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The influence of oxytocin and vasopressin on men's judgments of social dominance and trustworthiness: An fMRI study of neutral faces

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ABSTRACT

Cues signaling trust and dominance are crucial for social life. Previous studies on the effects of oxytocin (OT) nasal sprays on trustworthiness evaluations have been inconsistent and its influence on dominance is unknown. Vasopressin (AVP) may also influence social cue perception, but even fewer investigations have evaluated this possibility. We evaluated the effects of intranasal OT and AVP compared to placebo control during three double-blinded functional magnetic resonance imaging sessions. Twenty males received a pseudo-randomized order of nasal spray conditions and rated the trustworthiness and dominance of neutral faces. OT increased facial dominance ratings compared to placebo. Neuroimaging results revealed an inverse relationship between brain activation and face ratings for OT compared to placebo in regions involved in processing emotional expressions. Specifically, the right superior temporal gyrus was attenuated as ratings increased and the left precuneus selectively diminished with increasing dominance ratings. Additionally, OT increased functional connectivity between frontoparietal regions and the right amygdala for faces rated as highly dominant, but OT increased connectivity between the fusiform gyrus, hippocampus, and bilateral ventral tegmental area (VTA) for faces perceived as highly trustworthy. Overall, OT increased the perception of dominance but did not influence trustworthiness judgments. However, we observed regional neural effects for OT that differed between judgments of trustworthiness and dominance. AVP attenuated left temporoparietal junction activity as face ratings increased, a result consistent with AVP influencing mentalization. AVP also led to increased left amygdala and right VTA connectivity with the putamen, which is consistent with cue-driven, habitual responses.

1. Introduction

Facial features are central in predicting the social abilities and traits of others (Mueller and Mazur, 1996; Todorov et al., 2005). Models by Oosterhof and Todorov (2008) indicate that trustworthiness and dominance are the primary dimensions used to infer social cues from faces. The biological substrates that signal facial trustworthiness or dominance, including the brain mechanisms of these processes are less understood. Trust enables us to form cooperative partnerships and alliances against threats (Rousseau et al., 1998), while dominance is fundamental for establishing superordinate and subordinate relationships within social hierarchies (Byrne and Bates, 2010). The neuropeptides oxytocin (OT) and vasopressin (AVP) may contribute to the perception of trust and dominance based on their role in social bonding (Young and Wang, 2004) and social interactions (Heinrichs et al., 2009).

Prior studies indicate that OT influences the perception of facial cues and modulates several different functions. These include attention toward different facial features (Guastella et al., 2008), improved recall of faces compared to landscapes or objects (Rimmele et al., 2009), and increased salience of social information (Averbeck, 2010; Bartz et al., 2011). OT decreases vigilance toward unfamiliar, dominant faces in rhesus macaques (Ebitz et al., 2013). OT has also had diverse behavioral effects on trust across different contexts, including a variety of relevant game theory paradigms (e.g. Baumgartner et al., 2008; Kosfeld et al., 2005), but these have been difficult to replicate and have been subject to critical review (Nave et al., 2015). Among facial perception studies, Theodoridou et al. (2009) found OT to increase perceived trustworthiness and attractiveness when those two ratings were collapsed together, while Lambert et al. (2014) observed that OT enhanced the categorization of trustworthy faces. However, to our knowledge, no study has found a simple effect for OT on facial ratings of

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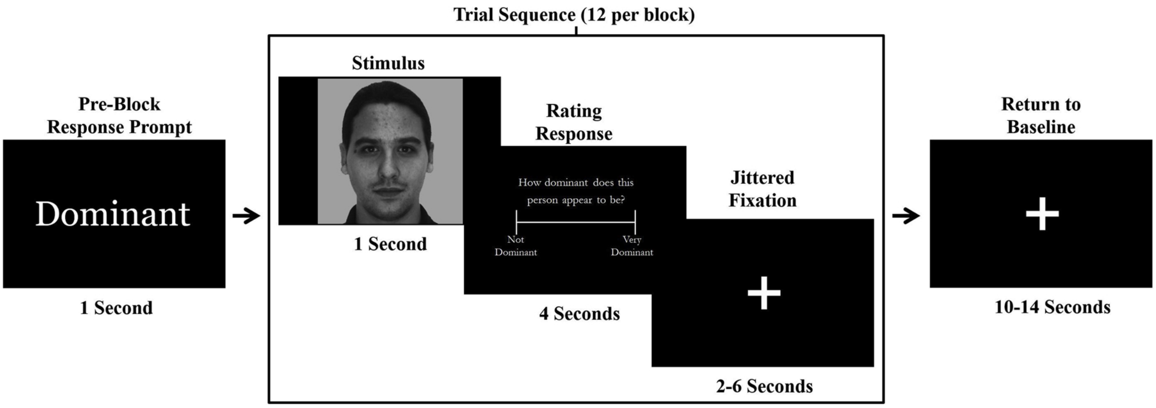

Fig. 1. Task design and trial structure. A prompt lasting 1 s preceded each block of 12 trials and indicated which response, “Trustworthy” or “Dominant,” were presented in those trials. Trials began with a 1 s presentation of a face stimulus, followed by 4 s presentation of the visual analog scale recording values on a range of 1–100, and trials ended with a jittered 2–6 s fixation period. For the final trial of a block, the fixation was replaced by a jittered return-to-baseline period of.10–14 s.

trustworthiness.

AVP has been linked to perceiving social dominance. Prior studies report increases in aggressive facial expressions in men when viewing unfamiliar male faces displaying neutral expressions (Thompson et al., 2004, 2006). These responses are similar to those evoked by angry faces in a control condition. Thompson et al. (2006) also reported that AVP increased autonomic responses toward threatening social stimuli, indicating an influence over arousal mechanisms. An influential model of facial perception associates perceived dominance of neutral faces with the approach-related dimension of competence and the avoidance-related dimension of threat (Todorov and Engell, 2008). Thus, the effects of AVP on threat may be related to threat. However, it is unclear whether this might arise from processing facial traits or from enhancing social salience in general.

Judgments of trustworthiness negatively correlate with amygdala activity across numerous studies (Adolphs et al., 1998; Todorov and Engell, 2008; Winston et al., 2002), but positively correlate with activity in dopaminergic reward processing regions including the ventral striatum and orbitofrontal cortex (OFC) (Mende-Siedlecki et al., 2012). Unlike trustworthiness, dominance is not specifically linked to emotional valence (Chiao et al., 2008; Todorov and Engell, 2008); however, trust and dominance are related. Oosterhof and Todorov (2008) reported that threat judgments negatively correlate with trust judgments, but positively correlate with dominance judgments.

In the current study, we evaluated three core hypotheses about the influence of OT and AVP on social perception in males: 1) OT and AVP modulate trustworthiness judgments toward neutral faces relative to placebo control, 2) OT and AVP modulate social dominance judgments toward neutral faces compared to placebo control, and 3) OT and AVP influence regional brain activation and connectivity associated with trustworthiness and dominance judgments relative to placebo control. We collected functional Magnetic Resonance Imaging (fMRI) data to investigate brain activation changes associated with these hormones and regional connectivity differences associated with hormone influences on facial judgments.

We made several *a priori* predictions about potential influences of OT and AVP on judgments, brain activation, and functional connectivity. We predicted that OT would increase ratings of trustworthiness while reducing amygdala activation and functional connectivity during trustworthiness judgments. We predicted that AVP would increase dominance ratings, increase activation within the right STG during those judgments, and that greater connectivity between the amygdala and brainstem regions associated with social vigilance would correlate with higher ratings of dominance when comparing AVP and placebo conditions.

2. Methods

2.1. Experimental procedure

Twenty male participants were recruited from The University of Texas at Dallas. We excluded females to avoid the potentially confounding interactions between hormone administration and menstrual cycle. Participants were screened for psychological disorders, as well as recreational drug or tobacco usage. This experiment was approved by the Institutional Review Boards of The University of Texas at Dallas and the University of Texas Southwestern Medical Center. Each person provided written consent to participate.

During each of three sessions, participants self-administered one nasal atomizer containing OT (24 IU), AVP (40 IU), or placebo. We obtained powdered Vasopressin from the Polypeptide Group (Strasbourg, France) that we had reconstituted using sterile saline solution by a compounding pharmacy, Pharmacy Solutions (Arlington, Texas). Sterile saline-based OT and placebo formulas equivalent to the AVP solutions in amount and perceivable properties (e.g. solution taste, smell, etc.) were then formulated and bottled for nasal spray administration at the University of Texas Southwestern Medical Center pharmacy which also maintained records of the blinded treatment conditions. Distribution of the nasal sprays was double-blinded and the order of nasal sprays participants received was counter-balanced in a pseudorandomized fashion. Previous research indicates that cerebrospinal fluid concentrations of AVP peak between 60–80 min (Born et al., 2002). To achieve peak efficacy, we began the first experimental task approximately forty-five minutes after nasal spray administration. During the intervening time between dosage and tasks in the first session, participants received task instructions and were shown examples of trials from both the face judgment and activity judgment tasks on a computer outside of the scanner.

2.2. Facial judgment task structure

One hundred forty-four face images were gathered from three face databases: CVL (Solina et al., 2003), AR (Martinez and Benavente, 1998), and the Karolinska face database (Lundqvist et al., 1998). Face images were split equally by gender and depicted Caucasian individuals facing forward with a neutral facial expression. All images were converted to greyscale (refer to Fig. 1).

The task was presented using E-prime 2.0 software (Psychology Software Tools, Sharpsburg, Pennsylvania) in eight blocks. Each block contained twelve trials consisting of two phases. First, each face stimulus appeared for 1 s. Second, participants had 4 s to rate the face (Fig. 1). We gathered data on two rating types: “How trustworthy is this face?” and “How dominant is this face?”. Only one of these two ratings appeared for every trial in a given block, such that each block contained only trust or dominance trials. Forty-eight unique faces were presented twice during each experimental session, for a total of 96 trials, to obtain ratings for trust and dominance. Prompts appeared for 1 s at the start of each block to cue participants about which rating to perform, "Trustworthy" or "Dominant," (Fig. 1). A 2–6 s jittered fixation cross appeared between the trials to provide the participant time to prepare for the next trial and to enable removal of periodic effects of the hemodynamic response (Huettel et al., 2009, p. 318–319). A 10–14 second fixation cross period separated each block to allow the hemodynamic response to return to baseline.

Ratings were performed by pressing a button on an MRI-compatible trackball device (Nata Technologies; British Columbia, Canada) using a visual analog scale package in e-prime downloaded from http://pfcgroot.nl/e-prime.html. This package generates a cursor that allows only horizontal movement within the bounds of a graphical representation of the scale. Ratings were recorded as integers ranging from one (not trustworthy/not dominant) to 100 (highly trustworthy/highly dominant). The paradigm took just under fourteen minutes to complete.

2.3. MRI acquisition

T2*-weighted echo planar images (EPI) sensitive BOLD contrasts were acquired with a Philips 3 T scanner fitted with a 32-channel phased array head coil using a 1-shot gradient echo- EPI sequence; Repetition Time (TR) = 2 s, Echo Time (TE) = 25 ms, field of view = 220 × 220 × 150, flip angle = 60°, and voxel size = 3.4 × 3.4 x 4 mm. The task was broken up into two runs of 232 volumes with each volume consisting of thirty-eight, 4 mm axial slices were obtained in an interleaved manner with no gap, providing whole-brain coverage. MP-RAGE 3D T1-weighted anatomical scans were also acquired.

All image preprocessing steps were performed using SPM12 (Wellcome Department of Imaging Neuroscience, London, UK). Functional images were realigned to the first volume via a six parameter, rigid body transformation. They were corrected for spikes in signal using ArtRepair, a quality control toolbox for SPM (http://cibsr.stanford.edu). We applied toolbox functions that use realigned images and the six rigid-body realignment parameters to replace outlier volumes containing scanner signal spikes or spikes from motion in excess of 3 mm with the linear interpolation of values from the two nearest non-outlier volumes. Images were resliced to the first volume using a fourth-degree spline interpolation, slice-time corrected, coregistered to the T1 image, normalized into standard MNI space (Montreal Neurological Institute), and resampled to a final 3 × 3 x 3 mm voxel size. Spatial smoothing was performed using an 8 mm full-width at half-maximum (FWHM) Gaussian kernel.

All comparisons of BOLD responses related to the task were performed in random-effects, epoch-related analyses in two stages. First, we estimated general linear models for each experimental session by entering the durations and onsets for each trial in a given run according to the judgment type, trustworthiness or dominance, and participants' ratings were entered as subject-level parametric modulators. Implicit contrasts were created for each judgment condition and the respective response regressors in a voxel-wise manner using a general linear model that convolves task designs with the canonical hemodynamic response function in SPM12. Covariates entered at this level were age and years of education. A temporal high-pass filter of 128 s was included to remove low-frequency signal drift. A first-order autocorrelation model was used to account for serial autocorrelations.

At the second level, contrast maps from the GLM were entered into SPM12′s flexible factorial design. Subject and session were specified as regressors of no interest. Treatment and task rating conditions were collapsed into a single factor to allow more freedom in contrasting different combinations of interest. The condition factor was entered as a non-independent measurement to correct for the fact that – due to repetition of stimuli – the error term of this factor violated the assumption of sphericity. A flexible factorial model was also generated for the parametric modulator regressor to isolate brain regions that might track linear trends related to behavioral responses.

Using the generalized psychophysiological interactions toolbox (McLaren et al., 2012), we also performed task-related functional connectivity analyses by seeding 5 mm radius spheres at the amygdalae (L: -24, -1, -16; R: 26, 1, -18) and ventral tegmental area (L/R: -5/5, -15, -14), respectively in MNI space. Amygdala activation is frequently observed to be modulated by OT and AVP and a large number of OT and AVP 1a receptors observed there and (Loup et al., 1991; Zink and Meyer-Lindenberg, 2012). The VTA seed was chosen because OT release in the hypothalamus can directly affect VTA activity during social reward in mice (Hung et al., 2017). Seed locations were selected based on the center of the amygdala regions in the automated anatomical label (AAL) atlas (Tzourio-Mazoyer et al., 2002), and previous study in VTA (Murty et al., 2014). For the connectivity analysis, the original first-level GLM was revised to additionally include psychophysiological terms for the trustworthy, dominance, and their linear parametric modulation conditions, respectively and a flexible factorial model was then created using the resulting contrasts.

Whole-brain inferences were made by comparing specific contrast maps created at this level at a voxel-wise threshold of $P < .001$, uncorrected and cluster corrected at $P < .05$. Cluster sizes were estimated from the residuals of the second level GLM analyses using AFNI's 3dClustSim with the spatial autocorrelation function option (Cox et al., 2017). All image results were visualized in MNI coordinates using the xjView toolbox (http://www.alivelearn.net/xjview).

3. Results

A Pearson's chi-square test indicated that individuals were successfully blind to condition being no better than chance at guessing condition (OT, AVP, or placebo) ($\chi^2 = 1.83$, $df = 2$, $p = .40$). To account for potentially confounding mood effects participants completed the Positive and Negative Affect Schedule (PANAS) (Watson et al., 1988) before nasal spray administration, prior to entering the scanner, and at completion of each session. The only mood difference observed resulting from a treatment effect was for self-reported attentiveness, $F(2, 38) = 4.35$, $p = .020$, $\eta_G{}^2 = .021$, which was driven by higher scores during placebo sessions ($M = 3.75$, $SD = 0.93$) than either OT ($M = 3.42$, $SD = 1.10$) or AVP ($M = 3.43$, $SD = 1.15$).

A two-way, repeated measures ANOVA revealed that participants rated faces as being more dominant ($M = 51.97$, $SD = 6.63$) than trustworthy ($M = 47.18$, $SD = 7.71$), but this difference was not significant, $F(1, 19) = 3.67$, $p = .071$. We found no main effect for neuropeptide treatment, $F(2, 38) = 1.40$, $p = .26$. However, this ANOVA did reveal a rating type by treatment interaction, $F(2, 38) = 3.72$, $p = .033$, $\eta_G{}^2 = .020$. We hypothesized hormone interactions for both tasks, with OT increasing trustworthiness ratings and AVP increasing dominance ratings. However, separate Bonferroni corrected ANOVAs run on the mean ratings for each judgment revealed the omnibus interaction to be driven by dominance ratings, $F(2, 38) = 4.35$, $p = .020$, $\eta_G{}^2 = .045$, not trustworthiness ratings, $F(2, 38) = 1.18$, $p = .316$, $\eta_G{}^2 = .006$. To limit multiple comparisons, we restricted subsequent pairwise Bonferroni *post hoc* t-tests to dominance ratings. These indicated that the task by treatment interaction was driven by OT ($M = 53.78$, $SD = 6.71$) increasing ratings of dominance over placebo ($M = 50.39$, $SD = 5.16$), $p = .031$ (Fig. 2).

3.1. Whole-brain BOLD activation

We analyzed OT and AVP treatment effects on regional activation compared to placebo for several contrasts of interest. We also compared treatment effects of OT and AVP to the placebo condition for BOLD response changes corresponding to behavioral ratings. This allowed us

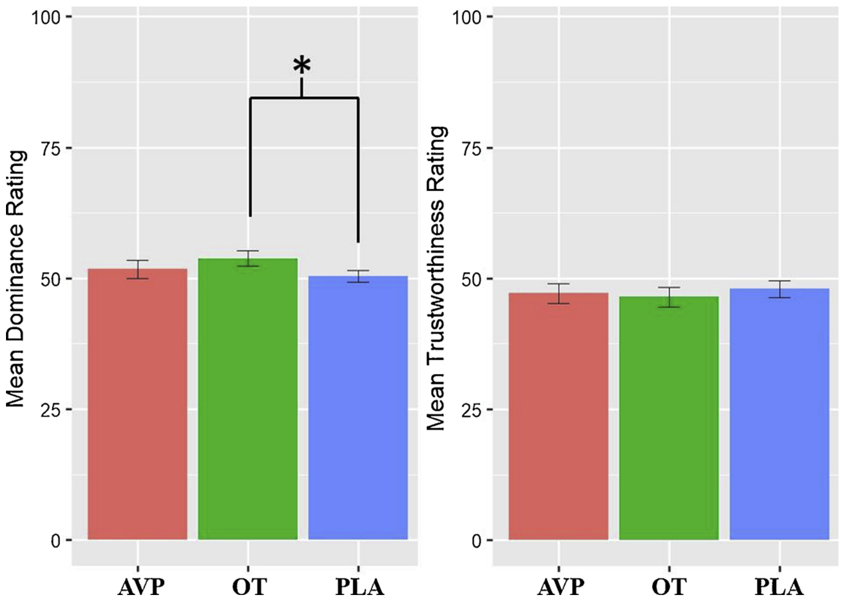

Fig. 2. Results of ANOVA and Bonferroni corrected post-hoc tests revealing differences in mean dominance and trustworthiness ratings between treatment conditions. Error bars: SEM. * < .05. AVP = Vasopressin, OT = Oxytocin, PLA = Placebo.

to investigate the hormones' effects on the linear relationships between activation and trustworthiness and dominance ratings. We only report BOLD differences relating to contrasts of these behavioral correlation maps as no significant changes were observed for simple treatment by task condition interactions. Our predictions for the whole-brain results were that OT would reduce amygdala activation and AVP would enhance STG activity, respectively, during trustworthiness and dominance judgments. None of these predictions held as stated.

In the OT condition compared to placebo, linear increases in ratings of either trustworthiness or dominance were accompanied by linear activation increases within a single cluster that included the left superior colliculus and the cerebellum and linear reductions in activation in several regions including the right posterior insula, Heschl's gyrus, parietal operculum, superior temporal gyrus (STG), the TPJ, and the left cerebellum (Fig. 3). These effects appear to be driven by the dominance task as linear increases in dominance ratings were associated with a nearly identical pattern of modulation with the addition of attenuated activity in the precuneus (see SI Table 1).

In the AVP condition, linear increases in dominance ratings were associated with linear reductions in activation within the left temporoparietal junction (TPJ) compared to placebo. An almost identical inverse relationship between ratings and TPJ activation was also observed when both dominance and trustworthiness judgments were collapsed together but was absent for trustworthiness judgments alone (see SI Table 1), suggesting that the effect was driven by the dominance task. Thus, the only result related to our hypotheses in this analysis was the observation of an effect on the STG, albeit attenuated rather than enhanced and modulated by OT rather than AVP.

3.2. Connectivity

Psychophysiological interactions measure functional connectivity between *a priori* seed regions and observed regions (Friston et al., 1997). We performed functional connectivity analyses for the amygdala and VTA seed regions to evaluate potential task-related interactions. We observed regional connectivity changes associated with AVP over placebo for the amygdala and VTA seeds. We had predicted that AVP would increase connectivity between the amygdala and brainstem regions associated with social vigilance during dominance judgments but saw no results supporting this. Instead, AVP led to connectivity decreases between the left amygdala and both the anterior STG and the inferior frontal gyrus (IFG) across all task conditions and ratings. AVP led to increased connectivity between the left amygdala and right thalamus across all task conditions and ratings.

During trustworthiness trials associated with AVP over placebo, left amygdala connectivity decreased with the bilateral precentral lobule, but increased with the bilateral cerebellum, PCC, left putamen, and a cluster that included the right thalamus and bilateral midbrain (Fig. 4). We observed increased connectivity between the right VTA and right putamen during trustworthiness trials, but decreased connectivity with the midbrain.

We next evaluated whether seed-based connectivity between

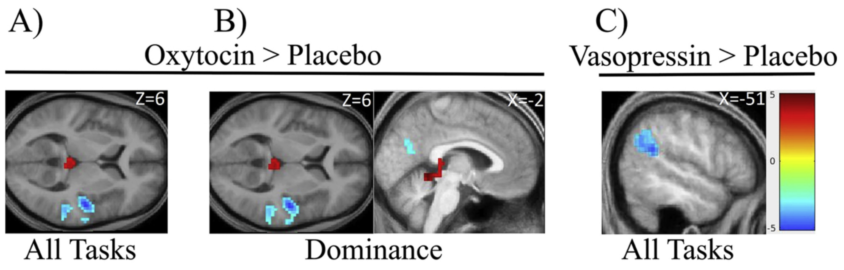

Fig. 3. Regional differences in correlations between regional BOLD response and task ratings resulting of contrasting OT or AVP treatments versus placebo for various task conditions. A) Increasing (red) and decreasing (blue) regional responses relating to OT regardless of rating type. B) Regional responses relating to OT during dominance ratings. C) Regional inverse correlations irrespective of rating type for AVP versus placebo. A nearly identical cluster was observed relating to dominance ratings alone for AVP versus placebo. Results are shown as t-score values for voxels significant at $p < .001$ uncorrected and cluster size corrected for $p < .05$ in AFNI's 3dClustSim (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

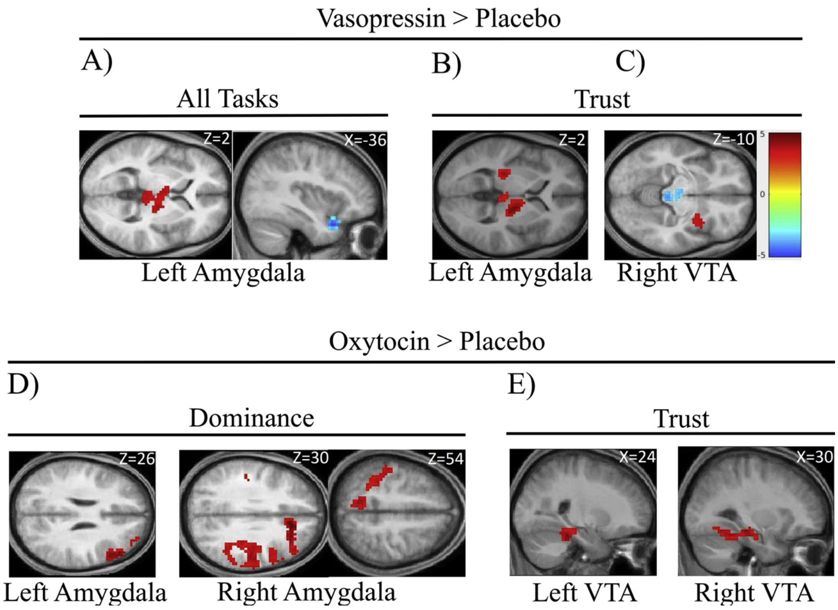

Fig. 4. Differences in connectivity patterns for amygdala and VTA seed regions when contrasting OT or AVP treatments versus placebo for various task conditions. A) Increasing (red) and decreasing (blue) connectivity with the left amygdala during AVP sessions regardless of rating type. B) Increasing and decreasing connectivity with the left amygdala for AVP treatment during trust evaluations. C) Increasing and decreasing connectivity with the right VTA for AVP treatment during trust evaluations. D) Increasing correlations between amygdala connectivity and dominance ratings when comparing OT treatment versus placebo. E) Increasing correlations between VTA connectivity and trust ratings when comparing OT treatment versus placebo. Results are shown as t-score values for voxels significant at $p < .001$ uncorrected and cluster size corrected for $p < .05$ in AFNI's 3dClustSim (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

regions was modulated by judgment ratings. We observed relationships between judgment ratings and functional connectivity relative to placebo for AVP. AVP was associated with increased connectivity between the right amygdala and right anterior cingulate cortex (ACC) during dominance judgments. The AVP condition led to decreases in functional connectivity between the left VTA and right temporal pole for trustworthiness ratings.

OT did not reduce general amygdala connectivity during trustworthiness judgments as predicted but it is worth noting that many previous facial judgment studies showing reduced amygdala connectivity used neutral faces to as a baseline contrast for emotional expressive faces (Tully et al., 2018). OT was seen to increase connectivity related to dominance ratings between the right amygdala and a network of clusters that included the bilateral parietal and somatosensory cortices and the right precentral gyrus, lateral frontal cortex, and the right MCC/dACC (Fig. 4). Of these regions enhanced by OT, only the MCC/dACC and medial, middle frontal gyrus was modulated by responses in both judgment conditions (See SI for fMRI results tables). OT increased connectivity associated with trustworthiness ratings for both left and right VTA seeds and regions of the right hippocampus, parahippocampal gyrus, fusiform gyrus, and the cerebellum.

4. Discussion

This study provides novel insights into the contributions of OT and AVP to social evaluations of neutral faces and the associated changes in neural activation and functional connectivity. Both neuropeptides yielded results that were unexpected and interesting. OT had a significant effect on behavioral ratings, brain activation, and task-related functional connectivity. While AVP did not significantly influence behavioral ratings, contrary to our prediction that it would increase ratings of perceived dominance, it showed distinct influences on brain activation responses and functional connectivity.

OT administration led to significant increases in ratings of social dominance of neutral faces, but not trustworthiness as we had expected. The influence of OT on the perception of dominance is a novel finding and may indicate that OT led to enhanced attention toward markers of facial dominance within the stimuli. Alternatively, genetic variations in OT sensitivity may help establish social hierarchies by prompting those with higher basal OT to more often perceive others as being relatively higher in social status than oneself. This tendency may promote prosocial behavior and willingness to cooperate when OT levels are elevated. Such an influence could result in a reduction in interpersonal conflict by promoting some individuals to adopt a subordinate status. Elevated baseline OT has been observed in dominant Rhesus monkeys (Michopoulos et al., 2011), which runs contrary to this idea; however, variation in the effects of these hormones across species is not uncommon (Goodson and Thompson, 2010).

Our findings failed to support our prediction that OT would increase trustworthiness ratings. OT trust effects have been difficult to replicate and have been subject to critical review (Nave, et al., 2015). Evidence suggests that the likelihood of observing a trust effect for OT varies based on the degree of social information and type of situational context presented (Bartz et al., 2011). Declerck et al. (2010) found that OT decreased cooperation during an interactive game when people lacked additional social information about others, while OT increased cooperation when additional social context was provided. In the present study, we provided no information regarding familiarity or in-group status of the trustee for the faces. The lack of modifying social factors may have reduced the influence of OT on trust judgments.

Our findings failed to support our prediction that OT would increase trustworthiness ratings. Theorodiou et al. (2009) previously found OT to increase perceptions of trustworthiness and attractiveness combined but the influence appeared from their report to be stronger for attractiveness and it is not clear whether the effect on trustworthiness could stand alone. No study has since observed a simple effect of OT on perceived trustworthiness (Lambert et al., 2014; Woolley et al., 2017). Evidence from intranasal OT research on other psychological constructs suggests that the likelihood of observing a trust effect for OT may vary based on the degree of social information and type of situational context presented (Bartz et al., 2011). For instance, Declerck et al. (2010) found that OT decreased cooperation during an interactive game when people lacked additional social information about others, while OT increased cooperation when additional social context was provided. In the present study, we provided no information to participants regarding the familiarity or in-group status of the faces rated, two factors that may increase the likelihood of an OT effect based on previous research (De Dreu et al., 2011; Scheele et al., 2013).

OT also influenced brain activation and functional connectivity. Across task conditions, linear increases in behavioral ratings during OT compared to placebo trials revealed enhanced activation in left superior colliculus, and cerebellum, attenuated activation in the right posterior STG and in a cluster including the right Heschl's gyrus, posterior insula and STG. Modulation of STG is a common effect of OT (Wang et al., 2017; Wigton et al., 2015). Attenuation of activity in this region in men has primarily been observed during implicit judgments, but enhanced activity has been seen for women, and one study in men (Labuschagne et al., 2012), during explicit judgments more similar to the task we employed (Wigton et al., 2015). This current imbalance regarding sex and task demand factors makes it difficult to determine the effect of OT on the relationship observed in the current study between STG activity and facial judgments. Our results may suggest that the perception of highly trustworthy and dominant faces attenuates STG activity. Alternatively, our results may reflect an OT effect on explicit facial judgments, which would suggest that perceiving faces as low on trust and dominance enhances STG activity.

When this contrast was restricted to dominance ratings, we observed a nearly identical pattern of activation, but with slightly greater coverage, suggesting that the dominance task drove the OT modulated relationship between behavioral and neural responses. Specifically, the left precuneus and right STG showed an inverse relationship with dominance ratings during OT compared to placebo sessions. The STG has been previously observed to correlate with ratings of dominant or submissive expressions (Chiao et al., 2008), demonstrating sensitivity based on the degree of social status information. For this reason, we anticipated observing an effect on the right STG during dominance judgments, although we predicted its activity would be enhanced, rather than attenuated, in association with a hormone increasing perceptions of dominance. Perhaps in this case sensitivity for more submissive faces was diminished by OT relative to the placebo condition, thereby raising the mean ratings and decreasing the degree by which the STG responded to these faces. The precuneus is commonly observed during social processing (Iacoboni et al., 2004; Northoff et al., 2006) and is responsive to emotional expressions, a function also associated with the right STG (Carvajal et al., 2013). The attenuation of precuneus activation may indicate that OT facilitated this trait-based facial judgment based on physical features associated with dominance alone and decreased automatic processing of emotional expression cues.

The connectivity results for this task were also related to dominance ratings, further suggesting that OT's effects are sensitive to the perceived dominance of the faces. Specifically, as dominance ratings increased, connectivity between the right amygdala and a network of cortical areas known to contribute to cognitive control, motor preparation and goal-directed attentional systems were enhanced including the IFG, ACC, DLPFC, sensorimotor cortices, and the TPJ (Kahnt and Tobler, 2013). The ACC, lateral PFC and sensorimotor were previously reported as being activated when people interacted with a high-status individual during a game (Zink et al., 2008). Enhanced connectivity in this network may suggest that OT primes goal-directed control and motor preparation systems even during the mere identification of dominant individuals. OT enhanced the correlation between trustworthiness ratings and bilateral VTA connectivity with the fusiform gyrus, hippocampus, and parahippocampal gyrus, potentially indicating that OT enhances dopamine mediated memory-encoding of trustworthy faces (Rimmele et al., 2009).

Research into AVP's influence on human social behavior lags well behind that of OT and remains exploratory. We found no AVP effect on behavior disconfirming part of our first hypothesis. We did find influences of AVP on neural responses during dominance ratings. AVP led to an attenuation of left TPJ activity as a function of behavioral responses, potentially signaling less engagement in theory of mind being necessary to promote high ratings in that condition. Connectivity results indicated greater connectivity for each of the left amygdala and right VTA seeds with the thalamus and right putamen while decreasing their connectivity with the left anterior temporal cortex. These results do not support our hypothesis that AVP may enhance communication in the social vigilance circuit between the amygdala and brainstem. Rather, these BOLD results may be consistent with AVP biasing facial evaluations toward habitual, perceptual cue-based judgments rather than judgments based on reward processing or social cognition. More work will be required to follow up on these findings related to AVP.

Our study only recruited male subjects, limiting the generalizability of the findings. It is important that future efforts integrate findings for neuropeptide administration in women. We administered conventional doses of 24 IU OT and 40 IU AVP while within-subjects studies often use the molecular equivalent doses of 24 IU OT and 20 IU AVP. Use of molecular equivalent doses is likely the best practice for limiting confounding participant experiences unrelated to

More precise understanding of the effects of these hormones on trust and dominance evaluation may be gained in future studies that include several variables not addressed by our data. We saw no behavioral effects when analyzing hormone, task, and face gender interactions but this might not be the case with a larger sample. The literature suggests a relationship between the effects of OT on facial attractiveness and trustworthiness, and attractiveness judgments are supported by reward processing regions (Mende-Siedlecki et al., 2012). We did not observe either hormone to modulate reward system activity, or connectivity between the VTA and other reward regions, during the trust judgments. This suggests that our results are unlikely to have been driven by facial attractiveness.

5. Conclusion

We modified levels of both OT and AVP combined with fMRI methods to investigate the neural mechanisms underlying trait evaluations of trust and dominance in others. This study aligns with recent reports showing a lack of an effect for OT on the overall perception of trustworthiness. We report the novel effect of OT increasing the perception of dominance. Like other studies, we observed OT to modulate STG activity, but the effect we observed is not typical in the few studies looking at intranasal OT in men during explicit facial judgment, thus rendering unclear the nature of the inverse relationship we observed between this activity and the behavioral responses for either judgment. When judging the dominance of faces, the left precuneus was selectively and inversely related to dominance ratings in addition to the effect on the right STG. This may indicate a diminished tendency to engage emotional expression processing when judging neutral expression faces. AVP demonstrated no influence on behavioral ratings but higher ratings for either task led to decreased activity in the TPJ and increased connectivity in subcortical networks potentially indicative of emphasis on habitual, perceptual cue-based processes during evaluations. These results demonstrate that the effects of OT and AVP on neural activity during social judgment depend not only on the type of social trait evaluated but also by the degree to which individuals may be perceived to reflect a trait.

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Conflict of interest statement

The authors declare no conflicts of interest.

CRediT authorship contribution statement

Adam R. Teed: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization, Investigation, Funding acquisition. **Kihwan Han:** Methodology, Formal analysis, Writing - original draft. **Jelena Rakic:** Investigation, Project administration, Writing - review & editing. **Daniel B. Mark:** Investigation. **Daniel C. Krawczyk:** Conceptualization, Supervision, Writing - review & editing, Funding acquisition.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.psyneuen.2019.04.014.

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