

Interactions in the hedonic experience of touch and emotion

A double-blind placebo-controlled study using intranasal oxytocin

Dan-Mikael Ellingsen



Master thesis, Department of Psychology

UNIVERSITY OF OSLO

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Interpersonal touch is a key means for communicating emotions in humans, and can be a powerful modulator of behavior. Perceived characteristics of the toucher, including his/her personality and emotional state, are among the factors likely to influence the hedonic touch experience in the touchee. The neuropeptide oxytocin (OT) is involved in a range of social interactions, and has been proposed promote prosocial behavior in humans. The present study investigated interactions in the hedonic experience of touch and emotion perception, and addressed the role of oxytocin in these interactions.

Thirty healthy individuals participated in a within-subjects placebo-controlled study where central OT levels were elevated through administration of a nasal spray. Participants watched faces with different emotional values while simultaneously receiving socially relevant touch or a control non-social vibratory stimulus on the forearm. After each stimulus pair, they rated characteristics of the faces (perceived anger, happiness, attractiveness and friendliness), or characteristics of the touch (perceived pleasantness and intensity). Throughout the experiment, participants' pupil responses to the tactile and visual stimuli were recorded as a measure of autonomic nervous signalling.

The results revealed that faces were rated as friendlier and less angry when accompanied by touch compared to vibration. Conversely, the reported pleasantness of tactile stimuli increased with happy faces relative to angry faces. OT was not found to increase positive perception of emotional stimuli. In contrast, participants rated angry faces as more angry with OT, supporting a view that its role in human social interactions is more complex than merely promoting positive social behavior.

INTRODUCTION

Pleasant and interpersonal touch

Interpersonal touch plays an important role for human communication, in both casual and intimate relationships (Gallace & Spence, 2010). Touch from another person can evoke powerful emotions in the touched person, positive or negative (Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006), depending on the identity of and the relationship with the toucher.

One specific class of unmyelinated C afferents (CT) has been hypothesized to have a crucial role for the hedonic aspects of touch in humans (Olausson, et al., 2002; Vallbo, 1999). These fibers are numerous in hairy skin, but absent in glabrous skin like the palm of the hand and the sole of the foot. CT afferents project to the insular cortex (Olausson, et al., 2002), which is, among other mechanisms, known to be involved in emotional processing, (Craig, 2002). CT fibers respond vigorously to light touch in slow velocities (3-5 cm/s) but responds less to slower and faster stimulation, providing an inverted U-shaped pattern that mirrors individual ratings of touch pleasantness, which also peaks at 3-5 cm/s (Löken et al., 2009). Thus, the CT-fibers are proposed to have a specialized role for the processing of hedonic, emotional and plausibly social aspects of touch.

Touch in the social setting can be closely linked with affect, and is thus a powerful modulator of emotional behavior. Fischer and colleagues (1976) conducted a study where employees in a library were told to either touch people briefly on the palm when they handed in books, or not to make any physical contact. The results showed that people who had been touched displayed a more positive evaluation of the library compared to the ones who had not been touched. In a related study, Crusco & Wetzel (1984) instructed waitresses to either touch customers on the hand, the shoulder, or not to touch them at all, when they returned the change after the customers had paid the bill. Customers who had been touched gave significantly more tips than the people who had not been touched.

The meaning of a perceived tactile stimulus in a social context depends on sensory factors like softness (Rolls, et al., 2003), temperature (Siri Leknes, Brooks, Wiech, & Tracey, 2008), and force and velocity (Loken, Wessberg, Morrison, McGlone, & Olausson, 2009), in addition to factors such as the emotional state of the touched person, the relationship with the toucher, and the body part that is touched (Lee & Guerrero, 2001). Moreover, it has been

suggested that touch preferences in adult life may be shaped by the relationship between stress and touch in early life (Reite, 1990).

Brain processing of pleasant touch involves a shared network with processing of pleasantness in taste and olfactory modalities, which involves orbitofrontal cortex activity (Francis, et al., 1999). The orbitofrontal cortex is involved in linking rewards with hedonic experience (Kringelbach, 2005), and has been found to respond to CT-activating touch of hairy skin relative to similar stimulation to glabrous skin which lacks CT-fibers (McCabe, Rolls, Bilderbeck, & McGlone, 2008), further supporting the hypothesis that CT-fibers are involved in the hedonic aspect of touch.

Oxytocin

Oxytocin (OT) is a neuropeptide of nine amino acids which is produced in the supraoptic (SON) and paraventricular (PVN) nuclei of hypothalamus, and released into the bloodstream via the posterior pituitary gland (Buijs, De Vries, Van Leeuwen, & Swaab, 1983) to peripheral destinations and through neural pathways to central destinations. Among brain regions rich in OT-receptors are the amygdala, hippocampus, striatum, hypothalamus, nucleus accumbens and midbrain structures (for a review of distribution of central OT, see Landgraf & Neumann, 2004). The OT system interacts with the dopamine and opioid systems (Insel, 2003). Peripherally, OT initiates milk production in lactating females, promotes contraction of the uterus, and has been proposed to play a role in sexual orgasm (Carmichael, et al., 1987). Centrally, this neuropeptide works as a neurotransmitter, and has been shown to be a powerful modulator of social behavior across a range of mammalian species (for a recent review, see Ross & Young, 2009).

So far, the most common way to investigate endogenous OT levels in humans has been to measure OT levels in blood plasma (however, see S. C. Carter, et al., 2007, for a potentially new noninvasive procedure involving saliva analysis). Not much is yet known about the relationship between such peripheral oxytocin measures and central mechanisms of OT in humans. However, exogenous OT can easily cross the blood-brain barrier (BBB) intranasally through the administration of a nasal spray (Born, et al., 2002). Thus, administration of a nasal spray containing OT provides a direct way to increase OT levels in the human brain.

Does OT promote prosocial behavior?

According to Uvnäs-Moberg (1998), OT coordinates the effects of positive social interactions and can be released endogenously by sensory stimuli perceived as positive, including touch, warmth and odors. Recently, a range of studies have investigated the modulatory effects of OT on social behavior in humans. One line of findings has led to the hypothesis that OT promotes prosocial and affiliative behavior in humans.

Kosfeld and colleagues (2005) found that relative to placebo administration, a single administration of intranasal OT (24 IU) increased the amount of money that male participants trusted to an anonymous stranger in a monetary game called the “Trust Game”. The person receiving the money units (“trustee”) could choose to keep the money or to give some of it back to the “investor”. A control experiment that replaced the trustee with a randomized computer, which supposedly involves a decision of risk and not trust, did not result in any difference between those who got OT and those who got placebo. Thus, it seems that OT did not affect the general willingness to take more risks, but specifically enhanced trust towards other humans.

A subsequent functional MRI study investigated the role of OT for the neural networks involved in the trust and risk experiments described above, and found that oxytocin-treated male subjects were more likely than placebo-treated subjects to continue trusting behavior even after betrayal in a Trust Game, i.e. a message that the trustees had kept all the money for themselves (Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008). The imaging data for the trust game revealed that relative to the OT group, the placebo group showed higher pre-feedback activation in the dorsal anterior cingulate cortex (dACC), a region frequently implicated in conflict monitoring (Botvinick, Cohen, & Carter, 2004). The OT group also showed a lower post-feedback increase in amygdala activation compared to placebo subjects. The amygdala is thought to signal salience, especially in the context of negative emotion, and has previously been reported to be sensitive to the presentation of faces perceived as untrustworthy (Winston, Strange, O'Doherty, & Dolan, 2002). In line with this evidence, a recent study reported increased ratings of trustworthiness and attractiveness for faces with neutral expressions after intranasal OT administration in both men and women (Theodoridou, Rowe, Penton-Voak, & Rogers, 2009).

In a related line of research, Zak and colleagues (2007) reported that intranasal OT administration leads to increased generosity, which is seen as a subset of altruism.

Participants receiving OT gave more money to the stranger than those who got placebo in an “Ultimatum Game”, but not in a “Dictator Game”. On the basis of their findings, the authors concluded that OT is specifically involved in generosity but not in altruism more generally.

A recent study investigated interactions of touch and endogenous OT release on the motivation to perform monetary sacrifice to strangers (Morhenn, Park, Piper, & Zak, 2008). One group of subjects went through a massage session followed by a round of the Trust Game, another group rested before the trust game, and a third group received only massage. Both the person administering the massage and the other players in the Trust Game were strangers to the participants. Measures of OT levels in blood plasma revealed that OT levels significantly increased in the massage+trust game group, but not in the rest+massage and massage only-group. The raise in blood plasma OT was accompanied by more trusting behavior in the Trust Game for the massage+trust group.

Social dysfunction and withdrawal in individuals suffering from autism spectrum disorder (ASD), obsessive-compulsive disorder, schizophrenia, and social phobia has been suggested to by a certain degree be accounted for by deficits in central OT functionality (Gurrieri & Neri, 2009; Lerer, et al., 2008). Intranasal OT has been suggested as a possible treatment for patients with ASD (Donaldson & Young, 2008), and recent studies have demonstrated increased social cooperative behavior (Andari, et al., 2010) enhanced emotion recognition (Guastella, et al., 2010) in ASD patients.

Together, these findings suggests a role for central OT in facilitating prosocial and approach behavior, specifically in increased trust towards strangers (Kosfeld, et al., 2005), even after betrayal (Baumgartner, et al., 2008), increased acts of generosity (Zak, et al., 2007), and increased perceived attractiveness and trustworthiness of neutral faces(Theodoridou, et al., 2009). Brain imaging findings indicate that activity of a network involving dACC and amygdala is modulated by OT in social interactions involving trust, possibly resulting in reduced uncertainty and suspicion about the trustworthiness of others (Baumgartner, et al., 2008). Moreover, it is suggested that touch may increase endogenous OT release specifically when followed by a social situation involving trust, an interaction which leads to increased trusting behavior (Morhenn, et al., 2008). Findings suggesting that OT enhances approach behavior may have clinical implications for patients with social deficit disorders like ASD, who might benefit from a treatment involving administration of exogenous OT (Andari, et al., 2010; Guastella, et al., 2010).

Fear and stress attenuation and amygdala activation

The increased prosocial effect that OT seems to have on human behavior may to a great degree be explained by a mechanism of reducing fear and stress responses to social situations.

Kirsch and colleagues (2005) reported that intranasal administration of OT attenuated amygdala responses to images of fearful and angry faces. It also significantly reduced amygdala responses to images of nonsocial threatening and fearful scenes, but the effect was more profound for the social stimuli. Another study found that OT attenuated amygdala responses to faces that had been fear conditioned with paired shocks (Petrovic, Kalisch, Singer, & Dolan, 2008). Furthermore, Domes et al. (2007) found attenuated amygdala responses to pictures of happy faces in addition to fearful and angry ones, which suggests that the modulatory effect is not limited to negative stimuli, but generalizes to emotionally laden stimuli irrespective of their valence.. It has been reported that the amygdala reacts to a spectrum of emotionally salient stimuli, and not limited to fearful and threatening emotional stimuli (Fitzgerald, Angstadt, Jelsone, Nathan, & Phan, 2006). Domes et al. (2007) interpret their findings to suggest that the attenuation of amygdala activity leads to less uncertainty related to all types of social stimuli, and thus results in more prosocial behavior. However, samples in all of these studies consisted of males only, and a recent study testing female participants found increases in amygdala activation in response to fearful facial expressions (Domes, et al., 2009), leading to the suggestion that there may be sex differences in the neural workings of OT in humans.

A recent study demonstrated that couples engaged in more positive relative to negative communication in a couple conflict after intranasal OT administration when compared to a placebo group. OT also reduced cortisol levels during the session compared to placebo, indicating reduced stress following administration of OT (Ditzen, et al., 2009).

Although there is some inconsistency in the literature about the exact nature of the modulatory effect of OT on brain regions involved in fear processing, like the amygdala (Domes, et al., 2009), evidence suggests that, at least in males, OT attenuates fear-induced amygdala responses to threatening social and non-social stimuli (Kirsch, et al., 2005), images of emotional laden faces (Domes, Heinrichs, Glascher, et al., 2007) and fear-conditioned face stimuli (Petrovic, et al., 2008). Together with the finding that OT reduced salivary cortisol levels, accompanied by more positive communication, in couple conflicts (Ditzen, et al.,

2009), these findings indicate that OT may increase prosocial behaviour by reducing fear and stress responses to social situations.

Identifying emotions

Recent evidence suggests that OT enhances memory encoding and recognition for positive social stimuli (Guastella, Mitchell, & Mathews, 2008; Marsh, Yu, Pine, & Blair).

Furthermore, OT has been shown to improve scores on a “Reading the Mind through the Eyes Test” (Domes, Heinrichs, Michel, et al., 2007), in which participants are shown a series of images of human eye regions, and judge the corresponding emotion. The effect was most profound in the “difficult” subset of pictures. In a subsequent study where participants were youth with ASD, the effect had the opposite pattern, i.e. OT enhanced the easy items but not the difficult ones (Guastella et al. 2010). In consequence, the authors suggested that the OT effect on social recognition may be strongest in items of moderate difficulties, and emphasized the importance of avoiding floor and ceiling effects. An eye-tracking study with healthy participants found that OT increased the duration and frequency of gaze to the eye region of neutral faces (Guastella, Mitchell, & Dadds, 2008). This finding points to a putative mechanism for enhanced emotion recognition after central OT increase, i.e. increased attention to emotionally salient features. Marsh and colleagues (2010) investigated the effect of OT on recognition of a range of emotions, using static “morphed” images of neutral faces with subliminal emotional cues present in intensities of 10-100%. They reported that OT enhanced recognition of happy expressions, but not any of the other emotions. This was suggested to implicate that OT may increase sensitivity to positive emotional cues, and thus increase perceptions of trustworthiness, facilitating prosocial and approach behavior. However, a similar study (Di Simplicio, Massey-Chase, Cowen, & Harmer, 2009) found weak or no effects of intranasal OT administration on recognition and classification of positive and negative emotion.

A more complex role for OT?

To sum up, the available literature suggests that OT supports affiliative and prosocial behavior in humans, which is often proposed to result from attenuated amygdala responses to emotionally salient stimuli (Domes, Heinrichs, Glascher, et al., 2007), and to a lesser extent nonsocial threatening stimuli (Kirsch, et al., 2005), and reduced cortisol levels (Ditzen, et al.,

2009). These mechanisms are suggested to underpin reduced stress in the face of social situations and thus promote prosocial behavior, like trust (Baumgartner, et al., 2008; Kosfeld, et al., 2005; Morhenn, et al., 2008), generosity (Zak, et al., 2007), gaze to the eye region of faces (Guastella, et al., 2008), enhanced memory and recognition of positive social stimuli (Guastella, et al., 2008; Marsh, et al., 2010), and enhanced trustworthiness and attractiveness perception (Theodoridou, et al., 2009).

However, recent evidence suggests that the role of oxytocin might be more complex than merely increasing positive social emotions. Shamay-Tsoory et al. (2009) reported that participants demonstrated more envy and gloating toward other players in a monetary game after administration of intranasal OT compared a control session using a placebo spray. They suggest that OT may have a more general effect of increasing the salience of social agents across a broader spectrum of social behaviors. Thus, the effects of OT lead to increased trustworthiness, generosity etc. in certain contexts and increased envy and gloating in competitive contexts. This is consistent with animal research showing that OT enhances social behavior as diverse as pair bonding (Williams, Insel, Harbaugh, & Carter, 1994), maternal care (Campbell, 2008) and maternal aggression to intruders (Bosch, Meddle, Beiderbeck, Douglas, & Neumann, 2005).

Pupillometry

Pupil diameter is an integrative product of sympathetic activation which stimulates the radial iris dilator muscle (active dilation of the pupil) and parasympathetic activation that stimulates the iris sphincter muscle (active constriction of the pupil). Contraction of the iris sphincter is initiated by cholinergic release through a pathway originating from the Edinger-Westphal complex of the oculomotor nucleus. Active constriction of the pupil is initiated by increase in light levels/luminance. Contraction of the pupil dilator, on the other hand, actively dilates the pupil, and is initiated by noradrenergic release through a pathway originating from the Locus Coeruleus (LC) nucleus in the brain stem. At any given time, the pupil size reflects a balance of these two processes. However, during constant light conditions, pupil dilation is an index of activation of the pupil dilator and inhibition of the iris sphincter, resulting from noradrenergic release initiated by sympathetic activity (Beatty & Lucero-Wagoner, 2000).

The pupillometry technique, which records pupil diameter at a high temporal resolution (50-60 hz/about once every 20 ms), represents a unique way to a direct assessment of sympathetic activity under constant light conditions, which is relatively inexpensive and convenient to use, since one person alone can execute recordings.

Pupillometry was a frequently used technique in cognitive research half a century ago, following the introduction of electronically based techniques providing high temporal resolution. Pupil dilation under constant light levels is associated with increased mental effort (Kahneman & Beatty, 1966), heightened arousal and cognitive interest (Hess & Polt, 1960) and responses to emotionally salient stimuli (Granholm & Steinhauer, 2004). Amount of pupil dilation as a response to a stimulus has also been suggested to index the degree of perceived pleasantness and unpleasantness of that stimuli (Whipple, Ogden, & Komisaruk, 1992; White & Maltzman, 1978). Recently, pupillometry techniques have gained renewed interest in the field of cognitive neuroscience (Granholm & Steinhauer, 2004), e.g. as a measure of cognitive load (Johnstone, van Reekum, Urry, Kalin, & Davidson, 2007). Pupil size was found to increase with the degree of uncertainty in a decision making study (Satterthwaite, et al., 2007). Furthermore, dilation of the pupil accompanies perception-switches when paying attention to visual and auditory ambiguous stimuli in which different possible interpretations of the stimulus rival for attention (Einhauser, Stout, Koch, & Carter, 2008). Another study demonstrated that sustained pupil responses to during tonic pain increased with pain intensity (Hofle, Kenntner-Mabiala, Pauli, & Alpers, 2008). Women's pupillary responses to pictures of their sexual partners have also been found to be subject to variation during the hormone cycle, with greatest responses during the fertile phase (Laeng & Falkenberg, 2007), which mirrors reports of variations in self-reported sexual interest (Adams, Gold, & Burt, 1978). Although pupillometry measures have been suggested to reflect range of phenomena, the crucial role of sympathetic nervous signaling for pupil dilation supports a more general interpretation of the pupillometry signal as an index of salience and cognitive load.

Unconscious processing of emotions

When meeting another human being, we immediately perceive a set of emotional cues, especially visual cues from the face region (Bar, Neta, & Linz, 2006) which helps us judge that person's emotional state, personality and motives. The processing of these visual cues in

the brain has both conscious and subliminal components (Winkielman, Berridge, & Wilbarger, 2005). Le Deux (2000) has suggested two pathways for the visual processing of emotional cues: a “high-road” projecting from thalamus to cortical areas in the occipital and temporal lobes that contributes to conscious appraisal of the emotional stimuli, and a “low-road” pathway projecting to subcortical structures like amygdala, which involves unconscious processing of the visual stimuli, but which is nonetheless involved in the modulation of behavior on an implicit level. The “low-road” is suggested to rapidly carry information about certain emotional cues, providing a robust first impression and enabling a quick judgment of the perceived object or individual.

A common method for studying the role of early subconscious processes in isolation from the conscious processing is known as backward masking. This method typically involves a brief (a few milliseconds) presentation of a stimulus, too short to be consciously noticed. The stimulus may for instance be a face with an emotionally salient expression, which is immediately followed by the image of a neutral face. The second (masking) stimulus is presented for a long enough period to be consciously perceived/interpreted (Esteves & Ohman, 1993). While only the masking image is reported as explicitly perceived and identified, the emotionally laden face efficiently modulates behavior. For instance, Winkielman and colleagues (2005) found that subliminally presented smiling faces increased consumption of juice that was offered after test completion, and the willingness to pay for it, while subliminal images of frowning faces resulted in the opposite effect, all in the absence of reported changes in mood.

Vuilleumier and colleagues (2003) demonstrated that subcortical circuits involving the amygdala were activated by images of fearful faces composed of only the lowest spatial frequencies (<6 cycles/image), but not by high-frequency versions (>24 cycles/image) of the same fearful faces, and suggested that emotional cues in the lowest spatial frequencies are processed in the subcortical “low-road”. By superimposing the lowest spatial frequencies of faces with emotional expressions (<6 cycles/image) over a neutral version of the same face in the rest of the bandwidth (>6 cycles/image), Laeng and colleagues (in press) created hybrid images that were explicitly identified by subjects as emotionally neutral, but that were nevertheless rated as less friendly when the superimposed low-pass emotional expression was angry, fearful or sad, relative to when the emotion was happy. Even when subjects were told that the images contained hidden emotions, and were asked to identify them, they were not able to distinguish hybrid-happy faces from hybrid-angry faces (Laeng, et al., in press).

The present study

In the present study, we addressed the question of how a socially relevant touch, relative to a non-social mechanical tactile stimulus, can modulate the perception of a social stimulus like a face with an emotional expression. Vice versa, we investigated how a face with a certain emotional expression can alter the hedonic aspects of a simultaneous interpersonal touch. A growing literature on the mechanisms of central Oxytocin has revealed an important role for this neuropeptide in human social behaviour. OT has been suggested to promote prosocial behavior by attenuating fear and stress responses to social situations and by facilitating emotion recognition (for a recent review, see Macdonald & Macdonald, 2010). Therefore, we investigated how increased levels of central OT via a nasal spray affected the perception of socially relevant touch, emotionally laden faces, and interactions of these.

We designed a within-subject, placebo-controlled paradigm where participants were shown a set of faces with different emotional expressions (happy, neutral and angry) and were asked to rate emotional characteristics (happiness and anger), and social characteristics (friendliness and attractiveness) of these faces. Simultaneously with presentation of the faces, they received socially relevant touch in the form of gentle strokes on the forearm and non-social control stimuli in the form of a mechanic vibratory stimulus. In addition to characteristics of the emotional faces, participants were asked to rate characteristics of the tactile stimuli (pleasantness and intensity). Moreover, we employed a subset of the hybrid faces used by Laeng et al. (in press). According to the suggestions in the literature that OT improves emotion recognition via modulation of amygdala activation, we expected intranasal OT administration to enhance the perceived salience of the subliminally presented emotional information contained in the angry and happy hybrid faces presented to our participants.

As pupil dilation response has been described to index heightened salience and cognitive load, we included pupillometry as an objective measurement of autonomic nervous activation, as a supplement the subjective reports which constituted the behavioural data.

Hypotheses

H1: Effects of touch on face perception

We hypothesized that socially relevant touch can contribute to a positive shift in emotion perception, as this type of gentle stroking touch is perceived as pleasant, and can be used to convey positive emotional information (Hertenstein et al. 2006). Specifically, we predicted that faces should be perceived as happier, less angry, more friendly, and more attractive with simultaneous socially relevant touch, compared to a non-social and emotionally neutral vibratory stimulus.

H2: Effects of face perception on the reported pleasantness of touch

We hypothesized that the hedonic experience of touch can be modulated by the emotional valence of a perceived face, since in non-laboratory settings, visual information is most likely used by the touchee to elucidate the intention of the toucher. Specifically, we hypothesized that the simultaneous perception of faces with happy expressions increases perceived touch pleasantness relative to faces with angry expressions. We predicted that this effect would be present only for socially relevant touch, and not for the non-social control stimulus.

H3: Effects of OT on perceived touch pleasantness

According to the view that OT mediates the benefit of positive social interactions and emotions (Uvnäs-Moberg, 1998), we predicted that OT would increase the hedonic experience, of a pleasant, socially relevant touch, but not of a non-social vibration. We expected the effects of oxytocin on touch perception to be limited to touch hedonics, and did not expect OT to alter reported intensity of tactile stimuli.

H4: Effects of oxytocin on face perception

a: We hypothesized that the perceived emotional value of a face can be modulated by central OT levels. According to the view that OT has an affiliative/prosocial behavior enhancing effect, faces should be perceived as happier, less angry, friendlier and more attractive with enhanced central OT levels. b: However, if OT has a more general “emotional salience” enhancing effect, as Shamay-Tsoory and colleagues (2009) suggest, this should be the case only for positive facial expressions, while negative emotional faces would be rated angrier, less happy, less friendly and less attractive. c: Furthermore, if OT enhances the ability to identify emotions (Domes, Heinrichs, Michel, et al., 2007), identification of hybrid faces should be enhanced by increased OT, whilst emotion recognition of explicit emotional expressions might be unaltered.

METHODS

Subjects

Thirtyone healthy volunteers (16 women and 15 men), age 20-39 (mean = 26.2, SD = 4.9), were recruited through ads put up on the University of Oslo (UiO) campus and through email requests sent out to students at the Dept. of Psychology, UiO. All participants gave written informed consent for the study, which was approved by the Local Ethics Committee. Inclusion criteria were right-handedness, fluency in Norwegian, non-pregnant, and age 18-55. Participants were paid 200 NOK per session. One female was excluded because she failed to return for the second test session, leaving a final study group size of 30.

Design

Each individual participated in two sessions on separate days, in counterbalanced order; one involving self-administration of a nasal spray containing oxytocin and one session involving self-administration of a nasal spray containing saline only. The study was double-blind, as neither the participant nor the experimenter who carried out the testing knew which session real OT had been administered. Pupil diameter was recorded during the experimental task, which was similar in both sessions. The participant watched faces with different emotions on a computer screen while receiving tactile stimulation on the left forearm, and rated qualities of the visual and tactile stimuli. Each session lasted for about two hours.

Stimuli

Tactile stimuli

Gentle stroking: Tactile stimulation consisted of 3 seconds duration soft strokes with a velocity of approximately 5 cm/s, a stimulus known to be very effective in activating CT-fibers (Löken et al., 2009). As C-fibers fatigue rapidly (Vallbo, Olausson, & Wessberg, 1999), the strokes were alternated between two parallel areas (~15 cm) of the left forearm. The strokes were administered with a silk glove by a research assistant who was concealed from the participant's view, behind a curtain. The silk glove was used in order to reduce variability caused by changes in the temperature and moisture levels of the skin of the hand. The smooth glove also reduced friction, thus making the stroking as smooth/soft as possible.

These characteristics make it comparable to the paint brush stimulation typically used in psychophysical studies addressing the functions of CT-fibers (Bjornsdotter, Loken, Olausson, Vallbo, & Wessberg, 2009; Loken, et al., 2009). In this setting, we were studying interactions between the appraisal of emotional and social touch, and not merely touch pleasantness. We argue that the soft stroking from a human hand is more socially relevant than a similar stimulation administered by a paint brush, and thus the ecological validity is enhanced.

Vibration: 3x1 sec 70 hz vibration was administered by a vibratory device on three successive areas of the dorsum of the left hand, with the same total duration as one stroking stimulus. Vibratory stimuli of this frequency mainly activate myelinated A β fibers and not CT-fibers (Bessou, Burgess, Perl, & Taylor, 1971). Therefore this stimulation was used as a control stimulus for the CT-activating touch, differing from the gentle stroking in social relevance and C-fiber activity, but not in stimulus intensity, the presence of motion, or attentional demand. Silk fabric identical to the silk glove was attached to the part of the device that was in contact with the skin, in order to make the stimulus as similar as possible to the stroking but without activating CT-fibers.

Visual stimuli

120 images of faces (20 males, 20 females) displaying angry, neutral and happy facial expressions were chosen from the Karolinska Directed Emotional Faces (Karolinska Hospital, Stockholm, Sweden, 1998).

Two hybrid images of each face (happy-neutral and angry-neutral) were made by filtering out high spatial frequencies of the angry and happy versions, keeping only frequencies of 1-6 cycles/image, and fuse it with a neutral expression of the same face in the rest of the bandwidth (7-128 cycles per image). For further description of this methodology, please refer to the relevant section of Laeng et al (in press)

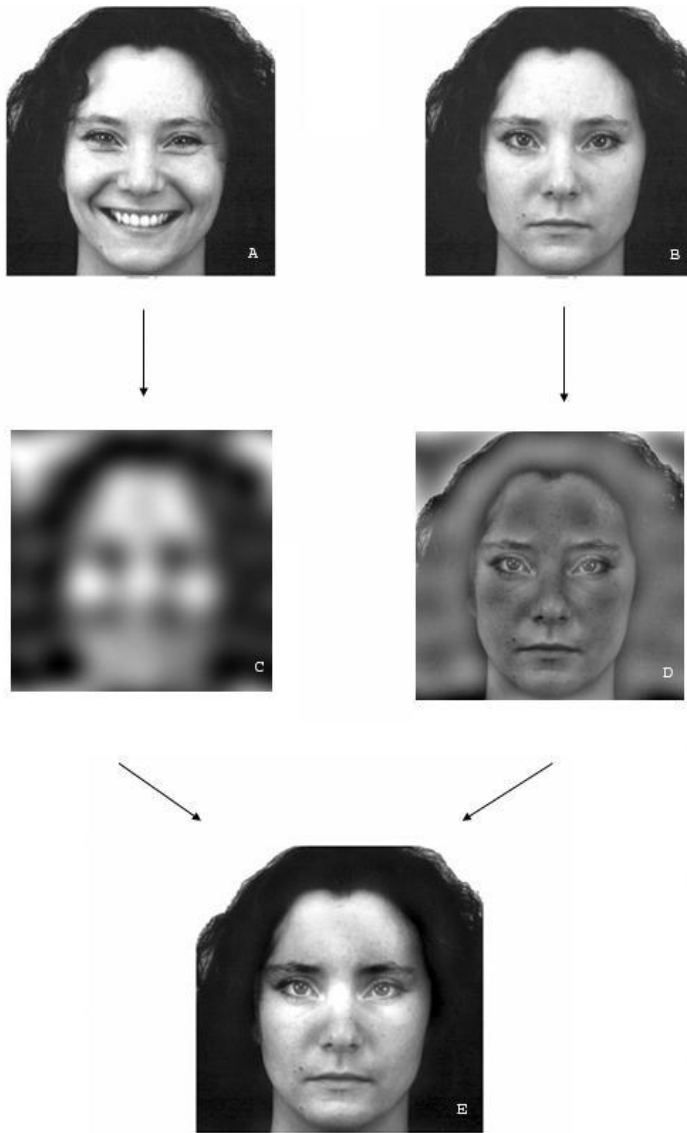


Fig. 1: The procedure of making a hybrid-face image. Spatial low-frequency information (1-6 cycles/image)(c) from an emotional salient face (a) is fused with spatial high-frequency information (d) from a neutral face (b), providing a hybrid-face (e)

The total of 200 images were pseudorandomized into two test protocols for use in sessions 1 and 2 (protocols A and B, each consisting of 100 images), such that faces of all the 40 persons depicted were presented during both sessions, but each image was presented only once. Within each protocol, image presentation was pseudorandomised according to the following rules: No more than two in a row of the same emotion; no two faces in a row of the same person; all five emotions in each 10-stimulus block; at least two of each gender in each block; the 5 touch blocks contain the same as the 5 vibration blocks in the same session, although they could come in a different order (i.e. the first vibration block could be similar to the fourth touch block). The order of presentation of the protocols (A, B, and their reversed-order counterparts A-reversed and B-reversed) was counterbalanced between participants. All of the faces in the pool were present in both version A and B, but different images. Half of

the participants were counterbalanced to complete the two versions in reversed order. Thus, all participants viewed the entire set of the 200 images, in one of four different orders (AB, BA, AB reversed and BA reversed).



Fig. 2. The visual stimuli (from left): angry, hybrid-angry, neutral, hybrid-happy and happy expressions

There was a significant difference of luminance between the female and the male faces in the original set of images ($p < 0.001$). Because the pupil sphincter muscle is affected by luminance, this difference may have led to systematic differences in pupil diameter due to activity of the pupil sphincter. To avoid this, we used a MATLAB script (The MathWorks, Inc.) to alter the background color of the images, which was originally white, so the net luminance became the same for all images. The faces themselves were left unaltered. The visual stimuli (11 x 11 cm) were presented on a computer monitor situated 104 cm in front of the participant, yielding a visual angle of 6 degrees, identical to that of Laeng et al. (in press).

Measurement/Materials

Behavioral measures

Subjective ratings of touch pleasantness and intensity, perceived mood (anger, happiness) of the displayed faces, and perceived attractiveness and friendliness of the displayed faces were collected using digital Visual Analog Scales (VAS). The questions were “How pleasant was the touch?” (anchors “Unpleasant-Pleasant”), “How intense was the touch? (anchors “Not noticeable-Intense”), “How angry was the person?” (anchors “Not angry-Angry”), “How happy was the person?” (anchors “Not happy-Happy”), “How attractive was the person?” (anchors “Unattractive-Attractive”), and “How friendly was the person?” (anchors “Unfriendly-Friendly”).

Pupillometry measures

The pupil diameter of the participant's left eye was recorded using the Remote Eye Tracking Device (RED; SMI-SensoMotoric Instruments® from Teltow, Germany) during each 3-second event. The operating distance for the RED is 0.5-1.5 m, and it records at a sample rate of 50/60 hz (approximately every 20 ms). The device's recording capabilities are not affected by the illumination of the room.

Pharmacological intervention

5 puffs in each nostril (10 in total) of a nasal spray containing Oxytocin (Syntocynon®, total dose: 40 IU) or placebo (saline) was self-administered 28-56 min (mean: 40, SD: 7.8) before the experiment started. Syntocynon® is commercially available in Norway, and is commonly used as a means of facilitating milk production in lactating women. Listed side effects include mild headache, nausea, and contraction of the uterus.

A number of studies have described the use of single doses of intranasal oxytocin in healthy male and female volunteers in experimental investigations (e.g. see Guastella, et al., 2008; Guastella, et al., 2008; Heinrichs et al. 2003; Kirsch, et al., 2005; Kosfeld et al. 2005; Petrovic, Singer, & Dolan, 2008; Theodoridou et al. 2009). These studies have not reported any significant adverse effects with intranasal doses up to 40 IU (see Heinrichs, et al., 2003).

Questionnaires

A number of self-report questionnaires were used as additional measures. These included standardized tests for measuring tactile communication (Tactype; Deethardt & Hines, 1984), ability to feel pleasure (hedonic tone) (a modified version of SHAPS: (a modified version of SHAPS: Snaith, et al., 1995), where we used a VAS with anchors Totally Disagree-Totally agree, instead of a likert scale with verbal categories), anticipatory and consummatory reward/pleasure experience (TEPS: Gard, Gard, Kring, & John, 2006), trait approach and avoidance motivation (BIS/BAS: Carver & White, 1994) and level of tactile and kinaesthetic mental imagery (subscales of the Questionnaire Upon Mental Imagery (QMI: Betts, 1909). In addition, a set of analogue mood rating VAS scales (See appendix) were administered at three points during each session: before the nasal spray administration, before the testing, and after testing.

Procedure

The participant was greeted by the experimenter, who presented verbal and written information about the study, and answered any remaining questions from the participant. Once this step was completed, the participant gave written consent to participate in the study. A mood rating VAS was filled in prior to the pharmacological intervention. The experimenter picked one out of two similar-looking nasal sprays identified by the shape of the cap. Neither the experimenter nor the participant knew which of the spray bottles contained active oxytocin. The participant then self-administered 5 puffs into each nostril (10 in total). A time interval of 20-45 min followed, for the nasal spray to take effect, in which the participants filled out the BISBAS, SHAPS, TEPS, Tactype and QMI questionnaires (in the first session only). The participants sat alone in a room during the waiting period, and were instructed not to engage socially during this period, but were allowed to read and go to the bathroom. Before the experiment started, the participant filled out a second mood rating. The chair height and the position of the eyetracker were adjusted to fit the individual, and an independent calibration procedure was performed to allow the localization of gaze by the eyetracker equipment. Specific instructions were given about the task, breaks, and the duration of the experiment, and the tactile stimuli were demonstrated by the experimenter. The participant was instructed to sit as still as possible during the experiment (and that the experimenter would tell them when they could move during the breaks between blocks). Participants were informed that an anonymous assistant would administer the tactile stimulation during the experiment. This person was concealed behind a curtain, and the participant was given earplugs in order to prevent auditory information to reveal the assistant's gender and other personal characteristics.

Prior to the experimental blocks, a baseline session was carried out to obtain baseline pupil diameter values of luminance, the visual stimuli, and the tactile stimuli. This consisted of one plain gray picture with the same mean luminance as the faces images, followed by six face images (3 male and 3 female) without any tactile stimulation, and finally six tactile stimuli (3 strokes and 3 vibratory, alternated) with concurrent plain gray images.

The experiment consisted of 10 blocks of 10 trials each. Between each block was a brief pause. The experimenter started the next block only after checking that the participant was ready. Each trial started with a fixation cross which was presented on the monitor for 5 seconds, followed by an image of a face for 3 seconds. Tactile stimulation was administered

concurrent with the visual stimuli. Following each visual-tactile stimulation, the participant responded to two visual analogue scales about the preceding tactile or visual stimulus. The pairs of questions were: touch pleasantness and intensity; anger and happiness; and attractiveness and friendliness. The order was pseudo randomized both between (with the rules: no more than two in a row of the same rating scale type; at least two of each of the 3 scale types in each 10-stimulus block) and within the pairs of questions, so the participants did not know which questions would be asked during the visual-tactile stimulation. Participants were informed of this before the experiment, and were instructed to pay attention to both the visual and the tactile stimuli in every trial, as the questions could be about either. Tactile stimulus type alternated between blocks. Half of the participants were counterbalanced to start with a vibration block and the other half with a touch block. The visual stimuli were presented in four different orders (AB, BA, AB-reversed and BA-reversed). List A consisted of 100 images, and list B consisted of another 100 images, and these lists were presented in a reversed order for half of the subjects.

After the experiment was completed, the participant filled out a third and final mood rating, followed by a debriefing period in which the participant was asked if he thought she/he got placebo or oxytocin, and to rate the confidence in the answer on a scale from 1-10. After session two the participant was also asked if she/he thought the assistant who administered the touch was male or female, why, and the confidence in the answer on a 1-10 scale.

Statistical analyses

Behavioral data

Behavioural data was analysed using Microsoft Excel and SPSS. VAS scores for each rating type were analysed in separate repeated-measures ANOVA with the factors; spray (Oxytocin; placebo); tactile (touch; vibration) face (angry; hybrid-angry; neutral; hybrid-happy; happy). Additional analyses were ran with between-subjects factors spray order (OT first; Placebo first), face order (AB; BA; AB-rev.; BA-rev.) and tactile order (started with touch; started with vibration). Specific a priori hypotheses were tested using paired, 1-tailed t-tests and repeated-measures Analysis of Variance (ANOVA).

Preprocessing of pupil diameter data

To prepare data of pupil diameter for analysis, the data was run through a preprocessing program made in MATLAB 7 (The MathWorks, inc.). First, the data was transformed from pixels to millimetres with a conversion rate of 16.72. Next, the following data points were excluded: 1) zero-values (eyeblinks and signal dropouts); 2) physiologically impossible data (pupil sizes of <1 mm and >9 mm); 3) within-trial outlier values (>2.5 SD from trial mean); 4) physiologically impossible pupil changes (dilation velocities faster than 0.702 mm/s and constriction velocities faster than 3.204 mm/s); 5) trials where less of 50% of data points remained.

As absolute pupil size differs across individuals, a measure of change in pupil diameter for each person was used. First, we calculated a grand mean based on all the values within each subject's two session. Then, the average of each trial was divided by the grand mean, resulting in a ratio value of mean pupil size change within a trial (1 = same as mean pupil dilation; >1 = greater than mean pupil dilation; <1 = lower than mean pupil dilation), a procedure adapted from Laeng et al. (2007).

RESULTS

H1: Pleasant touch causes a positive shift in emotion perception

To test if simultaneous pleasant touch contributes to a positive shift in emotional perception, we conducted separate t-tests (one-tailed) between touch and vibration trials for happy, angry, friendliness and attractiveness ratings. Anger ratings were significantly lower with touch ($M = 3.31$, $SD = 2.69$) compared to vibration ($M = 3.45$, $SD = 2.74$), $t(29) = -2.238$, $p = .02$ (see fig. 3a), and friendliness ratings were significantly higher with touch ($M = 5.3$, $SD = 2.41$) compared to vibration ($M = 5.13$, $SD = 2.36$), $t(29) = 1.909$, $p = .033$ (see fig. 3b). There were no significant effects on happy ($p = .14$) or attractiveness ($p = .22$) ratings.

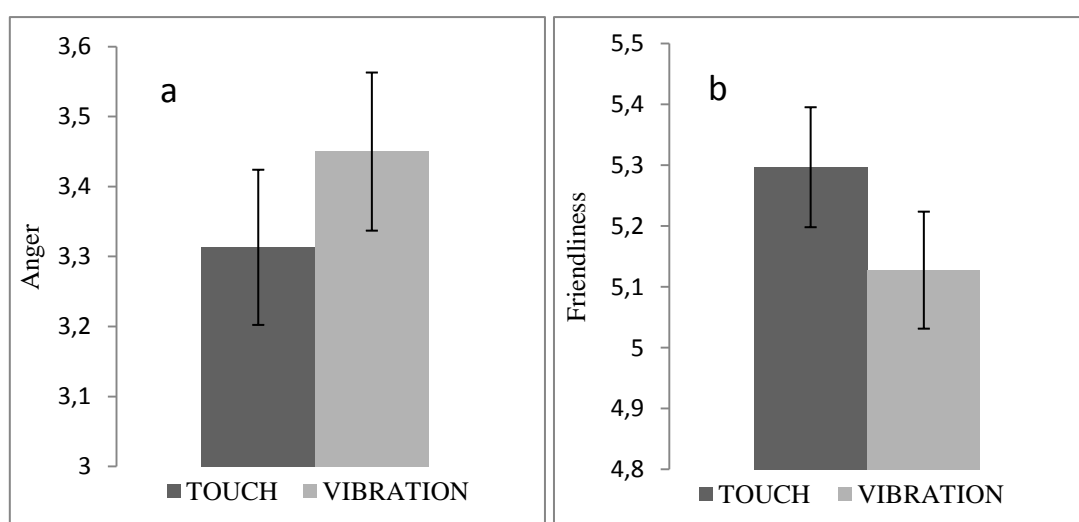


Fig. 3: Ratings of anger (a) and friendliness (b) paired with touch and vibration. Error bars represent standard error of mean

H2 and 3: Perceived pleasantness of socially relevant touch is increased by positive emotional stimuli, and OT:

To investigate if emotional valence and/or OT levels can modulate the pleasantness of socially relevant touch, we conducted a repeated-measures ANOVA with the factors spray (oxytocin and placebo), tactile (touch and vibration), and face (angry, hybrid-angry, neutral, hybrid-happy, happy), which revealed significant main effects of tactile condition, $F(1) = 47.343$, $p < .000$ and face emotion, $F(2.052) = 13.291$, $p < .000$, but not of spray type ($p = .619$). As expected, touch ($M = 6.73$, $SD = 1.41$) was rated as more pleasant than vibration ($M = 5.48$, $SD = 1.43$), and the significant linear effect of face revealed that pleasantness ratings were highest during the presentation of happy faces ($M = 6.39$, $SD = 1.41$), and lowest during angry faces ($M = 5.83$, $SD = 1.56$) (see fig. 4a). Also, there was a significant tactile *face

interaction, $F(3.44) = 4.15$, $p=.006$. The significant spray*face interaction, $F(3.45) = 2.63$, $p=.047$, indicated opposite effects of OT on pleasantness ratings during presentation of happy and angry faces, with increased ratings during angry faces, and decreased ratings during happy faces, compared to placebo (see fig. 4b). The interactions spray*tactile and spray*tactile *face were not significant.

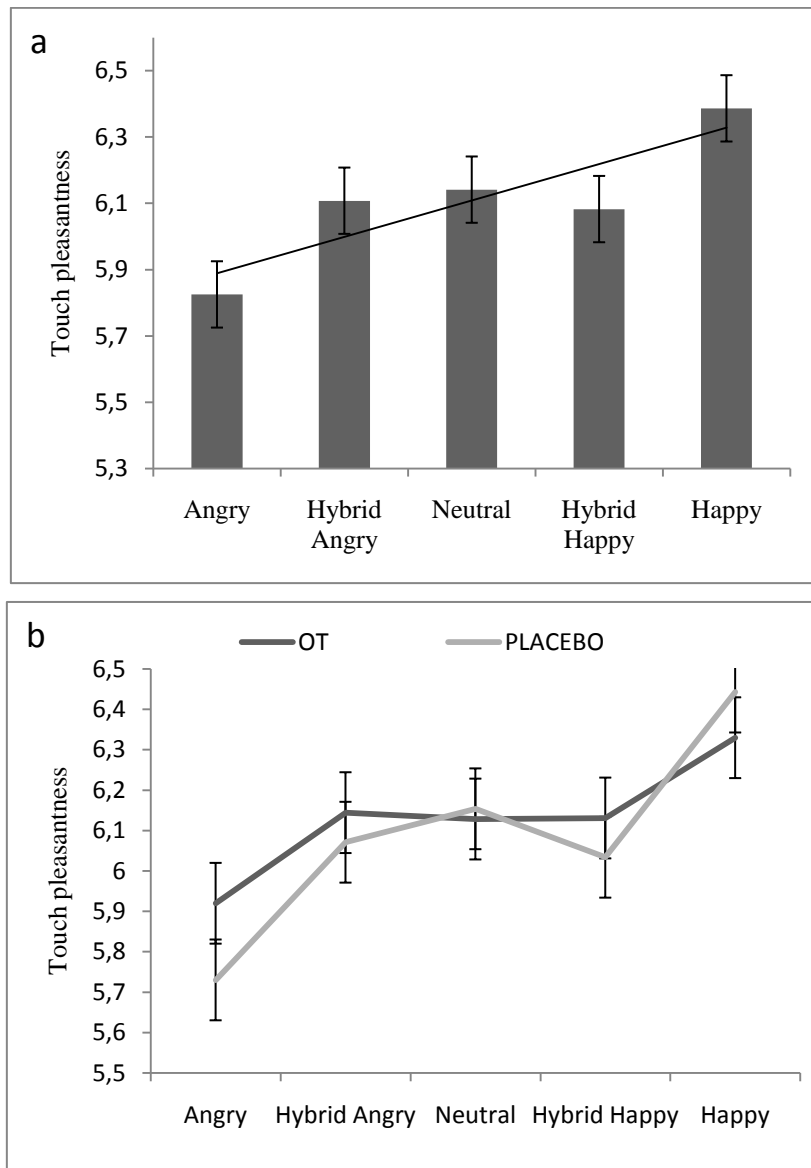


Fig. 4: Ratings of touch pleasantness under the different facial emotions both sessions (a) and divided between OT and placebo (b). Error bars represent standard error of mean.

Touch intensity

To investigate if perceived touch intensity differed between the touch and vibration stimuli, and if perceived touch intensity was affected by the emotional stimuli, we conducted a repeated-measures ANOVA with the factors spray (Oxytocin and placebo), tactile (touch and

vibration), and face (angry, hybrid-angry, neutral, hybrid-happy, happy), which revealed a nonsignificant trend towards a main effect of tactile, $F(1) = 3.853$, $p = .059$, with touch rated as more intense ($M = 5.68$, $SD = 1.48$) than vibration ($M = 5.42$, $SD = 1.49$). There was also a trend towards a main effect of spray, $F(1) = 3.384$, $p = .076$, that suggested higher intensity ratings during OT ($M = 5.65$, $SD = 1.48$) compared to placebo ($M = 5.45$, $SD = 1.49$). We also found a nonsignificant interaction trend of spray type and face type ($p = .059$).

H4a: OT increases prosocial behavior in general:

To test if OT had an overall effect of increasing happiness, attractiveness and friendliness ratings and decreasing anger ratings, we conducted separate paired t-tests (one-tailed) of VAS ratings between OT and placebo sessions for each rating type. There were no significant effects for angry ($p = .26$), happy ($p = .35$) or friendliness ratings ($p = .41$). Tentative support for the hypothesis was gleaned from a nonsignificant trend of increased attractiveness ratings in the OT session ($M = 4.28$, $SD = 2.28$) compared to the placebo session ($M = 4.15$, $SD = 2.1$), $t(29) = 1.147$, $p = .08$.

H4b: OT has a salience increasing effect:

To test if OT increases perceived salience of emotional stimuli, we conducted separate paired t-tests (two-tailed) between OT and placebo sessions for VAS ratings of angry and happy faces for each rating type. There were no significant differences in the happy ratings ($p = .22$) and attractiveness ratings ($p = .38$) of angry faces. Anger ratings of angry faces were significantly higher with OT, $t(29) = 2.143$, $p = .036$ (see fig. 5), and there was a trend towards lower friendliness ratings of angry faces with OT, $t(29) = -1.61$, $p = .056$. There were no significant differences in the ratings of happy faces (angry ($p = .32$), happy ($p = .49$), attractiveness ($p = .25$) or friendliness ($p = .34$)).

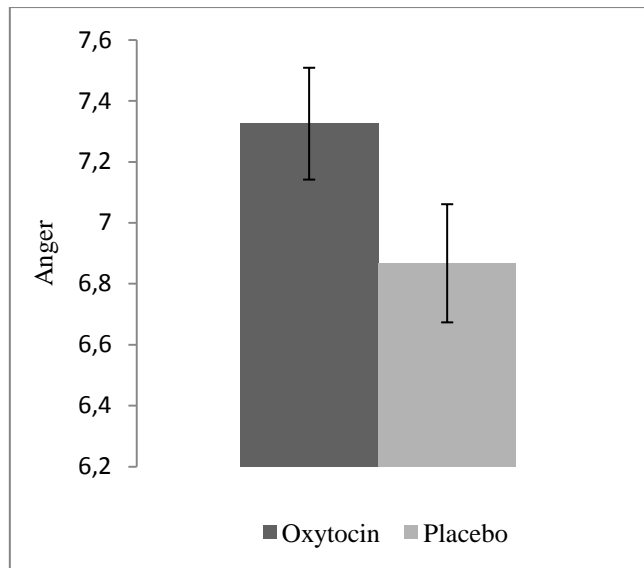


Fig. 5: Rated anger of faces with angry expressions. Error bars represent standard error of mean.

H4c: OT enhances recognition of emotions:

To validate that hybrid-angry and hybrid-happy faces were indeed rated differently, we conducted paired t-tests (two-tailed) between hybrid-angry and hybrid-neutral faces for anger and happiness ratings. As expected, hybrid-angry faces were rated as more angry ($M = 3.4$, $SD = 1.3$) than hybrid-happy faces ($M = 2.7$, $SD = 1.2$), $t(29) = 5.202$, $p = ,000$. Furthermore, hybrid-happy faces were rated as more happy ($M = 3.4$, $SD = 1.1$) than hybrid-angry faces ($M = 2.6$, $SD = 0.8$), $t(29) = 3.946$, $p = ,000$.

To test if OT enhances identification of emotional cues in hybrid faces, we conducted separate paired t-tests (two-tailed) between OT and placebo sessions of hybrid faces for anger and happiness ratings. There were no significant differences in the angry ($p=.46$) ratings of hybrid-angry faces, but there was a nonsignificant trend that hybrid-angry faces were rated as less happy with OT, $t(29) = -1.590$, $p=.059$). There were no significant differences in the anger ($p=.16$), happy ($p=.44$) ratings of hybrid-happy faces.

To further investigate possible interactions of tactile and emotions stimuli on the perception of faces, we conducted separate repeated-measures ANOVAs for each rating type, with the factors spray (Oxytocin and placebo), tactile (touch and vibration), and face (angry, hybrid-angry, neutral, hybrid-happy, happy).

Anger ratings

There were significant main effects of tactile condition, $F(1) = 5.01$, $p = .033$ (Greenhouse-Geisser) and face emotion, $F(4) = 108.4$, $p < .000$. The tactile*face interaction was significant ($p = .015$, GG). No other interactions were significant.

Follow-up post-hoc paired t-tests (two-tailed) between touch and vibration for the five emotions revealed that the tactile*face interaction was driven by lower ratings of angry faces with touch ($M = 6.86$, $SD = 2.3$) compared to vibration ($M = 7.33$, $SD = 1.8$), $t(29) = -2.36$, $p = .033$, and lower ratings of hybrid-happy faces with touch ($M = 2.63$, $SD = 1.8$) compared to vibration ($M = 3.01$, $SD = 2.0$), $t(29) = -3.132$, $p = .004$ (adjusted p-values after correction for multiple comparisons using the Holm-Bonferroni method (Holm, 1979)). There were no significant differences for hybrid-happy, neutral and happy faces.

Happiness ratings

As expected, there was a significant linear main effect of face emotion, $F(3.3) = 342.25$, $p < .000$. No other main effects or interaction effects were significant.

Friendliness ratings

There was a significant main effect of face emotion, $F(2.05) = 984.7$, $p < .000$, and a trend towards a main effect of tactile condition, $F(1) = 4.29$, $p = .066$. There was also a trend towards an interaction between tactile condition and face emotion, $F(5.194) = 3.23$, $p = .069$. No other interactions were significant.

As we found a significant overall effect of increased friendliness ratings with touch (relative to vibration) in the a priori test, we conducted post-hoc paired t-tests, between touch and vibration, to investigate this interaction trend. This revealed that touch significantly increased friendliness ratings ($M = 5.58$, $SD = 1.7$) compared to vibration ($M = 5.06$, $SD = 1.42$) for neutral faces only, $t(29) = 3.341$, $p = 0.006$ (Holm-Bonferroni adjusted)

Attractiveness ratings

There was a significant main effect of face, $F(2.6) = 77.93$, $p = .000$. No other main effects or interactions were significant.

Effects of perceived facial emotion, touch and enhanced OT levels on autonomic nervous signalling

To investigate the effects of facial emotions, touch and enhanced OT levels on pupil size, we conducted a repeated-measures ANOVA with the factors spray (Oxytocin and placebo), tactile (touch and vibration), and face (angry, hybrid-angry, neutral, hybrid-happy, happy). This revealed a significant main effect of face, $F(3.2) = 7.87$, $p < .000$, and a non-significant trend of spray, $F(1) = 3.124$, $p = .092$. Post-hoc t-tests revealed that pupil responses to angry faces were significantly larger than other emotion types, while the other facial emotions did not differ significantly, (least significant: $t(29) = 2.59$, $p = .017$ (Holm-Bonferroni adjusted)). There was no effect of tactile, $F(1) = .183$, $p = .67$. Moreover, there were no significant interaction effects.

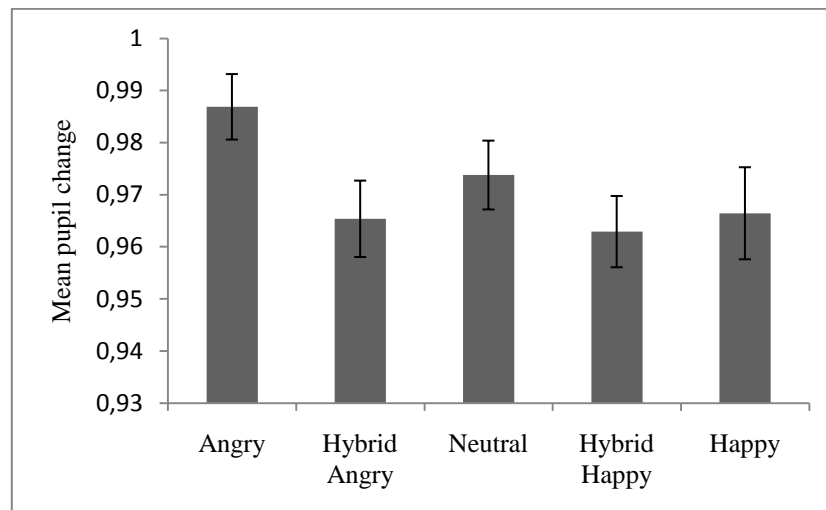


Fig. 6: Mean pupil change (ratio) in response to different facial emotions. Error bars represent standard error of mean.

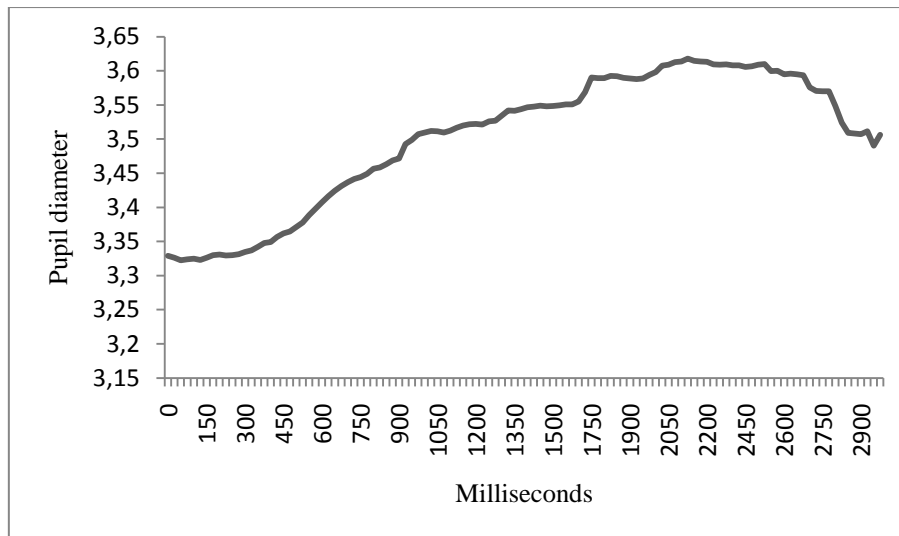


Fig. 7: Mean time curve (all subjects) during each trial of 3000 milliseconds.

Control measures

Order effects

We ran additional analyses to investigate possible order effects of spray, tactile condition, and the visual stimuli (see Methods section for details). There were no significant interactions involving order in any of the six rating types.

Debriefing results

Guesses about spray and gender of the toucher

As a part of the post-experiment debriefing, participants were asked what type of spray they believed they had administered. 17 out of 30 participants guessed the correct combination, which is slightly above chance level. They were also asked to rate their certainty of the answer, on a 1-10 scale (anchors: 1 = not certain at all, 10 = absolutely certain). Average was 5.8 (SD = 2.18).

After the second session, participants were also asked which gender they believed the experimenter was, and whether they thought it was the same person in both sessions. Three participants thought it was a male experimenter both times, twenty-two participants thought it was a female experimenter both times, two thought it was a male the first time and a female

the second time, one thought it was a female the first time and a male the second time, and one had no hypothesis.

Oxytocin and hormones: Information about their current phase in the menstrual cycle, specifically from self-report of the number of days since their last period, was gathered from female participants, to be able to control for possible hormonal changes that may interact with OT (McCarthy, McDonald, Brooks, & Goldman, 1996) -> rodents. However, as the number of female participants tested thus far is relatively low (N=15) and the distribution along the menstrual cycle unbalanced, it was not possible to conduct meaningful analyses on the effects of menstrual cycle relative to our other measures. Theodoridou et al. (2009) found no significant gender effects with a relatively large sample of subjects (N=96; 48 female).

Questionnaires and sociographic variables

Effects of mood

To investigate a possible mood altering effect of OT, we conducted a repeated-measures ANOVA with the factors spray (Oxytocin and placebo), time of rating (pre-spray, pre-experiment (after spray), post-experiment) and item (afraid, sad, irritable, happy, relaxed, anxious, and alert). As expected, there was a significant effect of item, which merely reflects the fact that items were rated differently (i.e. reports of sadness and happiness were different). There were no other significant main effects or interactions.

Effects of personality and gender

Data from the SHAPS, TEPS, TACTYPE, QMI and BIS/BAS questionnaires (see description of these scales in the Methods section) were collected, but not analysed yet. We are planning to test ten more participants before we address personality and gender variables.

DISCUSSION

In the present study, we investigated interactions in the hedonic experience of touch and emotion perception, and addressed the role of oxytocin in these interactions.

The results showed that images of faces were rated as friendlier and less angry when the faces were accompanied by a soft stroke on the forearm, compared to a mechanical vibratory stimulus. Vice versa, the reported pleasantness of tactile stimuli were altered by the emotional valence of simultaneously perceived faces, with touch pleasantness ratings increasing linearly with increasingly positive mood, such that touch hedonics were highest when paired with a happy face, and ratings were lowest when paired with an angry face. The socially relevant touch (i.e. the soft stroking) was always rated as more pleasant than the non-social vibration, but contrary to our expectations, the emotional valence of faces did not specifically alter pleasantness of social touch, but had the same impact on the hedonic assessment of non-social vibration. This may indicate that the emotional stimuli affected the experience of touch pleasantness more generally in our experiment, and not specifically for socially relevant touch. Furthermore, our results did not show any general effects of enhanced positive perception of emotional stimuli after intranasal OT, nor increased touch pleasantness. In contrast, participants rated faces with angry expressions as more angry after administration of intranasal oxytocin. Finally, we did not find any significant effects of OT on the perception of faces with subliminal emotional cues.

A socially relevant touch can be a powerful modulator of behavior (Gallace & Spence, 2010) in a range of social settings. Naturalistic studies have demonstrated that interpersonal touch can positively modulate attitudes and behavior (Crusco & Wetzel, 1984), even when the touch is not explicitly remembered (Fisher, et al., 1976). Moreover, recent animal research has found that dairy cows showed reduced anxiety towards contact with humans after they had been stroked on body parts often licked during social grooming (Schmied, Boivin, & Waiblinger, 2008). We predicted that gentle stroking would cause a positive shift in the perception of emotional faces. A priori hypothesis testing using paired, one-tailed t-tests revealed significant effects of increase in friendliness ratings and a decrease in anger ratings when participants had received simultaneous soft stroking touch compared to vibration. Soft stroking touch has been successfully shown to communicate positive emotion (Hertenstein, et al., 2006), and anecdotally this type of touch is used to communicate reassurance. Thus we speculate that the touch stimuli presented during emotional faces reduced perceived anger via

associative mechanisms whereby contiguous positively valenced information inhibited negative emotional information perceived in the images (Leknes & Tracey, 2008).

Touch is a key way for humans to communicate emotional messages (Hertenstein, et al., 2006), and the meaning of an interpersonal touch stimulus arguably plays an important role for the hedonic experience of that touch. Top-down factors like the characteristics of the toucher and the part of the body that is being touched are important, as are somatosensory factors such as softness (Rolls, et al., 2003), temperature (Leknes et al. 2008, and force and velocity of the touch (Loken, et al., 2009). The general effect of increased pleasantness from tactile stimuli was contrary to our predictions that this would be specific for social relevant touch, and not for non-social vibration. In the literature, however, there are examples demonstrating that emotional stimuli can modulate behavior that generalize beyond emotional or social aspects, and make our results seem less puzzling. Winkielman et al. (2005) reported that participants who had been subliminally primed with a smiling face consumed more juice that was offered after the experiment, and expressed more willingness to pay for it, compared to participants who had been primed with a subliminal angry face. Although these emotional messages were not consciously perceived, due to a masking paradigm (see introduction, the “Unconscious processing of emotions” section for details), our results demonstrate that general hedonic experiences may be altered also by fully consciously perceived emotional messages.

To account for possible differences in attentional demand of the two touch stimuli, we included ratings of touch intensity. We found that there was a trend towards that touch was perceived as more intense than vibration. Although this effect was not statistically significant, it underlines the possibility that unwanted variables may account for a part of the behavioral effects. We strived to make the vibration stimulus as similar as possible to the stroke stimulus without involving the activation of CT-fibers, but this method should be improved in future studies. Furthermore, the stroking touch stimuli were administered to a larger area of the skin, and thus activated more A β fibers than the vibration, which might have increased intensity of the touch.

Also contrary to our predictions, we did not find evidence that increasing central oxytocin levels enhanced touch-pleasantness. However, there was a significant interaction with face type that was driven by increased touch pleasantness during angry faces. This finding is consistent with previous results showing a social anxiety and stress-reducing effect of

intranasal OT administration (Ditzen, et al., 2009), suggesting that although OT may enhance emotion recognition of both positive (Marsh, et al., 2010) and negative emotions, as found in the present study, this neuropeptide may also reduce negative emotional effects of negative social stimuli.

Since OT is thought to be released during warm contact such as soft stroking touch and massages (Morhenn, et al., 2008; Uvnäs-Moberg, 1998), we hypothesised that enhancing central OT might cause participants to be more susceptible for enhanced enjoyment of socially relevant, pleasant touch. However, we did not find a main effect of oxytocin on touch hedonics. This null result must be interpreted with caution, since our controlled laboratory paradigm differed from naturally occurring interpersonal touch in a number of ways. Importantly, the touch did not occur in a familiar context, and the identity and gender of the toucher was concealed from the touchee. Endogenous OT can be released by positive sensory stimuli including warmth, pleasant odors, and touch (Uvnäs-Moberg, 1998). One limitation in research involving live humans is that endogenous OT levels can only be measured peripherally through blood plasma or saliva (Carter, et al., 2007). OT released into the blood stream cannot re-enter the brain, and not much is yet known about the relationship between such peripheral oxytocin measures and central mechanisms of OT in humans. While it is possible to study effects of elevated OT levels exogenously administered intranasally, this does not provide direct answers to the nature central OT release in social interactions/settings.

We did not find a general effect of OT of increasing positive perception of emotions from faces across emotional values, as would be predicted by findings showing that intranasal OT increases perceived attractiveness and trustworthiness of faces (Theodoridou, et al., 2009) and emotion recognition of positive emotions (Marsh, et al., 2010). In contrast, participants in our study rated angry faces as angrier after OT treatment. Similarly, there was a nonsignificant trend towards reduced perceived friendliness of angry faces in the oxytocin condition. These findings are compatible with a view that OT increases emotional salience, rather than increasing positive emotional perceptions per se (Shamay-Tsoory, et al., 2009). However, OT had no effect on the ratings of happy faces, which would be predicted to reflect enhanced perceived happiness, friendliness and attractiveness according to this view.

It has been demonstrated that OT has a role of enhancing emotion recognition of images depicting the human eye region (Domes, Heinrichs, Michel, et al., 2007), especially in moderately difficult cases that avoid “ceiling” and “flooring” effects (Guastella, et al., 2010).

Furthermore, Marsh et al. (2010) employed a paradigm using static images of faces with neutral expressions that were “morphed” with emotional expressions, resembling faces with subliminal or faint emotional cues. They reported that intranasal OT enhanced emotion recognition for happy expressions only. We argued that if OT enhances identification of explicit emotional cues, this may also be the case for implicit emotional information, such as that contained within the hybrid angry and happy images used here (Laeng et al., in press). However, besides a nonsignificant trend of lowered happiness ratings of hybrid-happy faces after OT treatment, we found no significant effects of OT on the perception of these hybrid faces. The fact that we did not find the predicted effects on hybrid faces might be explained by a difference in tasks used in our study and the ones used in Marsh et al. (2010) and Domes et al. (2007). In the study of Marsh et al., the participants viewed faces with varying intensities of emotional expressions (from 10-100%), and the task was to identify the facial expression by choosing one out of six emotions. In Domes et al., the task was to identify emotions from looking at images of human eye regions, by choosing from a set of alternatives. Both of these tasks were specifically about emotion identification and involved a forced choice of a set of predefined alternatives. In our study, we did not explicitly ask participants to identify the correct emotion of the hybrid faces, nor did we tell them that these faces contained hidden emotional cues. The task was to report, on a visual analog scale, their judgement of how angry, happy, friendly or attractive the face appeared. It is likely that participants in our study did not explicitly search for emotional salient cues in the hybrid faces, as these faces are consciously perceived as having neutral expressions (Laeng et al, in press). Thus, this conscious searching after emotions may be required for OT to have an effect. Another possible explanation is that the different visual stimuli engaged different mechanisms. The emotional cues of the hybrid images in our study was present in only the lowest spatial frequencies (<6 cycles/image), and supposedly initiates subcortical “low-road” processes, and without necessarily involving consciously explicit recognition of the cues (Vuilleumier, et al., 2003)Laeng et al. 2010, in press. This differs from the “morphed” stimuli used in Marsh et al. (2010) and the images of human eye regions used in Domes et al. (2007), where the emotional cues were present in the entire spatial bandwidth, and not solely activated subconscious processes. One possible interpretation of this is that OT may not interact with early “low-road” processing of visual stimuli, but rather work on processes involved in conscious judgment of emotional valence (Domes et al., 2007; Marsh, et al., 2010).

The reported effects of OT in social interactions are often quite specific. OT increases trusting behavior in social interactions, but not risky behavior in general (Kosfeld, et al., 2005), generosity, but not general altruism (Zak, et al., 2007), and enhances identification of emotions specifically in difficult tasks in healthy humans (Domes et al., 2007). Furthermore, Morhenn et al. (2008) found that only the interaction of massage followed by decision making involving trust resulted in an effect of increased trusting behavior, accompanied by increased plasma OT levels. Together these findings suggest that central OT may be involved in highly specific interactions in human social behavior. The results from our study support the view that the role for OT in human social behavior is indeed more complex than a general effect of increasing prosocial or affiliative behavior. Findings from animal research shows that OT is involved in protective behavior like maternal aggression against intruders (Bosch, et al., 2005) in addition to affiliative behavior as pair bonding (Williams, et al., 1994) and maternal care (Campbell, 2008). In humans, the recent finding that intranasal OT increased reportings of envy and gloating in a gambling game is inconsistent with a view that OT boosts positive emotions in all social settings. Our results show that threatening stimuli such as faces with angry expressions are perceived as more angry with increased central OT levels. The absence of OT effects on the perception of happy faces may be accounted for by a possible flooring effect, analogous to the ones demonstrated for difficulties in emotion recognition (Domes et al., 2007). Furthermore, our results showed increased pupil change in response to angry faces only, suggesting that these were more salient than the happy faces. One might speculate that the experimental setting was positively valenced in itself, so that the presence of a positive face did not represent any salient new information. The presence of an angry face, however, may stand out as more behaviorally interesting and emotionally salient in this setting.

Limitations

Many of the studies addressing the role of OT in humans have tested males only. Although some of the studies who have included both sexes in their samples have reported few effects of sex (Morhenn, et al., 2008; Shamay-Tsoory, et al., 2009; Theodoridou, et al., 2009), Domes et al. (2009) recently reported OT-induced increases in amygdala activation in response to fearful faces, which is the opposite of previous findings of amygdala reduction in males. The authors point to differences in steroid hormones and OT receptor affinity as

possible explanations for the findings, and stress that future studies should include both genders. As the sample size in the present study is relatively small (N=30), we have not yet addressed the question of sex differences, nor effects of personality traits. Our plan is to test ten more participants before we address these questions.

One limitation in our study is that all the personality questionnaires were answered after the nasal spray administration, which may have affected the scores in these. However, we did not find any effects of OT on the mood ratings, which were gathered three times throughout each session.

Another potential confound is the use of a within-subjects design in the present study, since this may be associated with learning effects. However, we did not find any significant effects nor interaction effects with session order and any of our other measures, suggesting that learning effects, if present, may have been small or variable between subjects.

Ecological validity may also be of concern in relation to the present study design. The kind of caressing touch we used usually belongs in a context where the touched person has some kind of relationship with, or at least knows the identity of the toucher. The fact that experimenter who was administering the touch was hidden from view, and never introduced visually to the participant, may have produced an element of uncertainty that may have affected the ratings.

Conclusion

Results from the present study demonstrated that socially relevant, pleasant touch can alter the perception of others' emotions, and vice versa that emotional characteristics of a simultaneously perceived face can affect the pleasantness of a tactile stimulus. In non-laboratory settings, a soft stroking or a caressing touch is usually a means of communicating positive emotions (Hertenstein, et al., 2006). Furthermore, visual information is most likely used by the touchee to elucidate the intention of the toucher. Contrary to our predictions, administration of intranasal OT did not cause a positive shift in the emotional perception, which would fit with the literature suggesting that OT promotes prosocial behavior. However, our finding that OT increased anger ratings of threatening stimuli (angry faces) is consistent with the hypothesis that OT increases salience to social stimuli, which suggests that the role for Oxytocin in humans may be more complex than previously assumed.

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