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Gender-specific effects of vasopressin on human social communication: An ERP study

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ABSTRACT

The quick and efficient perception of facial expressions represents a special and fundamental capacity of humans to engage in social communication. Here, we examined the effects of vasopressin (AVP, a neuropeptide) on the processing of same- and other-gender facial expressions among males and females. After receiving either AVP or placebo (PBO) intranasally in a randomized and double-blind manner, participants were asked to rate their approachability to facial expressions while event-related potentials (ERPs) were recorded. Males rated lower approachability scores to neutral and positive male faces relative to the scores to emotion-matched female faces after AVP but not following PBO administration. These behavioral effects were correlated with the AVP-induced increased P1 and decreased N170 responses to male faces among male participants. Females rated higher approachability scores to negative female faces than the scores to negative male faces after AVP but not following PBO treatment. These results suggest that AVP decreases friendly responses to neutral/positive male faces in males and increases friendly responses to negative female faces in females. Overall, these results demonstrate the gender-specific effects of AVP in response to same- and other-gender facial expressions, indicating there are sex- and context-dependent effects of AVP on socioemotional processes.

1. Introduction

Arginine vasopressin (AVP) is a social neuropeptide that regulates various social and emotional behaviors in a wide range of species (Albers and Bamshad, 1999; Albers et al., 2002; Heinrichs et al., 2009; Insel, 2010; Lindenberg et al., 2011; Viviani and Stoop, 2008). Animal studies have shown that AVP controls a variety of social behaviors, including both reproductive (e.g., parental and copulatory behaviors) and nonreproductive behaviors (e.g., offensive aggression, social memory, and social communication) (for reviews see Albers, 2015; Caldwell, 2017). AVP administration increases the amount of time spent taking care of pups among male prairie voles (De Vries et al., 1994), enhances the touch frequency of male *Callicebus cupreus* with their female partners relative to female strangers (Jarcho et al., 2011), and facilitates aggressive responses to a resident intruder in male Syrian hamsters (Caldwell and Albers, 2004; Winslow et al., 1993). Thus, both affiliative and aggressive behaviors can be induced by AVP in certain social contexts.

Based on findings from animal models, the past decade has witnessed a growing interest in exploring the modulatory effects of AVP on human social behaviors. As one of the most important forms of social communication (Ekman, 1993), facial expressions have been frequently used as stimuli to explore the role of AVP in social functioning (Guastella et al., 2010; Price et al., 2017; Rilling et al., 2017b; Thompson et al., 2006; Wu et al., 2018). In particular, AVP has been found to be associated with negative social interactions. Intranasal AVP administration increases agonistic facial motor patterns and decreases friendly perception in response to unfamiliar same-gender faces (Thompson et al., 2004; Thompson et al., 2006). Similarly, AVP diminishes the ability of males to recognize the emotions of other males,

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which may further stimulate intermale aggression due to a lack of empathy (Uzefovsky et al., 2012). Lastly, cerebrospinal fluid levels of AVP are positively correlated with aggressive life histories in individuals with personality disorders, an association that is stronger in males than in females (Coccaro et al., 1998). On the other hand, some evidence has suggested that AVP is involved in promoting social bonds. Intranasal AVP administration promotes cooperation among strangers (Brunnlieb et al., 2016; Feng et al., 2015; Rilling et al., 2012) and enhances the ability for males to detect sexual cues (Guastella et al., 2011). Furthermore, AVP 1a receptor (AVPR1a) repeat polymorphisms (RS3) are strongly associated with marital quality in males (Walum et al., 2008). Lastly, male plasma AVP levels are positively associated with distress in pair bonding relationships (Taylor et al., 2010). In females, AVP administration induces affiliative facial motor patterns and increases approachability ratings to other females, indicating that AVP could promote affiliative/friendly behavior (Thompson et al., 2006). Furthermore, AVP increases cooperation in females but not in males after their same-gender partners defect, suggesting that AVP can facilitate females' willingness to reestablish harmonious interpersonal relationships with other females (Rilling et al., 2014). Together, these studies indicate that AVP has gender-differentiated effects on human social behaviors and on associated emotional processing. Specifically, in males, AVP might promote male antisocial/aggressive responses toward other males in some contexts (Thompson et al., 2004; Thompson et al., 2006), but facilitate cooperation in others, especially when alliances have already been established (Rilling et al., 2014; Rilling et al., 2012). AVP may also facilitate prosocial responses toward potential mates (Guastella et al., 2011). In females, AVP appears to promote affiliative behavior toward other females (Rilling et al., 2014; Thompson et al., 2006). Therefore, it is possible that the effects of AVP on males and females are context-dependent and closely related to specific targets (e.g., same- or other-gender others).

Considering the gender-differentiated effects of AVP, it is important to explore not only the gender effects of participants but also the gender effects of interacting targets on AVP effects. Moreover, it is important to consider both neutral and emotional contexts, as AVP is more involved in modulating the processing of emotional cues than neutral cues (Naumann et al., 1991). Furthermore, previous studies have mainly focused on the processing of face stimuli in a context-free manner (i.e., participants of these studies were exposed to stimuli without contextual information) (Price et al., 2017; Rilling et al., 2014; Rilling et al., 2017b; Thompson et al., 2006), which diverges from the way in which people actually interact with others in daily life, whereby background information associated with others' emotions in involved (Frith and Frith, 2012). To address these issues, the current study investigated the temporal dynamics of potential effects of AVP on processing same- and other-gender facial expressions among males and females with the event-related potential (ERP) technique providing fine-grained temporal resolution. Relative to functional magnetic resonance imaging (fMRI), the main advantage of ERP lies in its millisecond-scale temporal resolution (Amodio et al., 2013) whereas disadvantages of ERP include its low spatial resolution and the fact that signals can only be detected from certain populations of neurons (Durston, 2010). More specifically, advantages of applying ERP in the present study include the followings: (i) ERPs can provide information on successive temporal dynamics far earlier than behavioral outputs, which are useful for uncovering mechanisms associated with the formation and regulation of a behavioral response. (ii) Given that very little work has been done to examine the effects of AVP on temporal dynamics of facial expression processing, the present findings might offer ERP markers for the modulation of AVP on emotional processing (i.e., revealing potential ERP components to be tested in future studies). (iii) Compared to fMRI, ERP can provide a realistic environment for social interactions such that sitting in a soundless room more closely reflects daily human communication settings than engaging amidst background noise; therefore, ERP may help to promote external validity.

In light of previous studies, the processing of facial expressions could be distinguished into at least two stages occurring within the first 200 milliseconds (ms) (Eimer and Holmes, 2007; Eimer et al., 2003; Olivares et al., 2015). In particular, valence appears to have an effect relatively early (roughly 100 ms) while arousal often has an effect later (200 ms and beyond) on the processing of facial expressions (Codispoti et al., 2007; Feng et al., 2014; Olofsson et al., 2008). On one hand, amplitudes of parieto-occipital P1 are enlarged by negative images rather than by positive and neutral images, indicating automatic and coarse processing in response to negative stimuli (Aguado et al., 2012; Delplanque et al., 2004; Luo et al., 2010). This “negativity bias” might be attributed to the fact that attention is automatically oriented toward threatening events in an evolutionarily adaptive manner (Öhman et al., 2001; Öhman and Mineka, 2001). On the other hand, parieto-occipital N170 is a face-specific component within 200 ms poststimuli (Rossion, 2014). N170 is sensitive to arousal and relevance irrespective of valence. For instance, high-arousal faces (e.g., fearful, sad and happy) evoke larger N170 amplitudes than low-arousal faces (i.e., neutral) (Almeida et al., 2016; Hinojosa et al., 2015; Krombholz et al., 2007; Williams et al., 2004), suggesting an enhanced attentional allocation to arousing/relevant stimuli (Batty and Taylor, 2003; Morel et al., 2014; Rossignol et al., 2005; Sun et al., 2017). By applying the ERP technique, this study was designed to uncover the effects of AVP on emotional processing at different temporal stages, which could help to uncover the mechanisms associated with the formation and regulation of a behavioral response.

Based on previous findings, we hypothesized that the effects of AVP on males and females are context-dependent and closely related to specific targets (e.g., same- or other-gender others and their emotional states). Specifically, AVP was expected to reduce approachability ratings toward male faces in males (Thompson et al., 2004; Thompson et al., 2006). These male faces may be perceived as more unfriendly, therefore eliciting larger P1 amplitudes. In addition, AVP was expected to increase approachability ratings of female faces in females (Rilling et al., 2017b; Thompson et al., 2006), as female faces might be perceived as more relevant/salient and therefore might induce stronger N170 responses.

2. Materials and methods

2.1. Participants

Forty-eight males (mean age 22.46, SD = 2.02) and 51 females (mean age 21.78, SD = 2.06) of 18–26 years of age participated in the present study. The participants were randomly assigned to AVP (n = 48, 24 males) or placebo (PBO) administration (n = 51, 24 males). There was no significant difference between the two groups with respect to age and education level among other demographic dimensions (see Supplementary Table S1 and S2). All participants had normal or corrected-to-normal vision and did not have any history of psychiatric or neurological illness or psychoactive drug use. Participants were instructed to abstain from alcohol and caffeine on the day of the experiment and from food and drink (except for water) 2 h before drug administration. Written informed consent was collected from all participants prior to the experiment. The study and the recruitment of participants were approved by the Ethics Committee of Beijing Normal University and were performed in strict accordance with the approved guidelines. One male participant from the PBO group was excluded from the ERP data analysis due to technical difficulties experienced during electroencephalogram recording.

2.2. Stimuli

Facial expressions were selected from the native Chinese Affective Face Picture System (Gong et al., 2011). Twenty-eight sad faces, 14 neutral faces, and 28 happy faces were selected, resulting in 70 adult

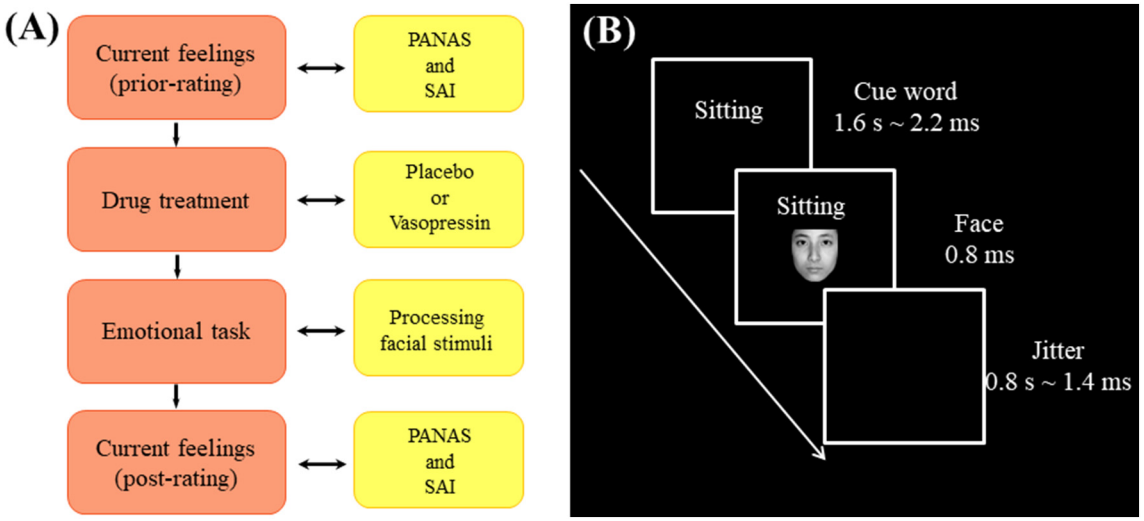

Fig. 1. Experimental procedure and design. (A). The experimental procedure. (B). Illustration of one trial of the emotion-rating task.

faces in total with an equal number of facial images of males and females. The valence and arousal of each picture were assessed on a 9-point Likert scale by a large sample of Chinese participants from a previous survey (Gong et al., 2011), showing that the three categories of faces have significantly different emotional valence scores and arousal scores. All images were normalized to the same luminance and contrast values. To investigate whether the effects of AVP in social processing are regulated by different social contexts, the high- and low-arousal context cues informing the situations in which those photos were putatively taken. Specifically, the neutral item was indicated by the word of "sitting". High and low-arousal positive items were indicated by the words of "reunion" and "traveling" respectively. The high-arousal and low-arousal negative items were indicated by the words of "bereavement" and "lost on the street" respectively. The arousal of cue words was validated by an additional group of 33 participants (mean age 22.70, SD = 2.90) who were recruited to rate arousal ("To what extent does this faces make you excited?") on a 9-Likert scale (from 1 "*not at all*" to 9 "*very much*"). A one-way ANOVA shows that each category of cue words shows significant differences in emotional arousal (F (4,128) = 16.136, $p < 0.001$, $\eta^2 = 0.335$; neutral words = 3.61 ± 0.31; high-arousal positive words = 5.91 ± 0.32; low-arousal positive words = 5.12 ± 0.31; high-arousal negative words = 6.72 ± 0.30; low-arousal negative words = 5.27 ± 0.32; pairwise comparisons: high-arousal positive words vs. low-arousal positive words, $p < 0.05$; high-arousal negative words vs. low-arousal negative words, $p < 0.001$; emotional words vs. neutral words, $p < 0.001$, positive vs. negative, $p > 0.05$).

2.3. Administration of AVP and PBO

The intranasal administration of AVP has been widely applied to humans and is regarded as an effective means to directly affect central processes through the blood-brain barrier (Born et al., 2002; Dhuria et al., 2010). In the present study, AVP and PBO solutions were formulated by a trained research assistant who did not interact with the subjects. The solutions were immediately sterilized before being transferred to a sterile conical tube and stored at −80 °C until further use. On the day of the study, the drug was transferred to a nasal spray bottle. All solutions were administered intranasally. Both the experimenters and participants were blind to the treatments that the participants received. Double-blind conditions were also maintained by the research assistant. The AVP group self-administered 20 IU AVP (ProSpec, https://www.prospecbio.com/Vasopressin) (Chen et al., 2016; Guastella et al., 2011; Guastella et al., 2010; Kenyon et al., 2013; Rilling et al., 2012; Rilling et al., 2017b; Uzefovsky et al., 2012). In each case, this required 6 nasal puffs to administer 0.5 ml of solution. The PBO group self-administered 6 nasal puffs of saline. Participants were instructed to place the nasal applicator in one nostril and to depress the lever until the spray entered the nostril, to breathe in deeply through the nose and to then place the applicator into the other nostril and repeat the process. After the experiment, all participants were asked to report what (AVP or saline) they thought they had received. The results show an average accuracy level of 53.68% across the participants, which does not significantly differ from the random level (χ^2 (1) = 0.52, $p = 0.47$). No significant difference was observed between the PBO and AVP groups for the male (45.83% vs. 45.83%, χ^2 (1) = 0, $p = 1$) and female participants (66.67% vs. 55.56%, χ^2 (1) = 0.66, $p = 0.42$).

2.4. Experimental tasks

Experiments were conducted in a dimly lit, sound-attenuated chamber with a CRT monitor set approximately 80 cm away from the participants' eyes. The participants were asked to perform an emotion-rating task adapted from previous studies (Price et al., 2017; Rilling et al., 2017b; Thompson et al., 2006). Specifically, participants were presented with emotional faces and were then asked to rate feelings of approachability related to each face. Specifically, the participants were presented with neutral, positive (happy) and negative (sad) facial expressions as well as cue words referred to the contexts under which the photos were putatively taken. Neutral expressions were associated with the term "sitting"; positive expressions were associated with terms "reunion" (high-arousal item) and "traveling" (low-arousal item); and negative expressions were associated with terms "bereavement" (high-arousal item) and "lost on the street" (low-arousal item). Cue words and facial expressions were always matched to emotional attributes and involved no conflict. Each association was presented 14 times during each of the three blocks of the task, resulting in 70 trials per block. For each trial, a cue word was presented (1600–2200 ms) followed by a facial expression (800 ms). Each trial ended with a jitter (800–1400 ms), during which a black screen was shown. Participants were instructed to respond to each facial expression by indicating on a 4-point Likert scale how much they wished to approach the person in the photo (from 1 "*not at all*" to 4 "*very much*"). To mitigate ocular artifacts in the ERP analysis windows, participants were asked to blink only during the jitter period. The procedure is illustrated in Fig. 1.

2.5. Mood measurements

The Positive and Negative Affect Schedule (PANAS) (Watson et al., 1988) and State Anxiety Inventory (SAI) (Spielberger, 1983) have been frequently used to determine the effects of AVP on emotional states in previous studies (Alvares et al., 2012; Di Simplicio et al., 2009; Thompson et al., 2006). For example, Thompson et al., 2006 found that AVP increased anxiety after an emotional task involving threatening stimuli. Accordingly, to examine whether AVP alters emotional responses to social stimuli by changing emotional states, participants in the current study also completed the PANAS and SAI prior to drug administration and at the end of the experiment.

2.6. Behavioral data analysis

Trials involving reaction times (mean [SD] = 524 [159] ms) of shorter than 200 ms were considered trial failures and were removed from further analysis (Duarte et al., 2004; Meyer et al., 2012). Removal of these trials resulted in the elimination of 1.14% of all trials (after rejection, mean [SD] = 540 [94] ms). Notably, since we did not identify any effects of contexts (i.e., high- vs. low-arousal) in either behavioral or neural responses, data taken from high- and low-arousal contexts were collapsed for the behavioral and ERP analyses.

2.6.1. Main tasks

Participants' self-reported approachability to each target in the photo and their RTs were analyzed. Four-way repeated measures analyses of variances (ANOVAs) were implemented with Drug (PBO vs. AVP) and Gender of participants (male subjects vs. female subjects) as between-subjects factors, and Emotional valence (neutral vs. positive vs. negative) and Gender of face stimuli (male faces vs. female faces) as within-subjects factors.

2.6.2. Mood measurements

Three-way repeated-measures ANOVAs were conducted on Drug (PBO vs. AVP), Gender of participants (male participants vs. female participants) and Test (pretest vs. posttest) on the PANAS and SAI scores.

2.7. EEG recording

The electroencephalogram (EEG) was recorded from 64 scalp sites using electrodes mounted on an elastic cap (Compumedics, Texas, USA), with an online reference to the left mastoid. The horizontal electroencephalogram (HEOG) was recorded with two electrodes placed laterally to the right and left eyes. The vertical electroencephalogram (VEOG) was recorded with electrodes placed above and below the left eye. All inter-electrode impedances were maintained below 10 kΩ. The EEG and EOG were amplified using a 0.05–100 Hz bandpass and continuously sampled at 500 Hz in each channel for offline analysis. EEGs were first re-referenced to the algebraic average of left mastoid and right mastoid and then to the average of all of the electrodes. Data were then corrected for ocular artifacts with algorithm implemented in the Neuroscan Edit 4.5 software (Compumedics, Texas, USA). The resulting data were then epoched from −200 to 800 ms relative to the onset of stimuli (i.e., faces), with baseline corrected from −200 to 0 ms. Afterwards, EEG data were low-pass filtered below 30 Hz. Artifact rejection was performed for all of the EEG channels, with the rejection criteria of ± 80 μV.

2.8. ERP data reduction and analysis

ERPs elicited by facial expressions were analyzed. Based on an inspection of grand-averaged ERP waveforms and from previous studies of emotion processing (Luo et al., 2010), the P1 and N170 components were measured. Occipito-temporal electrodes (PO7/PO8) were chosen for P1 (100–140 ms) and N170 components (170–210 ms) (Achaibou et al., 2008; Fu et al., 2012; Jemel et al., 2003; Magnée et al., 2008; Morgan et al., 2008; Vlamings et al., 2010), where the maximum amplitudes were observed for each component. The mean of amplitudes of these components were then analyzed in repeated measures ANOVAs with the factors of Drug (PBO vs. AVP) and Gender of participants (male participants vs. female participants) as the between-subjects factors, and Emotional valence (neutral vs. positive vs. negative), Gender of face stimuli (male faces vs. female faces) as well as Hemisphere (left vs. right) as within-subjects factors. *P*-values were corrected for deviations according to Greenhouse-Geisser correction if necessary. Bonferroni correction was used to draw multiple comparisons unless otherwise noted. All statistical analyses of behavioral and ERP data were conducted using SPSS 21.0 (IBM, Somers, USA). Statistical powers reported were calculated in G*Power 3.1.9.2 (Faul et al., 2007) using the effect size estimate (medium) and mean sample size taken from previous intranasal neuropeptide studies (Hasse Walum et al., 2016) while assuming an alpha level of 5%. The present study achieved a power of 71.25% in behavior, and a power of 70.34% in ERP results.

3. Results

3.1. Mood measurements

State mood and anxiety measured before drug treatment and after the experiment revealed neither main effect nor interactions related to drug administration (see Supplementary Tables S1 and S2), which is consistent with previous studies (Stoeva et al., 2015; Zink et al., 2010) and inconsistent with Thompson et al. (2006). Thompson et al. (2006) found that participants who received AVP reported higher anxiety after a faces processing task, the effect was absent in present study. This inconsistency may be attributed to the different emotional contexts examined in different studies. Thompson et al. (2006) included angry (threatening) faces, which may induce threatened responses and consequently alter the overall contexts of tests administered.

3.2. Behavior results

Behavioral results are shown in Fig. 2. Four-way repeated measures ANOVAs on the approachability ratings reveal a significant interaction of Drug × Gender of participants × Emotional valence × Gender of face stimuli (F (2, 190) = 5.809, p = 0.004, η^2 = 0.0011). First, for the neutral condition, males who received AVP reported lower approachability ratings to neutral male faces compared to neutral female faces (p = 0.000017), but the effect was found to be absent for the PBO group (Fig. 2A & 2B). On the other hand, female participants reported higher approachability ratings to neutral female faces than neutral male faces regardless of drug administration (p = 0.000015 for the PBO group; p = 0.000082 for the AVP group) (Fig. 2A). Second, in regard to positive valence, males who received AVP reported lower approachability ratings to positive male faces than positive female faces, but the effect was found to be absent for the PBO group (Fig. 2C & D). In contrast, females reported higher approachability to female faces than male faces regardless of drug administration (p = 0.000008 for the PBO group; p = 0.000041 for AVP group) (Fig. 2C). The post hoc comparisons show no significant differences between the AVP and PBO groups for all conditions (p > 0.05). Finally, in terms of negative valence, no significant difference was found between the approachability to male and to female faces among males (p > 0.05 for the PBO and AVP groups) (Fig. 2E). Females who received AVP reported higher approachability ratings to negative female faces compared to negative male faces (p = 0.0048), the effect was absent in PBO group (Fig. 2E & F). In addition, four-way repeated measures ANOVAs on the RTs did not reveal any significant effects related to drug administration. In short, males reported lower approachability ratings to neutral/positive male faces than neutral/positive female faces after AVP administration but not

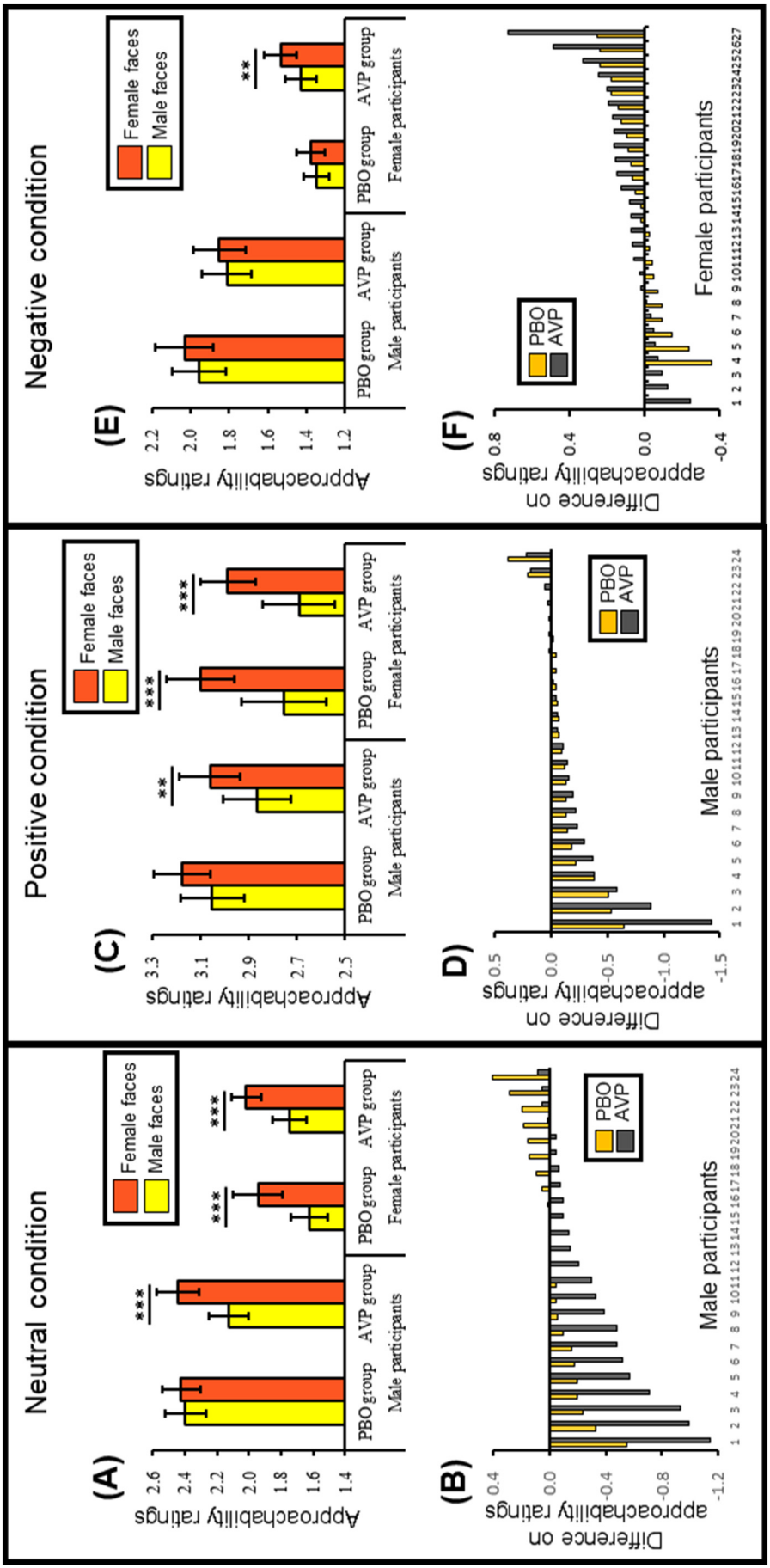

Fig. 2. Behavioral results. (A) & (C) & (E) The mean scores of approachability ratings as a function of Drug treatment, Emotional valence, Gender of face stimuli and Gender of participants. (B). Differences in approachability ratings between neutral male faces and neutral female faces for each participant in the PBO and AVP groups of males. (D). Differences in approachability ratings between positive male faces and positive female faces for each participant in the PBO and AVP groups of males. (F). Differences in approachability ratings between negative female faces and negative male faces for each participant in the PBO and AVP groups of females. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

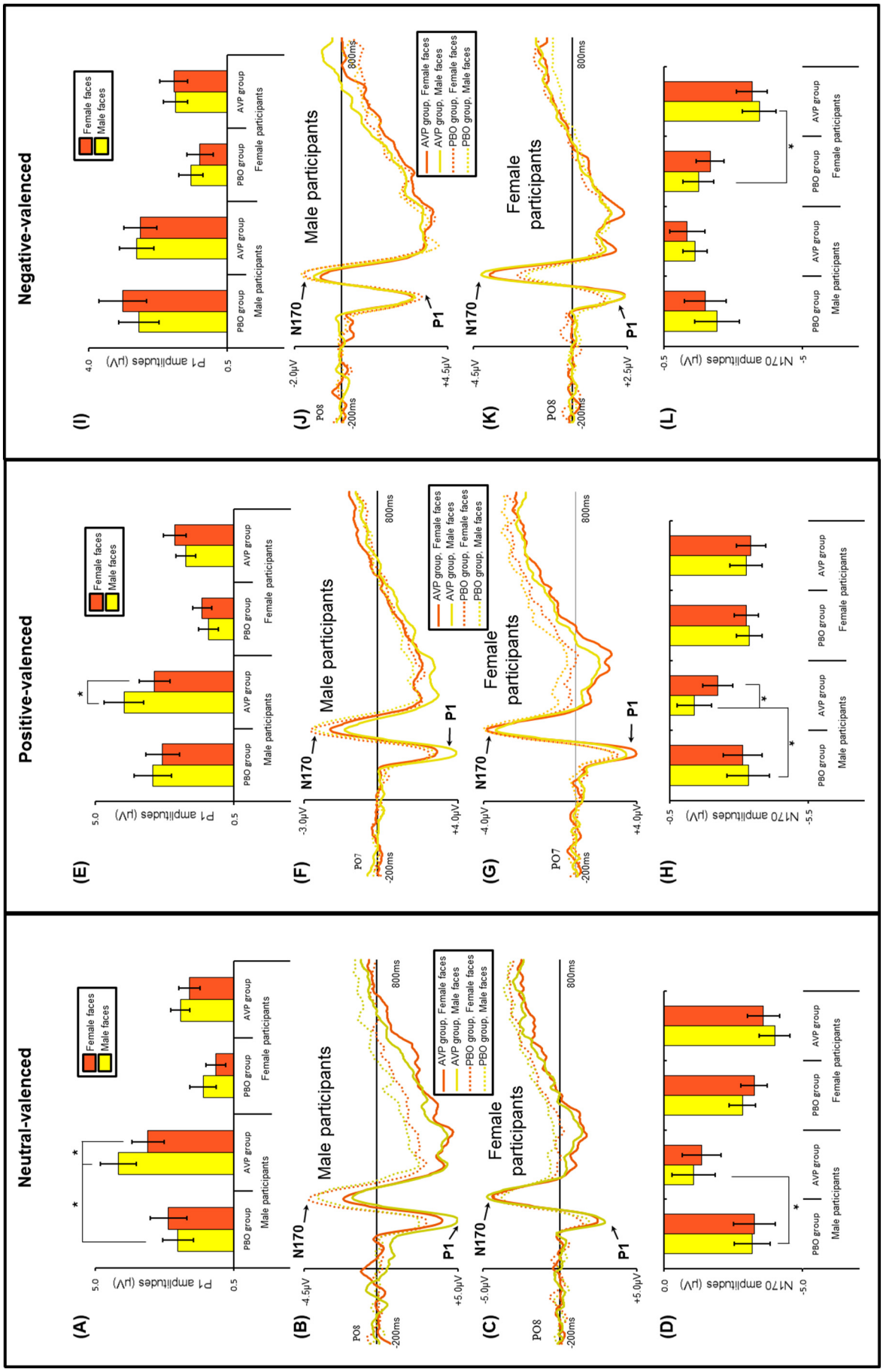

Fig. 3. ERP results of P1 and N170 components. (A) & (E) & (I). Bar graphs illustrate the mean P1 and N170 amplitudes as a function of Drug treatment, Gender of participants, Gender of face stimuli and Emotional valence. (B) & (C), (F) & (G) and (J) & (K). Grand average ERPs over occipito-temporal electrodes evoked by facial expressions among male and female participants in neutral, positive and negative conditions respectively. Please note that the positive-going component is plotted on the lower side of the y axis, while the negative-going component is plotted on the upper side of the y axis. (D) & (H) & (L). Bar graphs illustrate the mean N170 amplitudes as a function of Drug treatment, Gender of participant, Gender of face stimuli and Emotional valence. $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

after PBO administration. In addition, females reported higher approachability ratings to negative female faces than negative male faces after AVP administration but not after PBO administration.

3.3. ERP results

P1. Five-way repeated-measures ANOVAs on occipito-temporal P1 amplitudes revealed a significant interaction of Drug × Gender of participants × Emotional valence × Gender of face stimuli × Hemisphere (F (2, 188) = 4.058, p = 0.019, η^2 = 0.0036). First, for the neutral condition, male faces evoked larger P1 amplitudes on the right hemisphere in AVP-treated males compared to female faces (p = 0.024) and compared to PBO-treated males (p = 0.004) (Fig. 3A & B). This interaction between drug administration and the gender of stimuli was not found for the female participants (Fig. 3A & C). Second, in terms of positive valence, male faces evoked larger P1 amplitudes on the left (p = 0.006) and right (p = 0.007) hemispheres than female faces in AVP-treated males but not in PBO-treated males (Fig. 3E & F). This interaction of Drug administration and Gender of face stimuli was not found for the female participants (Fig. 3E & G). Third, in regard to negative valence, no significant interaction was observed between drug administration and the gender of stimuli in processing negative faces for both male and female participants (Fig. 3I & J & K). In brief, the P1 component exhibited stronger responses to neutral and positive male faces than emotion-matched female faces among AVP-treated males but not for PBO-treated males.

N170. Five-way repeated measures ANOVAs on occipito-temporal N170 amplitudes revealed a significant interaction of Drug × Gender of participants × Emotional valence × Gender of face stimuli × Hemisphere (F (2, 188) = 3.19, p = 0.043, η^2 = 0.002). First, for the neutral condition, N170 amplitudes on the right hemisphere in response to male faces were lower in the AVP-treated males than in the PBO-treated males (p = 0.02) (Fig. 3B & D). This interaction between drug administration and the gender of stimuli was not found for the female participants (Fig. 3C & D). Second, in terms of positive valence, N170 amplitudes on the right hemisphere in response to male faces were lower in the AVP-treated males than in PBO-treated males (p = 0.029). In addition, N170 amplitudes on the right hemisphere to male faces were lower than those to female faces in AVP-treated males (p = 0.03), but this effect was absent in PBO-treated males (Fig. 3F & H). This interaction between drug administration and stimulus gender was not found for the female participants (Fig. 3G & H). Third, in terms of negative valence, AVP-treated females showed increased N170 amplitudes on the left hemisphere in response to male faces than PBO-treated females (p = 0.012) (Fig. 3K & L). This interaction between drug administration and the gender of stimuli was not found for the male participants (Fig. 3J & L). In short, AVP compared to PBO decreased N170 responses to neutral/positive male faces among males and increased N170 responses to negative male faces among females.

3.4. Correlations

The results of the ANOVAs show that AVP induced different behavioral and ERP responses to neutral and positive female faces relative to responses to emotion-matched male faces in male participants. The bivariate (Pearson's r) correlation were employed to determine associations between differences in behavior (approachability ratings for male faces relative with those for female faces) and differences in ERP responses (ERP amplitudes for male faces compared to those for female faces) in males. Consistently, the results reveal that lower approachability ratings of neutral male faces relative to those of neutral female faces were related to enhanced P1 responses to neutral male faces relative to neutral female faces (all males: r = −0.406, p = 0.005; male AVP group: r = −0.306, p = 0.146; male PBO group: r = −0.406, p = 0.055) (Fig. 4A). Thus, the AVP treatment's reduction of approachability ratings for neutral male faces, relative to neutral female faces, is related to its enhancement of P1 responses to neutral male faces. Likewise, lower approachability ratings for positive male faces relative to positive female faces were found to be associated with weakened N170 responses to positive male faces relative responses to positive female faces (all males: r = −0.264, p = 0.073; male AVP group: r = −0.457, p = 0.025; male PBO group: r = 0.075, p = 0.734) (Fig. B). Thus, the AVP treatment's reduction of approachability ratings of positive male faces, relative to positive female faces, was found to be correlated with its weakening of N170 responses to positive male faces. For females the results show that approachability ratings in response to negative male faces were positively correlated with N170 responses to negative male faces (all females: r = 0.347, p = 0.013; female AVP group: r = 0.439, p = 0.022; female PBO group: r = 0.367, p = 0.078) (Fig. 4C).

4. Discussion

The current study investigated how AVP modulates the time course of the processing of same- and other-gender facial expressions among males and females. The results show that the effects of AVP on emotional processing at the behavioral and ERP levels depend on the gender of participants, emotional valence and the gender of stimuli. These findings support the account that the effects of AVP are constrained by the features of individuals and situations (Thompson et al., 2006).

In males, approachability responses to male and female faces differed for the AVP group but not for the PBO group such that AVP induced lower ratings of neutral and positive male faces than of emotion-matched female faces. Likewise, we found AVP to enhanced P1 responses to neutral and positive male faces. These results, in agreement with our hypotheses, suggest that male faces might capture more automatic attention at a very early temporal stage and presumably due to increased levels of perceived hostility induced by AVP administration (Thompson et al., 2006; Thompson et al., 2004). In addition, AVP administration weakened N170 responses to neutral and positive male faces relative to responses to emotion-matched female faces. Considering the critical role of N170 in encoding emotional arousal (Almeida et al., 2016; Williams et al., 2004), these results indicate that AVP might alter perceived arousal to male faces in relatively late temporal stage, as neutral and positive male faces may be perceived as less salient at this temporal stage. Hence, the differences in behavioral responses to male and female faces may be driven primarily by the reduced ratings of male faces. The correlational results further reveal that AVP's reduction of the approachability ratings of neutral male faces is related to its enhancement of P1 responses to neutral male faces while AVP's reduction of approachability ratings for positive male faces is correlated with its weakening of N170 responses to positive male faces, relative to female faces. Together our results are in line with previous observations showing that AVP can reduce approachability ratings of male faces in males (Thompson et al., 2006; Thompson et al., 2004). Specifically, the current and previous studies (Thompson et al., 2006; Thompson et al., 2004) consistently show that negative assessment effects of AVP are selective to neutral and positive stimuli rather than to negative stimuli among male participants. These data therefore support the idea that AVP promotes more negative assessments of faces not already perceived negatively.

In females, approachability ratings toward negative male and female faces differed in the AVP group but not in the PBO group. That is, AVP induced higher approachability ratings toward negative female faces than emotion-matched male faces. These results are consistent with our hypotheses and with those of previous studies indicating that AVP can increase approachability ratings to female faces in females (Rilling et al., 2017a; Thompson et al., 2006). In terms of ERP levels, AVP compared to PBO enhanced N170 responses toward negative male faces but not in the case of female faces. The correlational results reveal that AVP's reduction of approachability ratings to negative male faces was correlated with its enhancement of N170 responses to negative

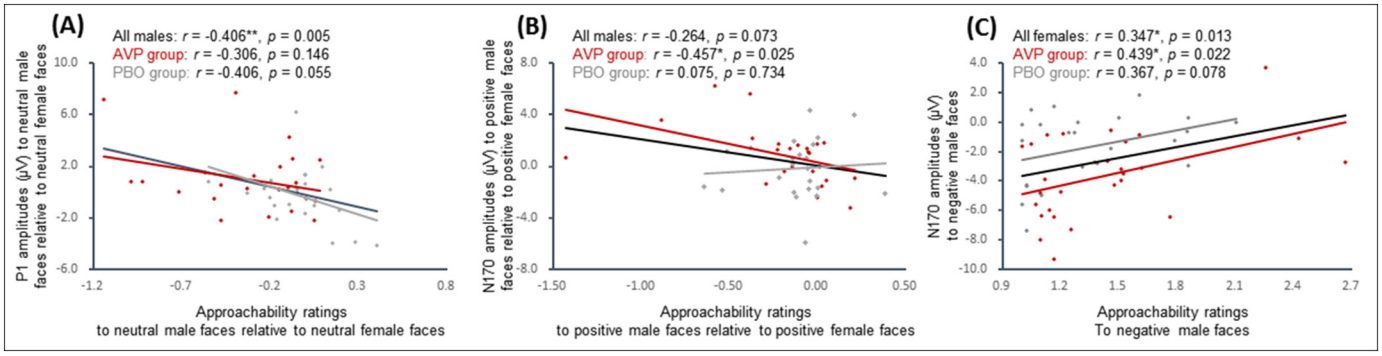

Fig. 4. Correlation between behavioral and ERP responses. (A) Correlations between differences in approachability ratings (neutral male faces relative to neutral female faces) and differences in P1 amplitudes (neutral male faces relative to neutral female faces) in male participants. (B) Correlations between differences in approachability ratings (positive male faces relative to positive female faces) and differences in N170 amplitudes (positive male faces relative to positive female faces) in male participants. (C) Correlations between approachability ratings and the mean N170 amplitudes of processing negative male faces in female participants. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

male faces. The results indicated AVP may also affect the way of processing male faces in females, perhaps in a negative way. Inconsistent with our hypotheses, the current study did not find any effects of AVP on ERP components parallel to higher approachability ratings of negative female faces among females treated with AVP, possibly because (i) variations of subcortical activation modulated by AVP could not be captured by scalp electroencephalographic recordings or because (ii) the statistical methods used were too conservative to capture such associations.

The results of the current study are consistent with previous findings showing that AVP promotes positive social assessments to female faces in females (Rilling et al., 2017b; Thompson et al., 2006) and weakens positive social assessment to male faces in males (Thompson et al., 2006; Thompson et al., 2004). However, none of these studies nor the current study show that AVP promotes positive assessments to female faces by males. The findings on females are consistent with the results of Thompson et al., 2006 and Rilling et al., 2017b in that AVP can promote positive social assessments to women in women. However, in the present study, this effect was only observed under negative condition, suggesting that the effects of AVP are stronger under specific social contexts. These differences might perhaps be a result of the testing contexts used in studies themselves, due to differences in stimuli used, or due to cultural differences between samples.

As observed in humans, sex-specific effects of AVP have been found in Syrian hamsters (Albers, 2012, 2015; Terranova et al., 2017). A large number of studies have found that AVP stimulates aggression in male hamsters and voles (Albers et al., 2006; Caldwell and Albers, 2004; Ferris Jr et al., 1997; Gobrogge et al., 2009), while AVP has the opposite effects in females. For instance, the injection of AVP into the anterior hypothalamus decreases offensive aggression in female hamsters, while the injection of the V1a receptor antagonist shows the opposite effects (Gutzler et al., 2010). Other studies have demonstrated that intracerebroventricular infusions of AVP delay the display of maternal aggression (Nephew and Bridges, 2008) and reduce maternal aggression in lactating rats (Nephew, Byrnes, & Bridges Nephew et al., 2010). Our findings, in line with previous studies conducted on humans (Rilling et al., 2017b; Thompson et al., 2006; Thompson et al., 2004), provide convergent evidence showing that AVP can promote negative and positive social responses in males and females, respectively.

Several limitations of the current study should be noted. First, the menstrual cycle phases of the female participants were not recorded. Thus, it is unclear whether the observed effects in female participants were influenced by cyclic hormones. Second, we did not observe any reliable effects of social contexts associated with drug treatment. Contexts associated with reproduction or aggression might play stronger modulatory roles than those employed in the present study. Third, there is no direct significant difference toward male or female faces between the PBO and AVP groups, suggesting the variance explained by the drug is small. Indeed, both the effect size and power of multi-interaction are relatively small. We believe that the relatively low power might be attributed to the fact that current intranasal routes of drug administration are not optimized for neuropeptides, leading to relatively small effect sizes as a general problem within field of intranasal neuropeptides (Walum et al., 2016). Walum et al. (2016) suggested that future studies could increase the reliability of neuropeptides findings in humans by employing following approaches: (i) by replicating findings from collaborative efforts, (ii) by collecting repeated measures from individuals performing the same task, and (iii) by depositing experiment data in a transparent manner. Fourth, the interpretation of ERP responses usually involves reverse inference (Hutzler, 2014; Poldrack, 2011), therefore specific functions associated with each ERP component remain future investigation. Finally, it should be noted that biological and social processes involved in human relationships are incredibly complex, which makes it likely that individual factors such as peptide regulatory mechanisms and/or face processing each play small though not necessarily unimportant roles and that their influences are likely to be very difficult to detect. Nevertheless, our main findings are consistent with previous observations on the effects of AVP on face processing.

5. Conclusion

In building on previous observations demonstrating the effects of AVP on social behaviors, we examined the role of AVP in processing same- and other-gender facial expressions among males and females. Our results indicate that the effects of AVP on human social communication depend on emotional valence, the gender of emotional face stimuli and the gender of participants. In short, AVP changes the way of processing same- and other-gender faces for males and females, and the observed pattern appears to be mostly consistent with AVP selectively weakening positive assessment to male faces in males while enhancing positive assessments to female faces in females. ERP data and correlational findings between ERP and behavior data further support these interpretations. These findings extend the knowledge of AVP on human social interactions and indicate sex- and context-dependent effects of AVP on socioemotional processes.

Conflict of interest

None of the authors have conflicts of interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yhbeh.2019.04.014.

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