Psychoneuroendocrinology (2014) 50, 220–226

Available online at www.sciencedirect.com

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The influence of Oxytocin on automatic motor simulation

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Received 22 April 2014; received in revised form 29 August 2014; accepted 31 August 2014

KEYWORDS
Oxytocin;
Automatic imitation;
Motor simulation;
Self-other distinction;
Mirror neuron system

Summary Motor simulation is important for imitation, action understanding, and a wide range of social cognitive skills. Furthermore, the neuropeptide hormone Oxytocin (OT) has also been related to social information processing in humans, improving perception of social stimuli and increasing altruism and trust. Surprisingly, however, a direct link between OT and motor simulation has never been systematically investigated. The current study examined this question using the imitation-inhibition task, a paradigm used to investigate automatic imitation behaviour and motor simulation. In this task, participants carry out simple finger movements while observing irrelevant movements that either match (congruent condition) or do not match (incongruent condition) the instructed movements. In a double-blind, placebo-controlled design, male participants were administered either OT ($N = 24$) or placebo ($N = 24$), and subsequently performed the imitation-inhibition task. To ensure specificity of OT effects to imitative behaviour, participants additionally performed a Stroop colour-word interference task (adapted to optimize similarities with the imitation inhibition task) to rule out general effects on cognitive control. As predicted, OT selectively influenced the congruency effect in the imitation-inhibition task but not the congruency effect in the Stroop task. This effect showed that OT led to a larger congruency effect by slowing down reaction times on incongruent trials when observed and own actions did not match. The findings suggest that OT leads to a decrease of control over automatic imitative behaviour mediated by increased self-other merging. Thus, for the first time, a link between OT and motor simulation is demonstrated, providing a window into the role of OT in motoric aspects of social cognition.

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http://dx.doi.org/10.1016/j.psyneuen.2014.08.021
0306-4530/

1. Introduction

Throughout history, humans have lived in tight relation to one another and formed groups in various contexts. Bonding behaviours have been shown to have several (evolutionary) advantages, both on a physical and cognitive level (Buss and Kenrick, 1998; Chou et al., 2011). One essential process by which relationships between people seem to be enhanced is imitative behaviour. Compelling studies indicate that being imitated by another person subsequently leads to increased liking of the other person, smooth interactions, and different forms of pro-social behaviour that generalize towards people not initially included in the imitative interaction (Chartrand and Bargh, 1999; van Baaren et al., 2004; Stel et al., 2008). Thus, a wide range of research provides evidence for the idea that imitation elicits positive consequences in social interactions, due to a shift towards interdependent orientation (Ashton-James et al., 2007). Other research suggests that imitation is based on a mechanism that directly matches the observed action onto a corresponding motor representation in the observer (Iacoboni et al., 1999). Such a motor simulation mechanism has not only been related to imitation but also to action understanding (Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2010). One way to investigate motor simulation is by automatic imitation paradigms where participants have to execute an action in response to an imperative cue while observing congruent or incongruent movements (Brass et al., 2000; see Heyes, 2011 for a review). Indeed, participants respond faster and more accurate when the observed action matches the instructed action (congruent) compared to a case where the observed action is different (incongruent) from the instructed action (Brass et al., 2000). This congruency effect indicates that movement observation leads to an activation of a motor representation in the observer, supporting the motor simulation idea. Furthermore, studies have documented that automatic motor simulation is sensitive to a number of social factors such as attributed intentionality and social attitudes (e.g. Liepelt et al., 2008; Leighton et al., 2010). While it has been shown that automatic imitation is influenced by hormone levels such as testosterone (Hermans et al., 2006), the influence of Oxytocin (OT) on this behaviour has never been investigated.

Interestingly, the neuropeptide hormone OT is strongly related to the processing of social information in humans (e.g. Bos et al., 2012; Heinrichs and Domes, 2008; Veening and Olivier, 2013). In particular, researchers have found improvement in perceiving social stimuli and increased empathy after OT administration (Domes et al., 2007b; Kéri and Benedek, 2009; Hurlemann et al., 2010; Marsh et al., 2010; Perry et al., 2010). Furthermore, when OT levels are increased, people seem to become more altruistic, trusting, and generous (Kosfeld et al., 2005; Baumgartner et al., 2008), possibly due to a reduction of anxiety (Meyer-Lindenberg et al., 2011; Viviani et al., 2011) and/or altering social information processing (Ellenbogen et al., 2012, 2013). Grillon et al. (2013), however, have shown that OT increases anxiety to unpredictable situations, suggesting that the response of OT is dependent upon the familiarity of the situation. This and other research has lead to nicknames such as ''the love hormone'' (e.g. Ferguson et al., 2002), indicating that OT plays a key role in social behaviour.

Given the role of OT in prosocial behaviour and affiliation, the question arises whether OT levels might also influence automatic motor simulation. The aim of the present study is to directly investigate the effect of OT on automatic motor simulation and to test the hypothesis that OT influences motor simulation. To this end, the imitation-inhibition task was used, a stimulus-response compatibility (SRC) paradigm that has been shown to be a reliable index of automatic imitation behaviour (Brass et al., 2000). In this task, participants carry out simple finger movements in response to imperative cues while observing irrelevant finger movements that either match (congruent condition) or do not match the instructed movement (incongruent condition). Since both OT and imitative behaviour seem to enhance prosocial behaviour, we expected a positive relationship between OT and automatic motor simulation. Thus, we predicted that increased OT levels would lead to a larger congruency effect (difference between incongruent and congruent trials) in the imitation-inhibition task as an index of a stronger influence of automatic imitative behaviour. In order to ensure that OT effects were specific to automatic motor simulation and were not related to general cognitive control processes, we also tested the influence of OT on the Stroop task (Stroop, 1935), which has a similar non-motor related interference condition. To optimize similarities between both tasks, the original Stroop paradigm was adapted to resemble the imitation inhibition task as closely as possible (e.g. using finger lifting responses). In this control task, we expected no change in interference effects.

2. Methods

2.1. Participants

Forty-eight healthy young adult men (age range = 18—32 years) participated in the study in exchange for 40 Euros, and provided written informed consent beforehand. Participants were recruited via the official recruitment website of the Faculty of Psychology and Educational Sciences. Ethical approval was granted by the institutional review board of Ghent University Hospital. Participants had no history of neurological disorders and were medication-free, as verified by questionnaires. To avoid sex differences in OT response, only males were recruited.

Both groups (OT versus Placebo) did not differ with respect to age (M_{OT} = 21.50, SD_{OT} = 3.11; $M_{PLACEBO}$ = 21.67, $SD_{PLACEBO}$ = 3.02) and education demographics (mostly psychology students), initial scores on Positive And Negative Affective Schedule (PANAS; Watson et al., 1988; Positive Affect: M_{OT} = 3.56, SD_{OT} = .45; $M_{PLACEBO}$ = 3.29, $SD_{PLACEBO}$ = .44; Negative Affect: M_{OT} = 1.57, SD_{OT} = .45; $M_{PLACEBO}$ = 1.69, $SD_{PLACEBO}$ = .58) or Interpersonal Reactivity Index (IRI; Davis, 1980; Perspective Taking: M_{OT} = 17.90, SD_{OT} = 3.86; $M_{PLACEBO}$ = 14.91, $SD_{PLACEBO}$ = 4.35; Empathic Concern: M_{OT} = 17.83, SD_{OT} = 4.52; $M_{PLACEBO}$ = 18.36, $SD_{PLACEBO}$ = 3.51; Fantasy: M_{OT} = 16.70, SD_{OT} = 5.17; $M_{PLACEBO}$ = 15.09, $SD_{PLACEBO}$ = 6.52; Personal Distress: M_{OT} = 10.35, SD_{OT} = 4.46;

$M_{PLACEBO}$ = 11.22, $SD_{PLACEBO}$ = 5.32), or experienced symptoms (all *p*s > .05).

2.2. Stimuli and apparatus

For the imitation-inhibition task (Brass et al., 2000), stimulus material consisted of images (300 × 200 pixels) depicting a hand in resting position or a hand performing an index or middle finger lifting movement (all from a third person perspective). At the time of the movement images, the number '1' or '2' was presented in the centre between the index and middle finger, signalling that participants had to perform either an index or middle finger movement respectively. As such, three types of trials were possible: (1) baseline trials in which a number was presented without a finger movement of the hand on screen, (2) congruent trials in which the number signalled a movement that corresponded to the movement observed on screen (e.g. '1' and index finger movement), and (3) incongruent trials in which the number signalled the opposite movement (e.g. '1' and middle finger movement). In this task, the observed number was the relevant dimension, whereas the observed hand movements were irrelevant.

For the Stroop task, stimulus material consisted of the Dutch translation of the words 'yellow' or 'blue' (font = Calibri, font size = 80) written in either yellow or blue ink. Furthermore, yellow and blue rectangles (of the same size as the corresponding words) could also be presented. Thus, there were again three types of trials: (1) baseline trials in which a coloured rectangle was presented, (2) congruent trials in which the word meaning and word ink corresponded (e.g. 'blue' written in blue ink), and (3) incongruent trials in which word meaning and word ink did not correspond (e.g. blue written in yellow ink). In this task, the ink colour of the word/rectangle was the only relevant dimension, with words written in blue ink requesting an index finger lifting movement and words in yellow ink signalling that the middle finger had to be lifted.

For both tasks, lifting movements were recorded with a custom-built response device using light sensors to measure reaction times and errors.

2.3. Procedure

Using a double-blind design, participants were randomly assigned to receive either intranasal OT (*n* = 24; 24 IU Syntocinon Spray, Novartis, Basel, Switzerland) or intranasal saline placebo (*n* = 24). As such, both participants and experimenter were unaware of the condition participants were assigned to. Participants completed measures of positive and negative affect (PANAS) and trait empathy (IRI), demographics, and medication use immediately after substance administration. However, because responses to OT do not typically emerge until approximately 45 min after administration (see e.g. Marsh et al., 2010 for a similar procedure), we did not expect responses on the questionnaires to be influenced by OT. Subsequently, participants received instructions for the imitation-inhibition task and the Stroop task. Forty-five minutes after substance inhalation, half of the participants started with the imitation-inhibition task, while the other half started with the Stroop task (additionally counterbalanced with substance randomization). Each task had a total duration of approximately 30 min, consisting of six blocks of 48 trials (16 trials for each type with congruent and incongruent trials being presented in a random order), with a total number of 288 trials. Each trial started with a black screen of 2000 ms. In the imitation-inhibition task, the hand in resting position was then presented for 2000 ms, while a movement and number were shown subsequently for 1300 ms. In the Stroop task, five fixation crosses were presented next to each other for 2000 ms and the words or rectangles were presented for 1300 ms. At the end of each trial, a black screen was shown for 700 ms in both tasks.

At the end of the experimental phase, participants again completed the PANAS to detect possible changes in affect. Furthermore, they filled in a questionnaire listing several adverse symptoms possibly related to OT (MacDonald et al., 2011).

2.4. Data analysis

A .05 significance level was used in all statistical tests. A 2 (Task: Imitation-inhibition or Stroop) × 3 (Congruency: Baseline, Incongruent, or Congruent) repeated measures ANOVA with Group (OT or Placebo) as between-subjects variable was used to analyze RTs and errors (homogeneity of variance assumption was met as demonstrated by non-significant Levene's tests). Furthermore, responses to the PANAS questionnaire were analyzed using a 2 (Valence: Positive or Negative) × 2 (Time: Pre or Post) repeated measures ANOVA with Group (OT or Placebo) as between subjects factor. Partial eta squared (η_p^2) and Cohen's *d* were used as measures of effect size.

3. Results

Both groups did not differ with respect to demographics (age, education), PANAS and IRI scores, or experienced symptoms (all *p*s > .05).

3.1. Reaction times

The three-way interaction between Task, Congruency, and Group was significant, $F(2,45) = 3.43$, $p < .05$, $\eta_p^2 = .13$, while all other main effects (including a Group effect, $F(1,46) = 1.04$, $p > .31$) and interaction effects were not significant (all *p*s > .37). Planned comparisons for the imitation-inhibition task revealed that the congruency effect (incongruent minus congruent trials) was significantly larger in the OT relative to the Placebo group, $t(46) = 2.22$, $p < .05$, $d = .65$ (see Fig. 1), indicating an influence of OT on motor simulation. Similar comparisons for the Stroop task indicated no effect of OT, $t(46) = 1.37$, $p > .18$. Since we expected OT to specifically increase RTs on incongruent trials rather than decrease RTs on congruent trials, we conducted planned one-tailed *T*-tests on the difference between incongruent/congruent and baseline trials. It was revealed that the difference between incongruent and baseline trials was significantly larger in the OT group when compared to the Placebo group, $t(46) = -1.74$,

$p < .05$, $d = .51$, while the difference between congruent and baseline trials did not differ significantly for both groups, $t(46) = .41$, $p > .30$. Similar planned comparisons for the Stroop task did not reveal any effect of group ($p > .18$) suggesting specificity of the observed effects on the motor simulation system. Additionally, a significant main effect of Task, $F(1,46) = 33.91$, $p < .001$, $\eta_p^2 = .42$ and Congruency, $F(2,45) = 49.40$, $p < .001$, $\eta_p^2 = .69$ were observed, as well as the interaction between these two factors, $F(2,45) = 10.27$, $p < .001$, $\eta_p^2 = .31$. As shown in Fig. 1, RTs were slower in the Stroop task (566.79 ms) compared to the imitation-inhibition task (489.37 ms), and were slower in incongruent (563.81 ms) trials compared to congruent trials (505.20 ms) and baseline trials (515.23 ms). Furthermore, the effect of Congruency was larger in the imitation-inhibition compared to the Stroop task. Finally, the order of tasks with which participants started (Stroop or imitation-inhibition task first) did not play a role (all $ps > .20$).

3.2. Accuracy

A significant main effect of Task, $F(1,46) = 8.02$, $p < .01$, $\eta_p^2 = .15$ and Congruency, $F(2,45) = 21.35$, $p < .001$, $\eta_p^2 = .49$ was observed, as well as a interaction between these two factors, $F(2,45) = 3.77$, $p < .05$, $\eta_p^2 = .14$ (Fig. 2). However, the three-way interaction with Group was not significant, $F(2,45) < 1$. All planned comparisons, as well as task order tests were not significant (all $ps > .30$).

No correlation between RTs and error rates was observed (all $ps > .24$), suggesting the absence of a speed-accuracy trade-off.

3.3. Questionnaires

PANAS: A 2 (Valence: Positive or Negative) × 2 (Time: Pre or Post) repeated measures ANOVA with Group (OT or Placebo) as between subjects factor was computed. A main effect of Valence, $F(1,46) > 50$, $p < .001$, $\eta_p^2 = .88$ and Time, $F(1,46) = 29.71$, $p < .001$, $\eta_p^2 = .39$ as well as an interaction between both factors, $F(1,46) = 9.81$, $p < .01$, $\eta_p^2 = .18$ was found. However, no main effect ($p > .77$) or interactions (all $ps > .05$) were detected. Thus, both groups showed a significant reduction in positive affect only. This was true for the Placebo group with higher scores on the initial ($M = 3.48$, $SE = .09$) compared to the final assessment ($M = 3.12$, $SE = .13$) and the OT group, initial assessment: $M = 3.38$, $SE = .09$; final assessment: $M = 3.01$, $SE = .12$. No correlations were found between positive (all $ps > .40$) and negative (all $ps > .21$) PANAS scores and RTs on the imitation-inhibition task.

4. Discussion

The present study sought to provide a missing link for the influence of OT on motor simulation, given that imitative behaviour is hypothesized to form the basis of a number

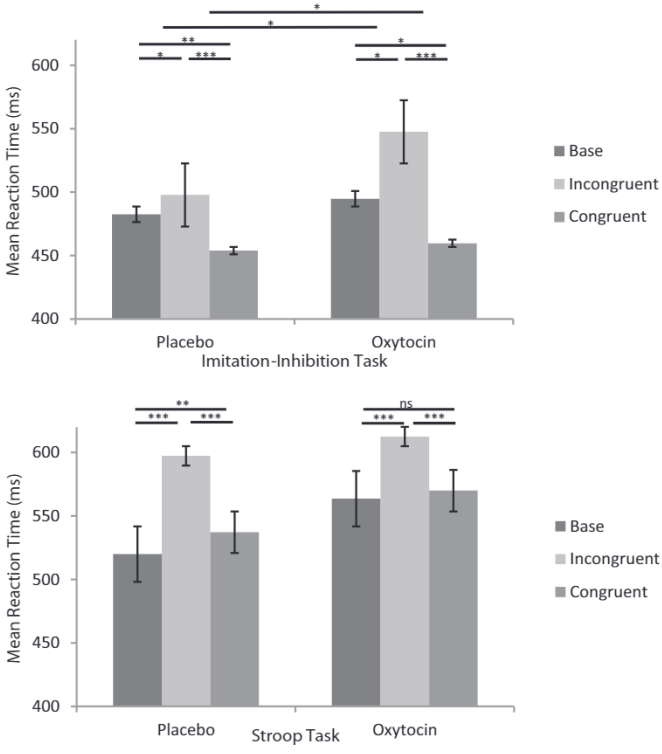

Figure 1 Mean reaction times (RTs; ms) on baseline, incongruent and congruent trials for the Placebo and Oxytocin group. The upper panel displays RTs on the imitation-inhibition task; the bottom panel displays RTs on the Stroop task. Error bars are standard errors of the mean. *p-value < .05, **p-value < .01, ***p-value < 001, ns: p-value > .05.

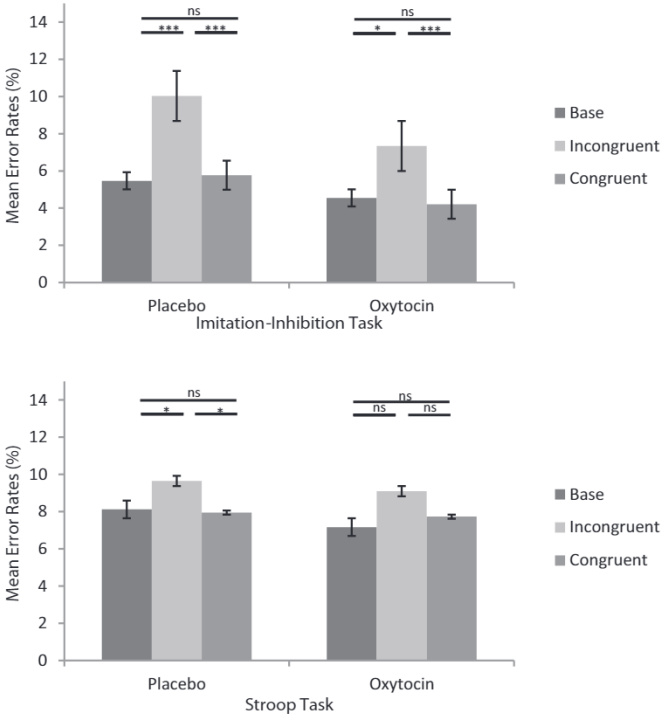

Figure 2 Mean error rates (%) on baseline, incongruent and congruent trials for the Placebo and Oxytocin group. The upper panel displays RTs on the imitation-inhibition task; the bottom panel displays RTs on the Stroop task. Error bars are standard errors of the mean. *p-value < .05, ***p-value < 001, ns: p-value > .05.

of social cognitive skills. Using a task that indexes such motor simulation, we predicted that OT would increase interference of automatic motor simulation but not interference during non-social cognitive control. As expected, OT increased the congruency effect (incongruent versus congruent trials) in the imitation-inhibition task but not the Stroop task, indicating a specific influence of OT on automatic motor simulation. Furthermore, supporting our hypothesis, OT seemed to selectively influence incongruent trials (compared to baseline trials), suggesting that its influence on automatic motor simulation is not caused by stronger response facilitation in congruent trials but by stronger interference in incongruent trials.

To our knowledge, our results provide first evidence for the hypothesis that OT has an influence on motor simulation. By showing that this effect is specific to the imitation-inhibition task, the results show that the influence of OT on automatic motor simulation is not due to general task processing or cognitive control processes but is restricted to interference in social situations. Yet, the mechanisms by which OT influences motor simulation are still unclear. One potential hypothesis is that OT exerts a direct impact on the brain circuits involved in motor simulation. Motor simulation has been strongly linked to the so-called mirror neuron system (MNS), which consists of the inferior frontal cortex and the inferior parietal cortex (see Brass and Heyes, 2005 for a review). Furthermore, it has been argued that the MNS plays a crucial role in social cognition (e.g. Rizzolatti and Craighero, 2004; Kaplan and Iacoboni, 2006; Bastiaansen et al., 2009; Brass et al., 2009). Thus, one possibility would be that the effect of OT on automatic motor simulation is caused by a facilitative effect on the MNS, which in turn leads to prosocial behaviour.

Alternatively, one could argue that OT decreases self-other distinction and therefore leads to larger interference costs. Interference effects in the imitation-inhibition task have previously been related to a brain network involved in self-other distinction including the temporo-parietal junction (TPJ) area and the medial prefrontal cortex (Brass et al., 2009, 2001; Spengler et al., 2010b). In particular, the TPJ seems to play a crucial role in the imitation-inhibition task as indicated by fMRI (Brass et al., 2005; Spengler et al., 2010b) and TMS/tDCS research (Sowden and Catmur, 2013). This line of work would suggest that OT impacts brain areas involved in self-other distinction.

In point of fact, the observation that OT administration increases the interference effect rather than increases the facilitation effect is more in accordance with the hypothesis that OT affects brain areas involved in self-other distinction such as the TPJ. Although direct evidence for this neuroanatomical hypothesis is still lacking, some indirect support comes from research in autism spectrum disorders (ASD). ASD has been linked to TPJ functioning (e.g. Lombardo et al., 2011), and recent research suggests that OT has positive effects on social processing in ASD (Green and Hollander, 2010; Yamasue et al., 2012; Miller, 2013; Tachibana et al., 2013). Furthermore, it has been demonstrated that individuals with ASD show larger interference effects in the imitation-inhibition task and deficits in the imitation-inhibition task have been linked to TPJ functioning in ASD (Spengler et al., 2010a). Thus, future studies could systematically and directly investigate the influence of OT on TPJ functioning in relation to autistic traits, which would provide important knowledge concerning clinical implications of OT in psychopathology.

While it is unclear why this interference of self-other distinction takes place, we believe that a self-other merging account is highly plausible. Research has shown that similarity between observer and observed person determines difficulties in distancing oneself from the other (Meltzoff, 1995; Kilner et al., 2003; Tai et al., 2004), and that individuals with increased self-focus show reduced automatic imitation (Obhi et al., 2014). Thus, this research indirectly indicates that self-other merging might be an important process by which self-other distinction operates, suggesting that shared representations between self and other are at the core of this mechanism.

There is one recent study, however, that seems to be at odds with the hypothesis that OT decreases self-other distinction. Colonnello et al. (2013) have demonstrated that perceptual judgements in a face recognition task requiring self-other distinction were enhanced by OT. In this task, photos of subjects were morphed onto unfamiliar faces (or vice versa), and participants were asked to distinguish other- and self-related features. Latency of self-other differentiation was reduced after OT administration. However, several important differences between the current task and the task used by Colonnello et al. (2013) might have contributed to the discrepant findings. First, there is a clear distinction between the task used by Colonnello et al. (2013), which is a pure perceptual task and the current paradigm which is a motor interference task. Self-other confusion in the current task is not about determining the identity of a person but rather the origin of a specific motor representation. It might well be that because OT enhances attention to social stimuli (Guastella et al., 2008; Ellenbogen et al., 2012; Leknes et al., 2013), several perceptual tasks involving social stimuli would improve. Secondly, during the face recognition task of Colonnello et al. (2013), participants were explicitly instructed to pay attention to self- versus other-related features of the stimuli. In the imitation-inhibition task, however, movements of the other person seen on screen are completely irrelevant for the task being performed. Thus, self-other differentiation might be much more covert in the current paradigm. Furthermore, superior performance in a face discrimination task might be related to enhanced amygdala function as indicated by previous work on emotional facial expressions (Kirsch et al., 2005; Domes et al., 2007a). However, further research combining perceptual and motor tasks is needed to better understand the impact of OT in the perceptual and motor domain. While research seems to suggest that OT effects are more pronounced in a social-interactive context (Veening and Olivier, 2013), our findings indicate that OT influences more basic mechanisms of social cognition as well. Indeed, a recent study by Zheng et al. (2014) has shown that OT modulates sensory experience much earlier in development than the previously described role of OT in social—emotional behaviours.

Finally, as predicted, OT specifically modulated congruency in a movement observation task but not a classical cognitive control task. Thus, we were able to rule out a general effect of OT, and confirm the specific role of OT in social cognition. Furthermore, it has to be noted that

no effect of OT were observed in error rates. However, previous literature suggests that RTs are more sensitive to (social) manipulations in the imitation-inhibition task (e.g. Leighton et al., 2010; Tomova et al., 2014). As such, we believe that the absence of effects in error rates is not surprising. Importantly, no evidence for a speed-accuracy trade-off was found. One limitation of the present study that hinders generalizability of the current findings, however, concerns the fact that, due to restrictions by the ethical committee, we only recruited men and moreover, that most of these participants were psychology students.

In sum, our results demonstrate, for the first time, a link between OT and motor simulation. We suggest that OT decreases control of automatic imitative behaviour by decreasing self-other distinction. This has implications for the effect of OT in a wide range of social situations, since it shows the influence of OT on a control mechanism important in social cognition.

Role of the funding source

This research was supported by Research Foundation Flanders Grant FWO10/ASP/321 to the first author.

Conflicts of interest

The authors declare no conflicts of interest.

References

Ashton-James, C., van Baaren, R.B., Chartrand, T.L., Decety, J., Karremans, J., 2007. Mimicry and me: the impact of mimicry on self-construal. Soc. Cogn. 25, 518—535.

Bastiaansen, J.A.C.J., Thioux, M., Keysers, C., 2009. Evidence for mirror systems in emotions. Philos. Trans. R. Soc. B: Biol. Sci. 364, 2391—2404.

Baumgartner, T., Heinrichs, M., Volanthen, A., Fischbacher, U., Fehr, E., 2008. Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. Neuron 58, 639—650.

Bos, P.A., Panksepp, J., Bluthé, R.M., van Honk, J., 2012. Acute effects of steroid hormones and neuropeptides on human social—emotional behavior: a review of single administration studies. Front. Neuroendocrinol. 33, 17—35.

Brass, M., Heyes, C., 2005. Imitation: is cognitive neuroscience solving the correspondence problem? Trends Cogn. Sci. 9, 489—495.

Brass, M., Bekkering, H., Wohlschläger, A., Prinz, W., 2000. Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. Brain Cogn. 44, 124—143.

Brass, M., Zysset, S., von Cramon, D.Y., 2001. The inhibition of imitative response tendencies. NeuroImage 14, 1416—1423.

Brass, M., Derrfuss, J., von Cramon, D.Y., 2005. The inhibition of imitative response tendencies: a functional double dissociation of imitative and overlearned responses. Neuropsychologia 43, 89—98.

Brass, M., Ruby, P., Spengler, S., 2009. Inhibition of imitative behaviour and social cognition. Philos. Trans. R. Soc. B: Biol. Sci. 364, 2359—2367.

Buss, D.M., Kenrick, D.T., 1998. Evolutionary social psychology. In: Gilbert, D.T., Fiske, S.T., Lindzey, G. (Eds.), The Handbook of Social Psychology. Oxford University Press, New York, pp. 982—1026.

Chartrand, T.L., Bargh, J.A., 1999. The chameleon effect: the perception-behaviour link and social interaction. J. Pers. Soc. Psychol. 76, 893—910.

Chou, K.L., Liang, K., Sareen, J., 2011. The association between social isolation and DSM-IV mood, anxiety, and substance use disorders: wave 2 of the National Epidemiologic Survey on Alcohol and Related Condition. J. Clin. Psychiatry 72, 1468—1476.

Colonnello, V., Chen, F.S., Panksepp, J., Heinrichs, M., 2013. Oxytocin sharpens self-other perceptual boundary. Psychoneuroendocrinology 38, 2996—3002.

Davis, M.H., 1980. A multidimensional approach to individual differences in empathy. JSAS Cat. Sel. Doc. Psychol. 10, 85.

Domes, G., Heinrichs, M., Gläscher, J., Büchel, C., Braus, D.F., Herpetz, S.C., 2007a. Oxytocin attenuates amygdala responses to emotional faces regardless of valence. Biol. Psychiatry 15, 1187—1190.

Domes, G., Heinrichs, M., Michel, A., Berger, C., Herpertz, S.C., 2007b. Oxytocin improves ''mind-reading'' in humans. Biol. Psychiatry 61, 731—733.

Ellenbogen, M.A., Linnen, A.M., Grumet, R., Cardoso, C., Joober, R., 2012. The acute effects of intranasal oxytocin on automatic and effortful attentional shifting to emotional faces. Psychophysiology 49, 128—137.

Ellenbogen, M.A., Linnen, A.M., Cardoso, C., Joober, R., 2013. Intranasal oxytocin impedes the ability to ignore task-irrelevant facial expressions of sadness in students with depressive symptoms. Psychoneuroendocrinology 38, 387—398.

Ferguson, J.N., Young, L.J., Insel, T.R., 2002. The neuroendocrine basis of social recognition. Front. Neuroendocrinol. 23, 200—224.

Green, J.J., Hollander, E., 2010. Autism and oxytocin: new developments in translational approaches to therapeutics. Neurotherapeutics 7, 250—257.

Grillon, C., Krimsky, M., Charney, D.R., Vytal, K., Ernst, M., Cornwell, B., 2013. Oxytocin increases anxiety to unpredictable threat. Mol. Psychiatry 18, 958—960.

Guastella, A.J., Mitchell, P.B., Dadds, M.R., 2008. Oxytocin increases gaze to the eye region of human faces. Biol. Psychiatry 63, 3—5.

Heinrichs, M., Domes, G., 2008. Neuropeptides and social behaviour: effects of oxytocin and vasopressin in humans. Prog. Brain Res. 170, 337—350.

Hermans, E.J., Putman, P., van Honk, J., 2006. Testosterone administration reduces empathetic behavior: a facial mimicry study. Psychoneuroendocrinology 31, 859—866.

Heyes, C., 2011. Automatic imitation. Psychol. Bull. 137, 463—483.

Hurlemann, R., Patin, A., Onur, O.A., Cohen, M.X., Baumgartner, T., Metzler, S., Dziobek, I., Gallinat, J., Wagner, M., Maier, W., Kenrick, K.M., 2010. Oxytocin enhances amydala-dependent, socially reinforced learning and emotional empathy in humans. J. Neurosci. 30, 4999—5007.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286, 1526—2538.

Kaplan, J.T., Iacoboni, M., 2006. Getting a grip on other minds: mirror neurons, intention, understanding, and cognitive empathy. Soc. Neurosci. 1, 175—183.

Kéri, S., Benedek, G., 2009. Oxytocin enhances the perception of biological motion in humans. Cogn. Affect. Behav. Neurosci. 9, 237—241.

Kilner, J.M., Paulignan, Y., Blakemore, S.J., 2003. An interference effect of observed biological movement on action. Curr. Biol. 13, 522—525.

Kirsch, P., Esslinger, C., Chen, Q., Mier, D., Lis, S., Siddhanti, S., Gruppe, H., Mattay, V.S., Gallhofer, B., Meyer-Lindenberg, A., 2005. Oxytocin modulates neural circuitry for social cognition and fear in humans. J. Neurosci. 25, 11489—11493.

Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U., Fehr, E., 2005. Oxytocin increases trust in humans. Nature 435, 673—676.

Leighton, J., Bird, G., Orsini, C., Heyes, C., 2010. Social attitudes modulate automatic imitation. J. Exp. Soc. Psychol. 46, 905—910.

Leknes, S., Wessberg, J., Ellingsen, D.-M., Chelnokova, O., Olausson, H., Laeng, B., 2013. Oxytocin enhances pupil dilation and sensitivity to ''hidden'' emotional expressions. Soc. Cogn. Affect. Neurosci. 8, 741—749.

Liepelt, R., von Cramon, D.Y., Brass, M., 2008. What is matched in direct matching? Intention attribution modulates motor priming. J. Exp. Psychol. Hum. Percept. Perform. 34, 578—591.

Lombardo, M.V., Chakrabarti, B., Bullmore, E.T., MRC AIMS Consortium, Baron-Cohen, S., 2011. Specialization of right temporo-parietal junction for mentalizing and its relation to social impairments in autism. NeuroImage 56, 1832—1838.

MacDonald, E., Dadds, M.R., Brennan, J.L., Williams, K., Levy, F., Cauchi, A.J., 2011. A review of safety, side-effects and subjective reactions to intranasal oxytocin in human research. Psychoneuroendocrinology 36, 1114—1126.

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

Meltzoff, A.N., 1995. Understanding the intentions of others: re-enactment of intended acts by 18-month-old children. Dev. Psychol. 31, 838—850.

Meyer-Lindenberg, A., Domes, G., Kirsch, P., Heinrichs, M.A., 2011. Oxytocin and vasopressin in the human brain: social neuropeptides for translational medicine. Nat. Rev. Neurosci. 12, 524—538.

Miller, G., 2013. Neuroscience. The promise and perils of oxytocin. Science 339, 267—269.

Obhi, S., Hogeveen, J., Giacomin, M., Jordan, C.H., 2014. Automatic imitation is reduced in narcissists. J. Exp. Psychol. Hum. Percept. Perform. 40, 920—928.

Perry, A., Bentin, S., Shalev, I., Israel, S., Uzefovsky, F., Bar-On, D., Ebstein, R.P., 2010. Intranasal oxytocin modulates EEG mu/alpha and beta rhythms during perception of biological motion. Psychoneuroendocrinology 35, 1446—1453.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169—192.

Rizzolatti, G., Sinigaglia, C., 2010. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. Nat. Rev. Neurosci. 11, 264—274.

Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2, 661—670.

Sowden, S., Catmur, C., 2013. The role of the right temporoparietal junction in the control of imitation. Cereb. Cortex (published online).

Spengler, S., Bird, G., Brass, M., 2010a. Hyperimitation of actions is related to reduced understanding of others' minds in autism spectrum conditions. Biol. Psychiatry 15, 1148—1155.

Spengler, S., von Cramon, D.Y., Brass, M., 2010b. Resisting motor mimicry: control of imitation involves processes central to social cognition in patients with frontal and temporo-parietal lesion. Soc. Neurosci. 19, 98—106.

Stel, M., van Baaren, R.B., Vonk, R., 2008. Effects of mimicking: acting prosocially by being emotionally moved. Eur. J. Soc. Psychol. 38, 965—976.

Stroop, J.R., 1935. Studies of interference in serial verbal reactions. J. Exp. Psychol. 18, 643—662.

Tachibana, M., Kagitani-Shimono, K., Mohri, I., Yamamoto, T., Sanefuji, W., Nakamura, A., Oishi, M., Kimura, T., Onaka, T., Ozono, K., Taniike, M., 2013. Long-term administration of intranasal oxytocin is a safe and promising therapy for early adolescent boys with autism spectrum disorders. J. Child Adolesc. Psychopharmacol. 23, 123—127.

Tai, Y.F., Scherfler, C., Brooks, D.J., Sawamoto, N., Castiello, U., 2004. The human premotor cortex is 'mirror' only for biological actions. Curr. Biol. 14, 117—120.

Tomova, L., von Dawans, B., Heinrichs, M., Silani, G., Lamm, C., 2014. Is stress affecting our ability to tune into others? Evidence for gender differences in the effects of stress on self-other distinction. Psychoneuroendocrinology 43, 95—104.

van Baaren, R.B., Holland, R.W., Kawakami, K., van Knippenberg, A., 2004. Mimicry and prosocial behavior. Psychol. Sci. 15, 71—74.

Veening, J.G., Olivier, B., 2013. Intranasal administration of oxytocin: behavioral and clinical effects, a review. Neurosci. Biobehav. Rev. 37, 1445—1465.

Viviani, D., Charlet, A., van den Burg, E., Robinet, C., Hurni, N., Abatis, M., Magara, F., Stoop, R., 2011. Oxytocin selectively gates fear responses through distinct outputs from the central amygdala. Science 333, 104—107.

Watson, D., Clark, L.A., Tellegen, A., 1988. Development and validation of brief measures of positive and negative affect: the PANAS scales. J. Pers. Soc. Psychol. 54, 1063—1070.

Yamasue, H., Yee, J.R., Hurlemann, R., Rilling, J.K., Chen, F.S., Meyer-Lindenberg, A., Tost, H., 2012. Integrative approaches utilizing oxytocin to enhance prosocial behavior: from animal and human social behavior to autistic social dysfunction. J. Neurosci. 10, 14109—14117.

Zheng, J.-J., Li, S.-J., Zhang, X.-D., Miao, W.-Y., Zhang, D., Yao, H., Yu, X., 2014. Oxytocin mediates early experience-dependent cross-modal plasticity in the sensory cortices. Nat. Neurosci. 17, 391—402.