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Age and Intranasal Oxytocin Effects on Trust-Related Decisions After Breach of Trust: Behavioral and Brain Evidence

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Age-related differences in cognition and socioemotional functions, and in associated brain regions, may reduce sensitivity to cues of untrustworthiness, with effects on trust-related decision making and trusting behavior. This study examined age-group differences in brain activity and behavior during a trust game. In this game, participants received "breach-of-trust" feedback after half of the trials. The feedback indicated that only 50% of the monetary investment into their fellow players had resulted in returns. The study also explored the effects of intranasal oxytocin on trust-related decisions in aging, based on suggestions of a modulatory role of oxytocin in response to negative social stimuli and perceptions of trust. Forty-seven younger and 46 older participants self-administered intranasal oxytocin or placebo, in a randomized, double-blind, between-subjects procedure, before they engaged in the trust game while undergoing functional magnetic resonance imaging (fMRI). Younger participants invested less into their game partners after breach-of-trust feedback, while older participants showed no significant difference in their investment after breach-of-trust feedback. Oxytocin did not modulate the behavioral effects. However, after breach-of-trust feedback, older participants in the oxytocin group showed less activity in the left superior temporal gyrus. In contrast, older participants in the placebo group showed more activity in left superior temporal gyrus after breach of trust. The findings may reflect reduced responsiveness to cues of untrustworthiness in older adults. Furthermore, the modulatory effect of oxytocin on left superior temporal gyrus activity among older adults supports the neuropeptide's age-differential role in neural processes in aging, including in the context of trust-related decision making.

Keywords: trust, decision making, aging, oxytocin, superior temporal gyrus

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Prosocial behavior, such as trusting, cooperating, and sharing, is intended to benefit others and has been shown to increase emotional fulfillment and overall well-being in older age (Beadle, Sheehan, Dahlben, & Gutchess, 2015; Fyffe & Wister, 2016; Newman, Vasudev, & Onawola, 1985). Trust, defined as accepting vulnerability based on positive expectations of another (Bailey & Leon, 2019; Rousseau, Sitkin, Burt, & Camerer, 1998), is important for promoting prosocial behavior (Van Lange, 2015) and may be required for cooperation to occur (Gächter, Herrmann, & Thöni, 2004). Despite its high interpersonal relevance, surprisingly little research has addressed trust-related decision making in aging (see Bailey & Leon, 2019 and Frazier, Lighthall, Horta, Perez, & Ebner, 2019 for reviews).

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The limited research that exists suggests that older adults may be overly trusting, possibly making them particularly vulnerable to deception and fraud (Lachs & Han, 2015; Lin et al., 2019; Spreng et al., 2017). In most instances of elder fraud another person gains the trust of an older adult for later exploitation (Peterson et al., 2014; Roberto & Teaster, 2011), with often devastating consequences such as declines in functional health and increased mortality (Dong et al., 2011; Wong & Waite, 2017). To address this "burgeoning public health crisis" among the elderly (Peterson et al., 2014), better understanding of processes underlying trust-related decision making among older adults is needed.

Trust-Related Decision Making and Aging

Trust-related decision making has been investigated using neuroeconomic paradigms (Rilling & Sanfey, 2011). More specifically, the trust game (Berg, Dickhaut, & McCabe, 1995) has been used to examine age-related differences in trust-related decision making (see Online Supplemental Materials Table S1 for a summary of the literature). In this economic-game paradigm, the investor is given a sum of money, which they can either keep for themselves or share in any amount with the trustee. Invested money is multiplied by a determined amount, after which the trustee can return money to the investor or breach the investor's trust and keep the entire sum. Most versions of the trust game allow for a mutually beneficial outcome for investor and trustee (Rilling & Sanfey, 2011). The trust game is generally played with either a different individual per round (i.e., one-shot) or with the same individual over multiple rounds (i.e., multiround).

Current evidence is mixed regarding age-related differences in the trust game (Rieger & Mata, 2015; see Table S1 in the online supplemental materials). Most one-shot trust game studies did not find age-related differences in trust. However, in one study that presented the faces of investors along with their reputations, older adults were more likely to invest into trustees with untrustworthy reputations (Bailey et al., 2016). This finding converges with evidence from multiround trust game studies, that older adults consistently invested more into an untrustworthy trustee over multiple interactions. That is, older adults may not trust others more or less than younger adults in a single interaction (especially when no additional information is provided) but may have difficulty detecting and/or learning from game partners' untrustworthiness over time. The present study examined age-related differences in investment behavior after younger and older participants received breach-of-trust feedback in the context of a series of one-shot trust games.

Age-Related Reduced Sensitivity to Cues of Untrustworthiness

Processes underlying greater trusting behavior in older adults are not well understood. Age-related differences in socioemotional functioning and associated neurobiological processes may underlie reduced sensitivity to cues of untrustworthiness and may drive greater trusting behavior in older adults (Castle et al., 2012; Spreng et al., 2017; Suzuki et al., 2019; Zebrowitz, Ward, Boshyan, Gutchess, & Hadjikhani, 2018; see also Frazier et al., 2019 for a review). Alternatively, it could be that older adults preferentially process and remember trustworthy compared with untrustworthy information (Castle et al., 2012; Suzuki, 2016, 2019; Zebrowitz et al., 2018), in line with the positivity effect that has been repeatedly found in the aging literature (Mather & Carstensen, 2005; Reed, Chan, Mikels, 2014).

Age-related decline in negative subjective arousal (i.e., loss anticipation and avoidance; Samanez-Larkin et al., 2007), episodic memory (Gutchess et al., 2005; Hoyer & Verhaeghen, 2006; Maillet & Rajah, 2013), and cognitive theory of mind (Bottiroli, Cavallini, Ceccato, Vecchi, & Lecce, 2016; Lecce, Ceccato, & Cavallini, 2019; see Ebner et al., 2016 for a review) could underlie this reduced sensitivity to cues of untrustworthiness in aging. For example, aging negatively affects both encoding and recall (Gutchess et al., 2005; Hoyer & Verhaeghen, 2006; Maillet & Rajah, 2013), which could lead to older adults not accurately remembering cues of untrustworthiness.

Changes with age in brain regions associated with processing social and affective information (e.g., the amygdala, insula, and superior temporal gyrus) may also contribute to older adults' reduced sensitivity to cues of untrustworthiness (Castle et al., 2012; Suzuki et al., 2019; Zebrowitz et al., 2018) and their increased risk for real-world financial exploitation (Spreng et al., 2017). The amygdala is a hub in brain networks that support social life (Bickart, Dickerson, & Barrett, 2014) and has been implicated in perceptions of trust and trust-related decision making such as in judgments of facial trustworthiness (Adolphs, Tranel, & Damasio, 1998; Santos, Almeida, Oliveiros, & Castelo-Branco, 2016; Zebrowitz et al., 2018; but see Suzuki et al., 2019). The insula is involved in negative subjective arousal (Knutson, Katovich, & Suri, 2014; Samanez-Larkin et al., 2007) and older adults show reduced insula activation to facial cues of untrustworthiness (Castle et al., 2012). The superior temporal gyrus constitutes another structure relevant in trust-related decisions making, given its involvement in emotional processing (see Grace, Rossell, Heinrichs, Kordsachia, & Labuschagne, 2018, for a meta-analysis) and theory of mind, and specifically in processing the intentions of others (Lewis, Rezaie, Brown, Roberts, & Dunbar, 2011; Olson, McCoy, Klobusicky, & Ross, 2013; Schultz, Imamizu, Kawato, & Frith, 2004). Thus, amygdala, insula, and superior temporal gyrus are particular regions of interest for the study of trust-related decision making in aging.

Modulatory Role of Oxytocin on Trust-Related Decision Making in Aging

There is evidence that the neuropeptide oxytocin is involved in attenuated response to negative social stimuli in younger adults (Striepens et al., 2012), including in contexts related to trust (Bartz, Zaki, Bolger, & Ochsner, 2011; De Dreu et al., 2015; Reyes et al., 2014; but see Grainger, Henry, Steinvik, & Vanman, 2019), possibly by modulating anxiety and social reward (Grace et al., 2018; Yoshida et al., 2009; Zink & Meyer-Lindenberg, 2012). For example, 24 IU (IUs) of intranasal oxytocin reduced activity in the amygdala in response to social betrayal of trust (Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008; Chen, Gautam, Haroon, & Rilling, 2017; Chen et al., 2016; De Dreu et al., 2015; Rilling et al., 2014; with sex differences in these effects). Intranasal oxytocin (24 IUs) also decreased insula activity to unreciprocated trust (Chen et al., 2016; Rilling et al., 2014; but see Chen et al., 2017) and negative social feedback (Gozzi, Dashow, Thurm,

Swedo, & Zink, 2017) and resulted in decreased insula and left superior temporal gyrus activity to negative social feedback in younger adults (Gozzi et al., 2017). This modulatory role of oxytocin was further supported by a meta-analysis documenting oxytocin-enhanced activity in left superior temporal gyrus during emotional processing (Grace et al., 2018).

The few studies on oxytocin's effect in aging suggest age (and in some cases age-by-sex) effects on behavior and brain activity (Campbell, Ruffman, Murray, & Glue, 2014; Ebner et al., 2015, 2016; Horta et al., 2019; but see Grainger et al., 2018, 2019). In particular, a double-blind, between-subjects design with younger and older men and women, in which 20 IUs oxytocin versus placebo were intranasally self-administered, found oxytocin-enhanced emotion recognition ability among older men (Campbell et al., 2014; see Ebner et al., 2015 for similar results with 24 IUs). Also, a double-blind, between-subjects design using intranasal oxytocin (24 IUs) in younger and older men and women suggested increased resting-state functional connectivity between the amygdala and the medial prefrontal cortex for the oxytocin compared with the placebo group, with this effect driven by younger women and, trendwise, older men (Ebner et al., 2016). However, other studies have not revealed age effects of intranasal oxytocin (24 IUs) on emotion recognition or theory of mind (Grainger et al., 2018). Also, another study from the same group found no effects of intranasal oxytocin (24 IUs) on facial trustworthiness and eye gaze patterns among younger or older adults (Grainger et al., 2019). These still scarce and inconsistent findings highlight the importance of additional research on oxytocin's role in younger and older adults, as specifically applied to trust-related decision making in aging in the present study.

Purpose of the Current Study

Synthesizing parallel literatures, the present study examined age-related effects on trust-related decision making after breach-of-trust feedback in a series of one-shot trust games. Based on emerging evidence of reduced sensitivity to cues of untrustworthiness in older adults (Castle et al., 2012; Spreng et al., 2017; Suzuki, 2016), we expected that younger and older participants would differ in their investment into trust game partners after breach-of-trust feedback, with younger participants responding to reduced investment after breach-of-trust feedback, while older participants would not adapt their investment after breach-of-trust feedback (Hypothesis 1). Furthermore, we hypothesized that there would be age-related differences in amygdala, insula, and superior temporal gyrus activity after breach-of-trust feedback, with greater activity in these regions of interest (ROIs) in younger relative to older participants (Hypothesis 2).

We also explored the role of intranasal oxytocin in modulating trust-related decision making, based on evidence that oxytocin increases trusting behavior after breach-of-trust feedback in younger adults (Baumgartner et al., 2008). Given the currently still sparse and mixed evidence on oxytocin effects in older adults (Campbell et al., 2014; Ebner et al., 2015, 2016; Grainger et al., 2018, 2019; Horta et al., 2019), we did not formulate specific hypotheses about the effect of oxytocin on investment and brain response after breach-of-trust.

Taken together, the current study aimed to advance the limited knowledge regarding age-related differences in trust-related decision making in response to breach of trust, both on the level of brain and behavior. The study also set out to explore a modulatory role of oxytocin on behavior and neural processes underlying trust-related decision making in aging.

Method

Participants

The full sample comprised 48 younger and 54 older generally healthy individuals who completed a larger project in the Department of Psychology, the Institute on Aging, and the McKnight Brain Institute at the University of Florida. For the present data analysis, one older man and two older women in the oxytocin group and one older man in the placebo group were excluded because of missing data on ≥25% of the trials on the trust game. Four additional older men in the placebo group were removed because of missing brain data. One additional younger man in the oxytocin group was excluded because his data was mistakenly overwritten. Thus, the final analysis sample in this study consisted of 47 younger (18–31 years., M = 22.45 years., SD = 3.00, 49% female, 53% oxytocin) and 46 older (63–81 years., M = 71.15 years., SD = 5.02, 61% female, 52% oxytocin) participants (see Table 1).

The Breslow-Day test confirmed a comparable distribution of younger and older participants in the oxytocin versus placebo condition across both men and women, χ^2_{BD} (1, 93) = .369, p = .543. Also, as summarized in Table 1, the age groups did not differ in self-reported physical, $F(1, 89) = .264$, $p = .608$, $\eta_p^2 = .003$, and mental health, $F(1, 89) = 3.59$, $p = .061$, $\eta_p^2 = .039$, negative affect, $F(1, 89) = .206$ $p = .651$, $\eta_p^2 = .00$, or plasma oxytocin concentrations at baseline (i.e., before intranasal administration), $F(1, 89) = .612$ $p = .436$, $\eta_p^2 = .007$. Older participants, however, were slower in sensorimotor processing speed, $F(1, 89) = 92.73$ $p < .001$, $\eta_p^2 = .51$, and had poorer short-term verbal learning, $F(1, 89) = 9.27$ $p = .003$, $\eta_p^2 = .094$, in line with previous findings (Hoyer, Stawski, Wasylyshyn, & Verhaeghen, 2004; Vakil & Blachstein, 1997). Older participants also reported more years of education, $F(1, 89) = 3.95$ $p = .050$, $\eta_p^2 = .04$, and higher positive affect, $F(1, 89) = 28.27$, $p < .001$, $\eta_p^2 = .24$, and these two variables were included as covariates in our behavioral analyses.

The treatment groups (oxytocin vs. placebo) did not differ in self-reported physical, $F(1, 89) = .016$ $p = .900$, $\eta_p^2 < .001$, and mental health, $F(1, 89) = .798$ $p = .374$, $\eta_p^2 = .009$, sensorimotor processing speed, $F(1, 89) = 1.19$ $p = .278$, $\eta_p^2 = .013$, short-term verbal learning $F(1, 89) = .958$ $p = .330$, $\eta_p^2 = .011$, years of education, $F(1, 89) = .516$ $p = .474$, $\eta_p^2 = .006$, positive affect, $F(1, 89) = .917$ $p = .341$, $\eta_p^2 = .01$, negative affect, $F(1, 89) = .143$ $p = .706$, $\eta_p^2 = .002$, or plasma oxytocin concentrations at baseline, $F(1, 89) = .074$ $p = .786$, $\eta_p^2 = .001$ (see Table 1). There was, however, an interaction between age group and treatment group in education, $F(1, 89) = 4.99$, $p = .028$, $\eta_p^2 = .05$, in that older participants in the oxytocin group reported more years of education than older participants in the placebo group, $F(1, 89) = 4.32$, $p = .041$, $\eta_p^2 = 0.046$, and younger participants in the oxytocin group, $F(1, 89) = 9.41$, $p = .003$, $\eta_p^2 = .096$.

Participants were recruited via university participant pools and recruitment services (HealthStreet) and through fliers across campus, town, and county. Volunteers were screened via telephone

Table 1
Sample Descriptive Data (Means and Standard Deviations/Percentage) for Demographic, Cognitive, Socioemotional, and Health Measures (n = 93)

Measure	Younger participants		Older participants	
	Placebo (n = 22) M (SD)	Oxytocin (n = 25) M (SD)	Placebo (n = 22) M (SD)	Oxytocin (n = 24) M (SD)
Demographics				
Age	22.92 (3.26)	22.03 (2.76)	70.93 (4.51)	71.35 (5.54)
Sex	50% women	48% women	68% women	54% women
Education	16.00 (2.80)	15.16 (2.04)	15.86 (2.23)	17.50 (3.40)
Cognition				
DSST	66.09 (12.29)	62.60 (8.04)	46.14 (8.87)	45.42 (7.51)
RAVLT	9.32 (1.81)	8.84 (2.04)	7.86 (2.57)	7.42 (2.59)
Affect				
Positive	2.85 (0.69)	2.81 (0.66)	3.60 (0.50)	3.39 (0.54)
Negative	1.25 (0.31)	1.15 (0.23)	1.20 (0.28)	1.26 (0.36)
Health				
Physical	8.27 (1.28)	8.64 (1.08)	8.73 (1.03)	8.42 (0.93)
Mental	8.50 (1.10)	8.44 (1.36)	9.14 (0.83)	8.75 (1.39)
Baseline plasma oxytocin	795.85 (124.82)	802.24 (148.47)	772.97 (122.4)	781.69 (132.21)

Note. Education was measured by total years of formal education. Sensorimotor processing speed was measured by total items correct in the Digit Symbol Substitution Test (DSST; Wechsler, 1981). Short-term verbal learning was measured by total items correct in the Rey Auditory Verbal Learning Test (RAVLT; Rey, 1964). Present mood was measured by the Positive Affect Negative Affect Schedule (PANAS; Röcke, Li, & Smith, 2009; Watson, Clark, & Tellegen, 1988). Subjective physical and mental health were assessed on single items on a scale from 1 = *poor*, 5 = *fair* to 10 = *excellent*. Plasma oxytocin concentrations at baseline were measured in picograms per milliliter (pg/ml).

interview for eligible age range, were English speaking, had normal neurological history, and were magnetic resonance imaging (MRI) eligible. Among the exclusion criteria were pregnancy (determined via pregnancy test for women of childbearing age), breastfeeding, psychological disorder, severe or progressive medical illness, known allergies to the preservatives in the nasal spray, any contraindication to MRI, and excessive smoking or drinking. All older participants scored ≥30 on the Telephone Interview for Cognitive Status (TICS; Brandt, Spencer, & Folstein, 1988).

Procedure

This study was part of a larger project (see Ebner et al., 2015, 2016, 2018; Horta et al., 2019; Lin et al., 2018; Plasencia, Luedicke, Nazarloo, Carter, & Ebner, 2019); only measures relevant to the present data analysis are reported in detail. The Institutional Review Board at University of Florida approved the study protocol. The study adopted a randomized, double-blind, placebo-controlled, between-subjects design. Participants underwent two visits: a screening visit to obtain written informed consent and to assess short cognitive, socioemotional, and health measures; and a study visit, following 2–10 days later, where participants self-administered the nasal spray and completed various computer tasks and questionnaires related to decision making and socioemotional functioning, some of which were conducted inside the MRI scanner.

For both visits, participants were instructed to stay well-hydrated but to abstain from smoking, caffeine, alcohol, and use of recreational drugs in the 24 hr, and from food, exercise, or engagement in sexual activity in the two hours, leading up to their appointment. All test sessions took place in the mornings, typically starting around 9 a.m., and included an intake survey covering current stress level, sleep the night before, and activities in the last 24 hr. Visits primarily took place at the Institute on Aging. Upon study completion, participants were debriefed and reimbursed. Approximately 1 week after the second study visit, participants received a follow-up phone call to assess any side effects of the spray. No consistent adverse side effects were reported.

Screening visit. After informed consent, participants completed short questionnaires related to experience in close relationships and personality (reported in Ebner et al., 2018; Plasencia et al., 2019), the Digit Symbol Substitution task (DSST; Wechsler, 1981), and the Rey Auditory Verbal Learning Test (RAVLT; Rey, 1964). They also underwent a blood draw to determine plasma oxytocin concentrations at baseline (see Plasencia et al., 2019 for details), saliva sampling, a health review covering all major bodily systems, and a brief contact with a licensed clinician for a health review to determine eligibility for study continuation.

Study visit. After 2–10 days, participants returned for their study visit. They responded to an MRI safety form and the brief Positive Affect Negative Affect Schedule (PANAS) followed by saliva sampling. Participants were randomly assigned to self-administer via nasal spray 24 IUs (one puff per nostril) of either oxytocin or placebo (i.e., a solution with identical ingredients except oxytocin). This procedure followed current standards in experimental intranasal oxytocin research on social cognition, including trust (see Guastella et al., 2013; Quintana et al., 2018), was directly modeled after Baumgartner et al. (2008), and aligned with recent studies that included older adults and social–cognitive tasks (Campbell et al., 2014; Grainger et al., 2018, 2019).

During the waiting period, participants were familiarized with the trust game (Figure 1; see description below), transported to the McKnight Brain Institute, and settled into the 3T MRI scanner.

Figure 1. Trial sequence and timing of the trust game adapted from Baumgartner et al. (2008). The slides depict what participants saw during the task. Participants played as the investor for both the trust (top) and lottery (bottom) trials. Each trial started with a 4-s screen informing participants what trial type they were about to play. Next, four response options (1 = 0 MU, 2 = 4 MU, 3 = 8 MU, 4 = 12 MU) appeared indicating that participants had 8 s to decide via button box press the monetary units (MUs) to invest on each trial. A fixation cross appeared for 4 s, followed by an 8-s waiting screen on which participants were informed that either their decision was being communicated to the trustee (trust trials) or that the lottery was being played (lottery trials). An 8- to 12-s jittered fixation cross concluded the trial. After half of the trust and lottery trials, a feedback screen appeared for 25 s informing participants that only 50% of the monetary investment had resulted in returns. The entire task took 14 min and 24 s, presented in two 7-min and 12-s runs. See the online article for the color version of this figure.

The trust game followed brief anatomical scans, approximately 45 min after self-administration of the nasal spray, and the scan session concluded with three additional functional tasks (see Ebner et al., 2016; Horta et al., 2019, for details).

Participants were then transported back to the Institute on Aging to complete questionnaires related to socioemotional functioning (see Ebner et al., 2015) and a short questionnaire about their experience with the spray and the MRI. Participants were debriefed about the general study goals and received $65 for study completion plus up to $8 depending on their earnings in the trust game.

Trust game. Figure 1 summarizes the trial sequence and timing of the repeated single-shot trust game used in the study, adapted from Baumgartner et al. (2008). As detailed in the online supplemental materials, participants were told that they would play several rounds of the game, each trial either with a different anonymous person (for trust trials) or a randomized computer-based lottery (for lottery trials; given this article's focus on trust-related decision making, we did not formulate predictions for the lottery trials).

In both trial types, participants played in the role of the "investor." Participants were informed that the monetary units (MUs) obtained in the game would determine their final dollar amount at reimbursement (1 MU = $0.25). Participants were given 12 MUs per trial to invest. For trust trials, participants were instructed that (a) any amount invested would be tripled for the trustee; (b) the trustee would then decide whether or not to repay the participant; and (c) if the trustee decided to repay the participant, both parties would receive an equal amount of MUs on that trial. Participants received no information pertaining to the likelihood of a trustee to repay. For lottery trials, participants were told that investments would either result in a doubled return or nothing at all, with chances of winning in each lottery trial between 33 and 66%. There were no instructions at the start of the task regarding the "breach-of-trust" feedback. After each block of 12 trials (i.e., after six trust trials and six lottery trials; half-way through the game and again at the end of the game), participants were informed that only 50% of the monetary investment into their fellow players had resulted in returns (that constituted the breach-of-trust feedback) and that only 50% of the monetary investment into the lottery had resulted in a win. As no feedback was provided on individual trials, it is unlikely that changes in investment after breach-of-trust feedback could be attributed to changing gaming strategy rather than the breach-of-trust manipulation. Only at the end of the experiment did the experimenter inform participants how much they had made in the game. Participants received up to a maximum of $8 (in addition to their study compensation).

We created two parallel presentation lists, one of which started with a trust trial and the other with a lottery trial. These two lists were counterbalanced across participants (matched within Age Group × Treatment Group). Within each list, trust and lottery trails were presented in a pseudorandomized order, with no more than three of the same trial types in a row.

Image acquisition. Brain images were acquired with a 3T Philips Achieva MR Scanner (Philips Medical Systems, Best, The Netherlands), using a 32-channel head coil. Whole-brain high-resolution three-dimensional T1-weighted anatomical reference images were acquired using an MP-RAGE sequence (sagittal plane, TR/TE/TI = 7/3.2/2750 ms, flip angle = 8°; in-plane FOV = 240 mm × 240 mm; imaging matrix = 240 × 240; 176

contiguous sagittal slices with 1 mm slice thickness, 1 × 1 × 1 mm isotropic voxels).

Functional images during the trust game were acquired across two runs (one before and one after the breach-of-trust feedback). Each run consisted of 226 functional images acquired using a T2-weighted echo-planar imaging (EPI) sequence (38 interleaved slices with zero interslice gap, TR = 2 s, TE = 30 ms, FOV = 252 × 252 × 133 mm, 80 × 80 × 38 mm matrix, flip angle 90°, in-plane resolution of 3.15 × 3.15 mm, slice thickness 3.5 mm). The 38 oblique axial slices were positioned parallel to the AC-PC line.

Analysis

Behavioral analysis. Sample descriptive analyses were conducted in SPSS25 (IBM SPSS Statistics for Windows, Version 25.0, IBM Corp., Armonk, NY). Multilevel modeling (MLM) was conducted in Stata 15.1 (StataCorp. 2017, Stata Statistical Software: Release 15, StataCorp LLC., College Station, TX).

We used MLM to determine age-related differences in cumulative investment (in MUs) during trust trials (dependent variable) with age group (younger vs. older) and treatment group (oxytocin vs. placebo) as between-subjects independent variables and feedback (prefeedback vs. postfeedback) as within-subject independent variable. We included years of education and positive affect as covariates given significant age-group main effects in these variables and a significant interaction effect between age group and treatment group in education (see Table 1). We predicted a significant two-way interaction (as determined by the Wald χ^2 Test) between age group and feedback (Hypothesis 1).

The return schedule differed for trust and lottery trials (see also Baumgartner et al., 2008). Also, we had no specific predictions for lottery trials. Therefore, we did not compare trust and lottery trials in the same model but ran a parallel (exploratory) analysis for lottery trials in the same manner as for trust trials.

fMRI analysis. Processing and analysis of brain imaging data were performed using Statistical Parametric Mapping (SPM12) software (www.fil.ion.ucl.ac.uk/spm). Standard preprocessing procedures in SPM12 were conducted, including slice time correction, realignment and unwarp, coregistration with structural data, spatial normalization into MNI space (Montreal Neurological Institute, Canada), resampled voxel size of 2 × 2 × 2 mm, and smoothing with an 8 mm Gaussian kernel for functional images.

Following Baumgartner et al. (2008), we defined a first-level (i.e., individual level) model for each participant. This first-level model consisted of four regressors of interest to model the "decision phase," defined as the time from onset of the 4-s trial type prompt to the time when the participant made their investment decision on that trial (see Figure 1). These four regressors of interests were: (a) trust prefeedback decision phase, (2) lottery prefeedback decision phase, (c) trust postfeedback decision phase, and (d) lottery postfeedback decision phase. The model also comprised eight regressors of noninterest for the fixation crosses (i.e., 4-s and 8–12 s [jittered] fixation per each trial type and feedback), four regressors of noninterest for the waiting phase (i.e., one per each trial type and feedback), and two regressors for the feedback slides (see Figure 1). We also included motion parameters, retrieved during realignment as regressors in the model. All regressors were convolved via canonical hemodynamic response function. We calculated a *t*-contrast image for Trust Post-Feedback > Trust Pre-Feedback at the individual level and created the second-level (i.e., group level) model based on this first-level *t*-contrast image. The second-level model considered age group and treatment group as between-subjects factors. To explore treatment effects for the age groups, we computed the second-level model *t*-contrast Oxytocin < Placebo for older participants using an exclusive mask of the same *t*-contrast for younger participants.

The ROIs masks for bilateral amygdala, insula, and superior temporal gyrus were defined using the Automated Anatomical Labeling atlas (Tzourio-Mazoyer et al., 2002). We applied small volume corrections (voxel-wise: $p < .001$ uncorrected, cluster-wise: $p < .05$ FWE corrected) for these six ROIs. To explore effects in the whole brain, we applied a voxel-wise statistical threshold of $p < .05$ (FWE corrected).

Results

Behavioral Results

Table 2 presents descriptive data for investments by feedback (before vs. after breach-of-trust feedback) for trust trials in younger and older participants (separately as well as across the treatment groups). In support of Hypothesis 1, the age Group × Feedback interaction was significant for trust trials, Wald $\chi^2(1) = 5.57$, $p = .018$, $f^2 = 0.061$. Younger participants invested significantly less into their trust game partners after ($M = 43.32$, $SD = 13.59$) compared with before ($M = 47.57$, $SD = 13.51$) breach-of-trust feedback, whereas older participants did not significantly change their investments into trust game partners after ($M = 46.48$, $SD = 11.76$) compared with before ($M = 43.96$, $SD = 11.48$) the breach-of-trust feedback (see Table 2). No other effects

Table 2
Descriptive Data (Means and Standard Deviations) for Investment (in Monetary Units) by Feedback (Across Six Prefeedback vs. Six Postfeedback) for Trust Trials in Younger and Older Participants (Displayed Separately as Well as Across the Treatment Groups)

	Younger participants			Older participants		
Feedback phase	Placebo *M* (*SD*)	Oxytocin *M* (*SD*)	Combined *M* (*SD*)	Placebo *M* (*SD*)	Oxytocin *M* (*SD*)	Combined *M* (*SD*)
Prefeedback	47.82(13.64)	47.36(13.70)	47.57(13.51)	42.91(14.06)	45(8.69)	43.96(11.48)
Postfeedback	44.91(13.64)	41.92(13.70)	43.32(13.59)	43.64(14.06)	49.17(8.69)	46.48(11.76)

Note. Monetary units ranged from 0 to 72. The combined column displays means and standard deviations of investment collapsed across treatment groups within age groups.

were significant: age group, Wald $\chi^2(1) = .91$, $p = .339$, treatment group, Wald $\chi^2(1) = .25$, $p = .619$, feedback, Wald $\chi^2(1) = .38$, $p = .538$, age Group × Treatment group, Wald $\chi^2(1) = .80$, $p = .370$, Treatment Group × Feedback, Wald $\chi^2(1) = .03$, $p = .871$, or Age Group × Treatment Group × Feedback, Wald $\chi^2(1) = 1.13$, $p = .287$.[1]

Also, for lottery trials, there were no significant effects: age group, Wald $\chi^2(1) = .49$, $p = .486$, treatment group, Wald $\chi^2(1) = .50$, $p = .480$, feedback, Wald $\chi^2(1) = .46$, $p = .496$, Age Group × Treatment group, Wald $\chi^2(1) = .3$, $p = .582$, Age Group × Feedback, Wald $\chi^2(1) = .05$, $p = .826$, Treatment Group × Feedback, Wald $\chi^2(1) = 3.22$, $p = .073$, and Age Group × Treatment Group × Feedback, Wald $\chi^2(1) = 1.01$, $p = .315$.

fMRI Results

Age group did not predict differences in bilateral amygdala, insula, or superior temporal gyrus activity when contrasting Trust Post-Feedback > Trust Pre-Feedback; thus, not supporting Hypothesis 2. Furthermore, there was no effect for treatment group on bilateral amygdala, insula, or superior temporal gyrus activity. However, treatment group did predict activity in left superior temporal gyrus for the contrast Trust Post-Feedback > Trust Pre-Feedback, peak MNI coordinate $x = -42$, $y = -2$, $z = -12$, small-volume correction: peak level $t = 4.06$, cluster level $p_{\text{FWE-corr}} = .028$, kE = 43. As depicted in Figure 2, older participants in the oxytocin group showed less, while older participants in the placebo group showed more, left superior temporal gyrus activity after breach-of-trust feedback. This effect was not present in younger participants. The whole-brain analysis did not result in any significant effects.

Discussion

The current study investigated the extent to which age affected trust-related decision making after breach of trust and explored the modulatory role of oxytocin on these effects. We found that younger but not older participants reduced their investments after breach-of-trust feedback. Furthermore, older participants in the oxytocin group showed reduced left superior temporal gyrus activity after breach-of-trust feedback. The novel findings generated from this research are discussed next.

Younger Adults Invested Less After Breach of Trust, While Older Adults did Not Change Their Investments

Our findings that younger participants decreased, while older participants did not change, their investments into game partners after breach-of-trust feedback contribute to a growing body of evidence that aging may be associated with reduced sensitivity to cues of untrustworthiness (Castle et al., 2012; Ebner et al., 2018; Spreng et al., 2017; Suzuki, 2016; Suzuki et al., 2019). For example, previous research has shown decreased sensitivity to untrustworthy faces (Castle et al., 2012; Suzuki et al., 2019; Zebrowitz et al., 2018), reputations (Bailey et al., 2016), and actions (Bailey, Petridis, McLennan, Ruffman, & Rendell, 2019; Rasmussen & Gutchess, 2019; Suzuki, 2016) among older adults. The age-related differences observed in our study also generally align with evidence from repeated trust game paradigms, and variations such as the Broker Investment Task (Bailey et al., 2016; Rasmussen & Gutchess, 2019; Suzuki, 2016; Webb, Hine, & Bailey, 2016). Going beyond these previous results, the present study evidenced age-differential response to breach-of-trust feedback when playing with different anonymous game partners over several rounds of the trust game.

It is possible that older adults countered the breach of trust with prosocial behavior in the form of not-decreasing investments (i.e., withholding punishment). This interpretation is in line with evidence that older adults are more motivated than younger adults to maintain relationships, take others' needs into account, and help others, especially when in need (Hoppmann, Coats, & Blanchard-Fields, 2008; Sze, Gyurak, Goodkind, & Levenson, 2012). Also, older adults prioritize (Lawton, Kleban, Rajagopal, & Dean, 1992) and show greater (Mather & Carstensen, 2005) emotion regulation and adaptive conflict resolution than younger adults (Birditt & Fingerman, 2005; Gross et al., 1997). That is, older participants' stable investments into their game partners even after breach of trust may have served an emotion-regulatory function. However, it is also possible that the breach-of-trust feedback used in our study was not sufficiently aversive (and may have been interpreted as standard) to warrant a change in older adults' investment. It will be interesting to delineate in future research the role of prosociality (e.g., trusting behavior) as an emotion-regulatory strategy and in the context of conflict resolution in aging.

Oxytocin Modulated Brain Response (But Not Trusting Behavior) After Breach of Trust in Older Adults

Oxytocin modulated neural response to breach of trust in older adults: older participants in the oxytocin group showed decreased left superior temporal gyrus activity after the breach-of-trust feedback, whereas older participants in the placebo group showed increased activity in this region after breach-of-trust feedback. This finding is in line with evidence of oxytocin-decreased superior temporal gyrus activity to negative social feedback (Gozzi et al., 2017; Grace et al., 2018) and may reflect oxytocin-induced downregulation of brain response to breach of trust in older adults, supporting an age-differential role of oxytocin in neural processes, including in the context of trust-related decision making.

There was no effect of oxytocin in young adults' neural response to breach of trust. These age-differential findings align with an emerging literature suggesting that intranasal oxytocin may differentially affect younger and older adults' brain response (Ebner et al., 2016; Horta et al., 2019) as well as behavior (Campbell et al., 2014; Ebner et al., 2015). The literature discusses that age-related differences in socioemotional proficiency (Hoppmann, et al., 2018; Mather & Carstensen, 2005; Sze et al., 2012) and associated neurobiological processes, including changes in brain structure and function (Ebner et al., 2016; Horta et al., 2019), gonadal hormones (Ebner et al., 2015; Grace et al., 2018; MacDonald, 2013; MacDonald & Feifel, 2013), baseline oxytocin levels (Plasencia et al., 2019), and gene expression (Quintana et

[1] Results from MLMs with baseline plasma oxytocin concentration included as a covariate were comparable with those reported in the main text. Note that plasma oxytocin concentrations were not assessed on the same day as the intranasal oxytocin administration took place.

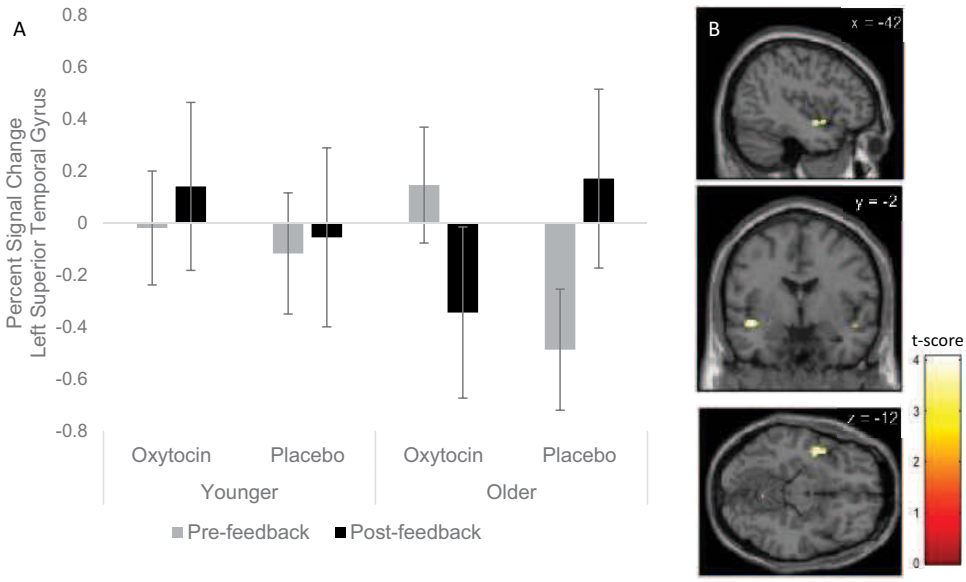

Figure 2. (A) Bars depict means and error bars depict standard errors of percent signal change (*t*-score) in left superior temporal gyrus (peak MNI coordinates: $x = -42$, $y = -2$, $z = -12$) by age group, treatment group, and feedback. Older participants in the oxytocin group showed less left superior temporal gyrus activity after the breach-of-trust feedback. In contrast, older participants in the placebo group showed more left superior temporal gyrus activity after the breach-of-trust feedback. There were no significant treatment effects for bilateral amygdala, bilateral insula, or right superior temporal gyrus. (B) Sagittal, coronal, and axial slices for peak activation of the left superior temporal gyrus in the *t*-contrast of Oxytocin < Placebo for older participants, using an exclusive mask of the same *t*-contrast for younger participants, are shown. Small volume corrections were thresholded voxel-wise at $p < .001$ uncorrected and cluster-wise at $p < .05$ FWE corrected. See the online article for the color version of this figure.

al., 2019), could explain why oxytocin intervention does not exert the same effects in younger and older adults' brains and behaviors. The examination of mechanisms involving age variations is a necessary and promising future direction for research on oxytocin (Ebner, Maura, Macdonald, Westberg, & Fischer, 2013; Ebner et al., 2015, 2018; Huffmeijer, van Ijzendoorn, & Bakermans-Kranenburg, 2013; Lussier, Cruz-Almeida, & Ebner, 2019; Sannino, Chini, & Grinevich, 2017), including in the context of trust-related decision making and prosociality.

Insula activity was not modulated by age or oxytocin. Insula activity has been shown to be associated with the motivation to avoid losses, that is, is responsive to negative subjective arousal (Samanez-Larkin et al., 2007) and social aversion (Bickart et al., 2014). It is possible that the breach-of-trust feedback in the present trust game did not constitute a sufficiently large loss to promote insula-mediated negative subjective arousal. Additionally, our trust game paradigm may not have provided enough salient social information to trigger an insula-mediated response. Previous work that found oxytocin-induced modulatory effects on insula activity in response to untrustworthiness used facial images to depict game partners (Chen et al., 2016; Rilling et al., 2014).

While we observed oxytocin modulation on left superior temporal gyrus activity among older adults in response to breach of trust, intranasal oxytocin administration did not affect investment behavior. Research shows that brain effects are not always reflected in behavioral effects (Chen et al., 2017; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Horta et al., 2019). In fact, one possibility could be that the behavioral measures in the present study were not sufficiently sensitive. Conditions under which behavioral and brain effects of oxytocin align will have to be determined in future studies, especially in studies with older adult samples.

There is also evidence that oxytocin's prosocial effects vary by group membership in that oxytocin promotes prosociality for members of the in-group while it promotes hostility toward members of the out-group (De Dreu & Kret, 2016; van IJzendoorn et al., 2012). In the present study's trust game, game partners were not known to participants and they did not personally meet them nor saw facial images of them during the game. Thus, our study design did not allow for testing variations in oxytocin effects as a function of in-group versus out-group membership of game partners. Variations by group membership on trust-related decisions making after breach of trust among younger and older adults will have to be addressed in future research.

Limitations and Future Directions

Our study advances understanding of age-related differences in trust-related decision making in response to breach of trust. Results from this work also inform the modulatory role of oxytocin in aging, contributing to an emerging field of research. However, there are some design limitations with relevance for interpretation of our findings, that can be developed into promising research extensions moving forward, as discussed next.

A meta-analysis published after the closure of the current study suggests that studies examining oxytocin's effects on social cognition should have at least 64 participants in each group for between-subjects designs and 34 participants for within-subjects designs to be adequately powered (≥80%) to detect moderate effect sizes between treatment groups or conditions (Leppanen, Ng, Tchanturia, & Treasure, 2017). Future research on oxytocin function in aging will benefit from taking these recommendations into consideration to replicate and extend the current findings.

Relatedly, our study was not sufficiently powered to include sex as a factor in the analyses. There is growing evidence of differences in oxytocin's effects across men and women, which could be a function of interactions with gonadal hormones or sex differences in social function at baseline (Ebner et al., 2015; Grace et al., 2018; MacDonald, 2013; MacDonald & Feifel, 2013). More systematic investigation into age-by-sex variations in oxytocin's effects, including on trust related-decision making and prosocial thought and action, are warranted.

Finally, interactions between endogenous (naturally occurring) oxytocin levels on functional effects of exogenous oxytocin are not yet well understood (see also Lussier et al., 2019, for a discussion). We did not find an effect of endogenous plasma oxytocin on trust-related decision making or evidence of an interaction with intranasal oxytocin administration. Of note, however, plasma oxytocin levels were not assessed on the same day as the oxytocin administration and the game paradigm took place. Mechanistic research is needed to determine the extent to which endogenous oxytocin levels moderate effects of intranasal oxytocin administration on brain and behavior, including in older adults and with respect to trust.

Conclusion

The present study provides novel evidence of age-related differences in trust-related decision making after breach of trust and suggests a modulatory role of oxytocin on left superior temporal gyrus activity after breach of trust among older adults. These findings contribute to the increasing evidence of age-related reduced sensitivity to cues of untrustworthiness. It is possible that greater trusting behavior after breach of trust disproportionately exposes older adults to financial exploitation and fraud. However, it is also possible that older adults counter trust violations with increased prosociality, which could benefit conflict resolution and lead to improved social interactions. Moving forward, investigations addressing these possible interpretations will advance understanding of factors contributing to and processes underlying decisions of trust and prosocial behavior in aging.

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