action matching in isolation from a given social context. Whereas actions such as copying someone's finger tapping may not signal a concrete social intent, yawning, smiling, pouting or frowning certainly do carry important social relevance (see also Hess and Fischer, 2013). Displaying and mimicking these types of behaviours may therefore have relevant consequences for social bonding. If oxytocin facilitates affiliation and bonding, it is plausible that it would differentially modulate the mimicry of gestures and facial expressions according to their social signal value.

When individuals mimic other people's facial muscle movements, they respond to the emotion expressed, its meaning and the intention of the expresser. Mimicry is most likely to occur when there is a shared understanding and thus a shared reaction to a stimulus, implying that mimicry signals social intentions (Hess and Fischer, 2016, 2013). For example, mimicking expressions of happiness communicates affiliative motives to share the happy state of mind (Hess and Fischer, 2013; Martin et al., 2017), and mimicking other people's sadness signals an understanding of their suffering and willingness to help (Bavelas et al., 1986; Hess and Fischer, 2014). On the other hand, mimicry of other emotions such as anger does not signal a bonding intention, but rather an antagonistic intention (Hess and Fischer, 2013). Congruent expressions (e.g. frowning) to displays of anger are thus unlikely to increase affiliation and might in fact convey hostile intention and initiate agonistic interactions (van der Velde et al., 2010; Van Kleef, 2010). The case of fear deserves some more elaboration. Fear is a signal that there is a threat in the environment, and may elicit mimicry when the threat is also perceived by the other person. In this case, the mimicry would be a response to the warning signal, and not an affiliative response. It is also worth noting that fear mimicry has not been consistently found in

experimental research: some researchers have found it (Laird et al., 1994; Magnee et al., 2007), whereas others have not (Lundqvist and Dimberg, 1997; Moody et al., 2007). In any case, fear mimicry does not signal a clear bonding intention.

1.3. Present study

Based on the above research and theoretical grounding, we hypothesised that oxytocin would facilitate facial mimicry of emotional displays, but only when the mimicry is an affiliative response and thus facilitates social bonding. That is, we expected oxytocin to increase facial mimicry of happiness and sadness, but not of anger and fear. We tested our hypotheses in a double-blind design where adult males were administered a nasal spray of either oxytocin or placebo before completing a mimicry task.

2. Methods

2.1. Participants

We calculated the required sample size using G*Power 3.1 (Faul et al., 2009) under the "MANOVA: Repeated measures, between factors" analysis, with the expected effect size $f = .2$, $\alpha = 0.05$, $power = .95$, $number\ of\ groups\ (Oxytocin\ or\ Placebo) = 2$, $number\ of\ measurements\ (5\ different\ types\ of\ emotions) = 5$, and $correlation\ among\ repeated\ measures = 0$. A total sample size of 68 participants were needed for this study. In a similar between-subject study on oxytocin and emotion mimicry, data from 60 participants was used (Korb et al., 2016). However, given the recent statistical and methodological considerations for the interpretation of intranasal oxytocin studies on humans, suggesting that intranasal OT studies are generally underpowered (Walum et al., 2016), we decided to collect a larger sample size.

One hundred and forty-five Caucasian males ($M_{age} = 24.5$; $SD_{age} = 5.7$) residing in Cambridge, United Kingdom, were randomly assigned to an oxytocin group ($n = 71$) or a placebo group ($n = 74$). Two additional individuals participated but their data were excluded from the final sample because of a technical difficulty with their video data (they were in the oxytocin group). Participants were invited through various mailing lists, including lab pools and student lists, posters distributed around the city and university buildings, social media, and word of mouth. They were instructed that the study tested the effects of oxytocin on social behaviour.

Inclusion criteria included being Caucasian, male⁵, between 18 and 55 years old, not diagnosed with any psychological problems in the past 5 years, being fluent in English, and not taking any medicine regularly. Participants' age did not differ between oxytocin ($M = 24.62$) and placebo ($M = 24.49$) conditions, $t(143) = -0.138$, $p = .89$. Participants taking temporary medicine for cough/cold were asked to take part in the study at least one week after they had stopped taking the medicine. They were also asked to abstain from food and drink (other than water) for 2 h before the experiment and from alcohol, smoking, and caffeine for 24 h before the experiment. Each participant was paid £25. Ethical approval was granted by the Cambridge Research Ethics Committee. Before the experiment, written informed consent was obtained from all participants according to the Declaration of Helsinki.

⁵ We did not include female participants in the current study for two main reasons: First, most human studies that manipulate OT experimentally have tested males only (see MacDonald and MacDonald, 2010) and we wanted to be able to compare our results to the rest of the literature. Second, females' menstrual cycle and oral contraception use have been shown to affect intranasal oxytocin's influence on socio-emotional tasks (Theodoridou et al., 2009) as well as the perception of emotional stimuli (Conway et al., 2007; Pearson and Lewis, 2005).

2.2. Overview of procedure

The study used a randomized, double blind between-subject experimental design. Participants were individually tested at a university hospital in a single visit during which they received either oxytocin or placebo, and completed a facial mimicry task. To ensure that groups did not differ on potential confounders, before the experimental session participants completed a series of questionnaires, including the Adult Attachment Scale (Collins and Read, 1990) and the Autism Spectrum Quotient Scale (Baron-Cohen et al., 2001). At the face-to-face visit, a medical doctor briefly talked to the participant to confirm details of their medical history and suitability for the study. The medical doctor then instructed the participant on how to self-administer a single dose of either 24 IU oxytocin (three puffs per nostril, each with 4IU OT) or placebo intranasally.⁶ To monitor any potential adverse reactions to oxytocin, participants had their blood pressure measured three times during the study: once after signing the consent form (before receiving the spray), once 35 min after having received the spray, and a third time at the end of the study.

After oxytocin administration participants waited in a quiet room. The mimicry task was the first task completed after treatment, and started approximately 50-min after the spray had been administered. Participants were in the testing room alone when doing this task. Following that, participants completed a series of other tasks related to social cognition and behaviour. This paper only reports our measure of mimicry.

2.3. Facial mimicry task

A procedure adapted from van der Schalk et al. (2011a) was used to measure facial mimicry, which required participants to watch a series of videoclips of individuals expressing different emotional states. Participants were seated on a comfortable chair about 70 cm from a computer screen, where all instructions, questions and videoclip stimuli were displayed. Their facial expressions were video recorded throughout the whole task through a webcam (Logitech C920 Full HD 1080p).

Participants were told to watch each expression closely and to keep their hands on the table (or mouse) during the task. This was to prevent participants from touching their faces, which would reduce the reliability of the facial expression coding. In order to draw participants' attention to the emotional expressions and to prevent them from guessing the true purpose of the task, they were told that the procedure assessed emotional recognition. To bolster this cover story, after each expression they were asked to rate on a 5-point Likert scale 'how intense was the emotion expressed?' from 'not at all' to 'very intense'. These ratings were also used to confirm that treatment did not influence how participants perceived the intensity of emotional stimuli. Participants were not told they would be video recorded during this particular task. However, as part of the consent procedure participants had been informed that portions of the study would be filmed.

The stimulus material included video clips of anger, fear, sadness and happiness displays, as well as neutral expressions, of different models adapted from the Amsterdam Dynamic Facial Expressions Set (ADFES, van der Schalk et al., 2011b). ADFES includes dynamic emotion expressions by North-European and Mediterranean, female and male models, and it has excellent recognition rates. Facial expressions are based upon prototypes of the 'basic emotions' as described in the Facial Action Coding System (FACS) Investigator's Guide (Ekman and Friesen, 1978). Each clip lasts 5 s and the model changes from a neutral facial expression to an emotional display (except in the neutral videos),

reaching apex at approximately 1 s.

Fig. 1 illustrates the experimental procedure. For each emotion, video clips of eight different models (four males and four females) were presented consecutively, in a randomised order. The order of the clips within each emotion block was randomised, as well as the order of the emotion blocks. At the beginning of the task, participants were presented with eight clips displaying dynamic neutral expressions by the same models and were asked to rate, on a 5-point Likert scale, how much they liked the model, and how negative or positive they felt about them. Friendliness and positivity ratings were used to confirm that treatment did not influence how participants perceive the models used as experimental stimuli. We did not instruct participants to keep a still face while watching the videos in the neutral block. This block was used to obtain a measure of participants' emotional expressivity in a neutral situation. At the end of all emotion blocks, participants completed a second neutral block (also with eight clips), which was aimed to neutralise potential emotional states induced as part of the task, and reduce carry over effects for subsequent tasks. Therefore, the final neutral block is not used for the purposes of the present study.

2.4. Facial expression coding

Participants' facial expressions were coded using OpenFace, an open source software for coding of facial behaviour (Baltrusaitis et al., 2016). Muscular activity of eleven different facial action units were coded using OpenFace's Action Unit Extraction Function (Baltrusaitis et al., 2015). The potential facial units used to detect mimicry of each of the four emotional states are illustrated in Fig. 2 – these were the FACS action units used as target codes by ADFES models (van der Schalk et al., 2011b). Please note that expressions of anger as displayed in ADFES also involve activity in AU7 (Lid tightener); however, extraction of this facial unit is not available in the current version of OpenFace. Therefore, only the remaining action units were used for this emotion.

In the final analysis, the following 11 action units were used: AU1, AU2, AU4, AU5, AU6, AU12, AU15, AU17, AU20, AU23, AU25.

Only the time during which participants were watching the video clips was considered for facial coding; all remaining recorded expressions (e.g., during instructions, while participants were giving ratings, etc.) were excluded from the analyses. Each second of participants' recorded expression corresponded to an average of 30 image frames. Given that the stimuli presentation during each emotion block lasted for 40 s (8 models x 5 s per video), each block consisted of a total of 1200 frames per participant. The software succeeded in identifying facial muscular activity (or lack thereof) in 97.7% of the frames; however, in 2.3% of the frames the software failed to detect a face due to extreme head motion or face occlusion due to face touching. The final number of frames did not differ by condition or emotion type ($p > 0.60$). Each image frame of the participants' recorded expressions was coded for the presence (1) or absence (0) of activity of each of the 11 facial action units.

For each image frame participants received a score corresponding to each facial action units of each emotional category that were expressed. That is, we calculated all the 11 AUs in neutral, happiness, anger, sadness, and fear, whether or not this AU was typical or not in this emotion.

The scores of each AU were averaged across all frames within each of the five emotion blocks. Participants therefore received 11 AU scores for each emotion block (that is, we had a score for AU1, AU2, AU4, AU5, AU6, AU12, AU15, AU17, AU20, AU23, AU25 for neutral, happiness, anger, sadness and fear), and each score ranged between zero and one. A score of zero indicated total absence of that particular AU in an emotional block whereas a score of one indicated an AU shown in all frames for that emotion block—that is, the higher the score, the more a certain facial unit the participant expressed when watching a certain emotion video. All analyses were conducted using R Studio 3.

⁶ The sprays were provided by Newcastle Specials Pharmacy Production Unit (Royal Victoria Infirmary, Queen Victoria Road, Newcastle upon Tyne, NE1 4LP). The ingredient was not disclosed by the supplier for commercial reasons.

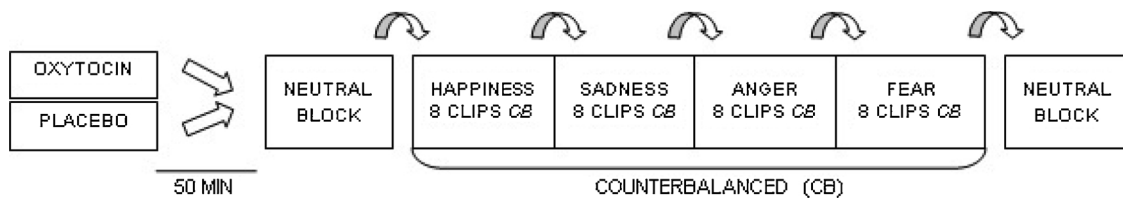


Fig. 1. Summary of the experimental procedure.



Fig. 2. Emotions (clockwise: happiness, anger, sadness and fear) and corresponding action units expressed by the models and coded in participants' recorded expressions; snapshots of the four expressions were reproduced with permission from the ADFES (van der Schalk, Hawk, et al., 2011).

3. Results

3.1. Preliminary analyses

Oxytocin and placebo participants did not differ in attachment, including closeness, $t(143) = -0.56$, $p = .58$, dependence, $t(143) = 0.50$, $p = .62$; anxiety, $t(143) = -.15$, $p = .88$, and avoidance, $t(143) = 0.02$, $p = .98$. Groups were matched on autistic traits, $t(143) = 1.24$, $p = .22$.

We also checked whether treatment influenced participants' perception of the experimental stimuli used for the mimicry task. Treatment did not influence how 'positive' participants felt about the models as indicated during the initial neutral block, $b = .12$, $p = .35$; neither did it influence how friendly they judged the models to be, $b = 0.14$, $p = .15$. Across the other four emotional blocks, treatment did not influence participants' ratings of how intense the emotions expressed by the models were, $b = 0.05$, $p = .53$. Taken together, these results suggest that oxytocin did not influence participants' perception of the models or facial expressions used in the mimicry stimuli.

3.1.1. Presence of facial mimicry

To assess whether our paradigm successfully elicited facial mimicry, we first verified whether patterns of facial activity as measured by AUs differed in response to congruent vs. incongruent emotion blocks for participants in the placebo condition. For example, AU6 activity during the happiness emotion block is 'congruent', but in all other emotion blocks it is 'incongruent'; therefore, higher activity in AU6 during happiness block (vs. others) is indicative of mimicry. AU4 activity in anger, sadness, and fear emotion blocks is all treated as 'congruent'; in 'happiness' and 'neutral' it is treated as 'incongruent'. Since in the

neutral block we did not instruct participants to keep a neutral expression, we treated it as an incongruent emotion block rather than an absolute baseline. We tested whether average activation of each AU in the congruent emotion block was higher than activation of that AU in all incongruent emotion blocks using contrast coding linear regression. It is worth mentioning that for different AUs, the number of incongruent blocks varied; accordingly, the emotion blocks that entered the contrast coding analysis also differed.

As shown in Table 1, all typical AUs for happiness (6, 12, 25) were more active during the happiness block than during incongruent blocks, suggesting that our stimuli successfully elicited mimicry of happiness. Similarly, two out of four typical AUs for sadness (4, 17) were more active in the sadness block than others, suggesting that participants mimicked sadness expressions. An average measure of all four typical AUs for sadness was also significantly higher in the congruent in comparison to incongruent blocks ($b = 0.05$, $p = .004$). However, only one typical AU for anger (AU4) was higher during congruent block vs. incongruent blocks, and an average measure of all typical AUs for anger did not differ between placebo and oxytocin groups ($b = 0.04$, $p = .15$). Similarly, no AUs typical of fear were higher during the fear block in comparison to incongruent blocks. Therefore, there was no strong evidence for mimicry of anger and fear.

Finally, a first inspection of the results also suggested an unusual high expression of AU23 across all emotion blocks (See Appendix for descriptive statistics for all AUs across all emotion blocks). AU23 is a lip tightener and may be a signal of upper concentration. Its more frequent occurrence might thus be due to the fact that our participants' were focused on the task. Therefore, the emotion mimicry using AU23 (anger) should be analysed with caution.

Table 1
Activation of relevant AUs during emotion-congruent vs. incongruent blocks, only among participants in the placebo condition.

Block	AU	M congruent block	M incongruent blocks	b
Happiness	AU6	.238	.147	.09**
	AU12	.311	.175	.13***
	AU25	.584	.494	.09*
Fear	AU1	.284	.258	.03
	AU2	.257	.253	.00
	AU4	.208	.165	.04
	AU5	.187	.135	.05
	AU20	.215	.289	-.08*
	AU25	.513	.494	.02
Sadness	AU1	.293	.258	.04
	AU4	.358	.165	.19***
	AU15	.323	.299	.02
	AU17	.211	.156	.05*
Anger	AU4	.390	.165	.22***
	AU5	.120	.135	-.01
	AU17	.178	.129	.05
	AU23	.862	.850	.01

* $p < .05$.

** $p < .01$.

*** $p < .001$; AUs in bold indicate evidence of mimicry.

3.1.2. Effects of oxytocin on emotion expressivity

We ran a multivariate regression model to confirm that oxytocin did not influence general AU expressivity—that is, participants' activity of different AUs while watching models displaying a neutral expression. As expected, the multivariate test showed no significant overall effect of oxytocin on AU expressions during the neutral block, Wilks's $\lambda = .93$, $F(1, 143) = 0.96$, $p = .48$, $\eta_p^2 = .07$. Among the 11 AUs, only AU23 was different in the oxytocin group compared to the placebo group, $b = -0.11$, $p = .02$, as there was less AU23 activation in the neutral emotion block by oxytocin group than the placebo group. The other 10 AUs did not differ between oxytocin and placebo conditions when watching the neutral emotion videos. We therefore suggest that oxytocin did not influence general (i.e. non-mimicked) facial expressions in response to neutral faces.

3.2. Main analysis

In the main analysis, we aimed to test whether oxytocin influenced emotion mimicry of happiness, sadness, fear and anger. For each of the four emotions, we ran two models. In the first model, we ran a linear regression with Treatment (placebo, oxytocin) as a predictor, and an average of all typical (i.e. congruent) AUs for each emotion block as outcome (e.g., the average of all happiness AUs—6, 12, and 25—in reaction to happiness videos, measured in that block; the average of all sadness AUs—1, 4, 15, 17—in reactions to sadness videos). In the second model, we ran a multivariate regression model, using Treatment (placebo, oxytocin) as a predictor, and all congruent AUs for each emotion block as outcomes (e.g. AU6, AU12, AU25 during the happiness block; AU1, AU4, AU15 and AU17 during sadness). This model was to test whether any effects were restricted to particular emotion congruent AUs.

For happiness, results indicated no effect of oxytocin on overall mimicry of happiness, $b = 0.05$, $t(143) = 1.30$, 95% $CI [-0.03, 0.13]$, $p = .20$, or either of the three congruent AUs (6, 12, 25), $ps > 0.05$. In contrast, we found a marginally positive effect of oxytocin on the mimicry of sadness, $b = 0.053$, $t(143) = 1.90$, 95% $CI [-0.002, 0.108]$, $p = .06$. Multivariate analysis suggested that oxytocin increased the activity of AU15 (lip corner depressor), $b = .11$, $t(143) = 2.02$, $p = .045$, as well as the activity of AU17 (chin raiser) in the sadness block, $b = .09$, $t(143) = 2.12$, $p = .036$; however, oxytocin did not significantly affect AU1 (inner brow raiser) or AU4 (brow lowerer), $ps > 0.05$. This suggests that oxytocin increased mimicry of facial

features of sadness, at least for the mouth and chin areas (Fig. 3).

Oxytocin did not influence overall mimicry of fear, $b = 0.003$, $t(143) = .18$, 95% $CI [-0.03, .03]$, $p = .86$, or any of the congruent AUs (1, 2, 4, 5, 20, 25), $ps > 0.05$. Finally, with regards to anger, participants in the oxytocin condition ($M = .35$, $SD = .14$) were marginally less likely to display mimicry than those in the placebo condition ($M = .39$, $SD = .11$), $t(143) = -1.83$, $p = .07$. Pair-wise comparisons suggested that this effect of oxytocin was driven by decreased activity of AU23, $b = -0.15$, $t(143) = -3.10$, $p = .002$. However, given that there was a Treatment difference of similar magnitude on AU23 in the neutral emotion block, the conclusion that oxytocin decreased the mimicry of anger may be premature. Indeed, when we removed AU23, there was no difference between the oxytocin group ($M = .23$, $SD = .16$) and the placebo group ($M = .23$; $SD = .13$) in anger mimicry, $t(143) = -0.04$, $p = .97$.

3.2.1. Exploratory analysis for happiness

Considering that mimicry of happiness occurs frequently and seems relatively independent of social context (Dimberg and Thunberg, 1998; Hinsz and Tomhave, 1991), we considered the possibility that any effect of oxytocin would be most noticeable among participants who displayed low levels of happiness during the initial neutral block, indicating reduced positive expressivity. Indeed, in the study of oxytocin's influence on social cognition, oxytocin is especially helpful for those who are low at baseline level (Bartz et al., 2010). To check for this interaction between oxytocin and general happiness, a regression model was run with Treatment (oxytocin versus placebo) as predictor, an average of happiness-congruent AUs (6, 12 and 25) in the neutral block as a moderator, and mimicry of happiness (the average of AUs 6, 12 and 25 in the happiness block) as outcome. This model revealed that the effect of oxytocin on mimicry of happiness was indeed qualified by an interaction with baseline happiness, interaction $b = -0.58$, $p = .01$.

As illustrated in Fig. 4, simple slope analysis indicated that, for participants who had expressed low happiness while watching neutral expressions (1SD below mean), oxytocin increased mimicry of happy faces, $b = .14$, $p = .01$, 95% $CI [0.04, 0.25]$, whereas no effect was observed for those who had already expressed high levels of happiness during the neutral block, $b = -.06$, $p = .26$, 95% $CI [-0.17, 0.05]$. These effects only applied to the average of happiness-congruent AUs, but not to any particular AU when tested separately ($ps > .05$). No analogous interactions were observed for the remaining three emotion blocks ($ps > .05$).

4. Discussion

In the present study, we found some evidence that a single dose of intranasally administered oxytocin facilitates quick and automatic mimicry of other people's facial expressions. Participants who had received oxytocin (versus placebo) were more likely to mimic facial features of sadness (i.e. pouting). In addition, we found that oxytocin increased mimicry of others' happiness, but only among participants who had expressed low levels of happiness while watching neutral faces. Because mimicry of both happiness and sadness fulfils a binding function, our results confirm the affiliative effect of oxytocin. Critically, no differences between treatment and placebo were found for facial expression while viewing neutral faces, confirming that the observed effects concerned mimicry and not general expressivity or emotionality. This was true for all AUs except 23 (lip tightening), which was less frequent for oxytocin than placebo, possibly reflecting the hormone's anxiolytic effects (Churchland and Winkielman, 2012).

We had initially predicted that oxytocin would facilitate mimicry of happiness/sadness but not fear/anger, given that mimicking the latter does not fulfil a clear bonding function. However, our mimicry task failed to elicit mimicry of fear rendering the treatment comparison irrelevant for this emotion. This is not entirely surprising: other researchers have also failed to find mimicry of fear (Lundqvist and

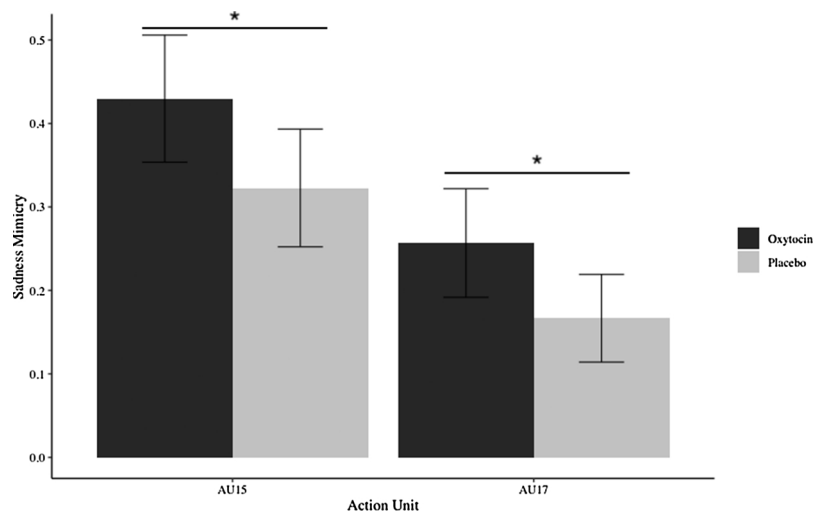


Fig. 3. Oxytocin increased facial mimicry in response to sadness videos for AU15 (lip corner depressor) and AU17 (chin raiser). Bars correspond to 95% confidence intervals. * $p < .05$

Dimberg, 1997; Moody et al., 2007), presumably because fear mimicry would normally occur in the face of an external threat, and not when simply watching another's fear face (Hess and Fischer, 2013). With regards to anger, we only found evidence for mimicry in the brow lowerer. In line with our prediction, brow lowerer activity during anger displays was equally frequent for participants in the oxytocin and placebo groups. However, to further confirm that oxytocin has differential effects on mimicry depending on its affiliative potential, our procedure should be replicated using experimental stimuli that are more conducive to mimicry of anger and fear. For example, researchers can use anger displays directed towards third persons (Hess and Fischer, 2013; see also Mumenthaler and Sander, 2012), or fear displays embedded in a threatening context (Laird et al., 1994), which are more likely to elicit mimicry.

Overall, our findings reinforce the notion that emotional mimicry is not entirely motor mimetic (Moody et al., 2007); rather, mimicry serves a social function, and therefore depends on the nature of the emotion displayed (Hess and Fischer, 2016). This view of mimicry as intrinsically meaningful within a social interaction helps reconcile inconsistent results from previous research. For example, whereas one study found that oxytocin increased finger movement mimicry (De Coster et al., 2014), another found that it reduced overt mimicry of actions that could promote disaffiliation with others (i.e. public yawning; Gallup and Church, 2015). As our present findings

preliminarily suggest, oxytocin might increase emotional mimicry when this holds potential affiliative effects. This highlights the importance of examining a range of gestures and/or emotional states in future mimicry research. Given that effects of oxytocin on prosocial tendencies are mostly parochial (see De Dreu, 2012, for a review), it also remains to be tested whether the present effects on sadness and happiness would be absent or reversed if the target was a threatening out-group member.

The observed effect of oxytocin on mimicry of facial features of sadness joins an ever-growing literature showing connections between oxytocin and other-oriented concern. For example, oxytocin was shown to increase perceptions of harm for victims (Krueger et al., 2013) and empathy to the physical pain of others (Riem, Voorthuis, Bakermans-Kranenburg, & van Ijzendoorn, 2014; Shamay-Tsoory et al., 2013). Our study is the first to show that these effects apply to automatic, unconscious behaviour at early perceptual levels of processing. Because our effects on mimicry of sadness were significant only for facial activity on the lips and chin (but not eyebrow), and marginal when using a composite measure of all sadness-congruent AUs, researchers should replicate this finding. However, it must also be considered that effect sizes in mimicry literature are typically small, due to the fact that participants are exposed to artificial, de-contextualised stimuli in a lab setting, which makes it difficult to take the other person's perspective. Researchers should consider replicating this study using an interactive,

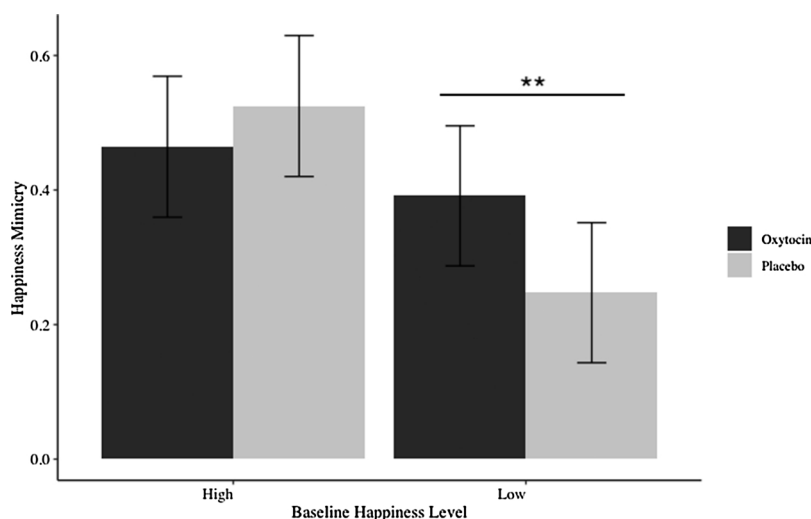


Fig. 4. Mimicry of happiness as a function of the interaction of happiness-congruent AUs during neutral block and condition (placebo vs. oxytocin). The graphed values for these variables were obtained from regression equations by using +1 SD as the value for high baseline happiness and -1 SD as the value for low baseline happiness. Bars correspond to 95% confidence intervals. ** $p < .01$.

naturalistic mimicry induction (Fischer et al., 2012) as well as other measures of facial activity (e.g., manual coding). If the effect is reliable, the low-level, spontaneous mimicry of sadness may be a key pathway through which oxytocin promotes complex forms of compassionate responding.

With respect to happiness, it was unexpected that oxytocin only amplified mimicry among participants who were less likely to smile while watching neutral faces. However, this may have been the case because, unlike other emotions, mimicking expressions of happiness is highly frequent and less variable across individuals. In fact, as long as the person is not an enemy (Likowski et al., 2008), smiles are often promptly reciprocated (Dimberg et al., 2000; Hinsz and Tomhave, 1991). Reciprocating a smile communicates that all is well and the person lacks any hostile intent, and therefore incurs a lower social cost than mimicking sadness, which cues intention to help (Bavelas et al., 1986). Further studies should replicate these effects in situations where gestural matching is less likely, such as when smiles are subliminally displayed.

Last but not least, a methodological note is in order. We adopted a novel way of coding facial mimicry, using an open-source software called OpenFace (Baltrusaitis et al., 2016). To date, the most common method for assessing mimicry has been facial electromyography (EMG). Despite its high precision and sensitivity, EMG mostly focuses on two major muscle groups in the face (Corrugator Supercilii and Zygomaticus Major), which reduces its potential for differentiating among discrete emotional states. More refined facial coding has been traditionally performed via laborious manual methods (Ekman and Friesen, 1978). Automated face analysis provides a promising methodological alternative, particularly considering its high concurrent validity with manual FACS coding (Cohn et al., 1999) and the ease with which it allows for the coding of numerous combinations of muscle contractions.

4.1. Conclusion

Our study provides some evidence to support the idea that oxytocin facilitates automatic responses to others' emotional displays in ways that are conducive to affiliation. Our findings contribute to our understanding of the role of oxytocin in attachment, empathy and reciprocity, and might have future therapeutic implications for the treatment of mental health conditions characterised by social difficulties.

Declaration of Competing Interest

The authors have no competing interests to declare.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.psyneuen.2019.104377>.

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