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Boys vs. girls: Gender differences in the neural development of trust and reciprocity depend on social context

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ABSTRACT

Trust and cooperation increase from adolescence to adulthood, but studies on gender differences in this development are rare. We investigated gender and age-related differences in trust and reciprocity and associated neural mechanisms in 43 individuals (16–27 years, 22 male). Participants played two multi-round trust games with a cooperative and an unfair partner. Males showed more basic trust towards unknown others than females. Both genders increased trust during cooperative interactions, with no differences in average trust. Age was unrelated to trust during cooperation. During unfair interactions males decreased their trust more with age than females. ROI analysis showed age-related increases in activation in the temporo-parietal junction (TPJ) and dorsolateral prefrontal cortex (dlPFC) during cooperative investments, and increased age-related caudate activation during both cooperative and unfair repayments. Gender differences in brain activation were only observed during cooperative repayments, with males activating the TPJ more than females, and females activating the caudate more. The findings suggest relatively mature processes of trust and reciprocity in the investigated age range. Gender differences only occur in unfair contexts, becoming more pronounced with age. Largely similar neural activation in males and females and few age effects suggest that similar, mature cognitive strategies are employed.

1. Introduction

Humans are by nature social beings. The development of their social skills and the maturation of the brain continue well into the twenties (Crone and Güroglu, 2013; Dumontheil et al., 2010; Tamnes et al., 2010; Sowell et al., 2001). Late adolescence and early adulthood can therefore be viewed as a developmental stage (Arnett, 2007), rather than a period of completed development without changes (for an overview of studies, see (Blakemore, 2012). The changes in social behavior occur in parallel with structural and functional maturation of the brain (Crone and Dahl, 2012; Steinberg, 2005) in a complex interdependent way (McClure et al., 2004; Blakemore and Choudhury, 2006), where a changing social context shapes social cognition and the brain (Blakemore, 2012; Nelson et al., 2005), and developing cognitions and underlying neural circuitry allow for more complex relationships that further shape cognitions and underlying neural circuitry. While several studies investigated social decision making in children, young adolescents and adults, data on the developmental processes from late adolescence into adulthood are still scarce (Frith and Frith, 2010). We therefore sought to investigate the development of social interactions in this particular group at the transition between adolescent and adult life.

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1.1. The development of trust and social reciprocity

During adolescence the priority of social interactions changes markedly from a family focus towards peer relations, which evolve into intimate, supportive, and communicative relationships (Nelson et al., 2005; Brown, 2004; Steinberg and Sheffield Morris, 2001). The formation of adult like relationships during late adolescence and early adulthood is bi-directionally associated with the development of social (cognitive) skills, such as enhanced mentalizing, sensitivity to the perspective of others and trust. While the majority of previous research in the field yielded important insights into the natural development of trust and social mechanisms such as reciprocity and cooperation (Steinberg, 2005; Eisenberg et al., 2005, 2002; Fett et al., 2014a; Smith et al., 2013), it lacked the ability to analyze these social interactions in a systematic way (Belli et al., 2012). Interactive games from economic sciences overcome this issue by enabling the study of real-time social interaction in controlled environments (Tzieropoulos, 2013). A now widely used paradigm to investigate trust, cooperation and reciprocity is the trust game (Berg et al., 1995). Here the first of two players, the investor, receives €10 and can give any amount between €0 and 10 to the second player, the trustee. The given amount is tripled and the trustee then can return any part of this amount to the investor. In first instance the best pay-offs for the trustee are reached by keeping the money. Thus, investing requires trust that a fair repayment will be made. In general, adults trust others with at least half of the initial endowment (Tzieropoulos, 2013; Johnson and Mislin, 2011; van den Bos et al., 2011), suggesting a natural tendency to cooperate. To date there have only been few developmental studies on age-related changes in trust and social reciprocity. Fett and colleagues showed that individuals become more inclined to establish cooperation from early adolescence until middle adulthood (Fett et al., 2014b). Similarly, Sutter and Kocher (2007) found that trust increases linearly until 22 years of age, showing stability in adulthood and a slight decrease thereafter. Research by Van den Bos and colleagues in younger individuals reported increasing trust from childhood to mid-adolescence and a slight decrease towards early adulthood (van den Bos et al., 2010), as well as increased first investments and enhanced learning over trials with age (van den Bos et al., 2012). Several possible mechanisms could explain the age-related changes in trust. A key mechanism that is increasingly employed with age is mentalizing (Fett et al., 2014a; Derks et al., 2015), which allows for a. better estimation of the social situation, the interaction partner and for improved strategic thinking (Dumontheil et al., 2010; van den Bos et al., 2011; Burnett et al., 2011; Chaudhuri and Gangadharan, 2003; Declerck et al., 2013).

1.2. The neural development of trust and reciprocity

Neuroeconomic studies implicated three brain systems in social decision making, that are dedicated to cognitive control, social cognition, and processing reward (Declerck et al., 2013). Only few studies investigated age-related changes in brain activity during social interactions in the trust game. Fett et al. (2014b) found increased brain activation in mentalizing regions, i.e. temporo-parietal junction (TPJ), posterior cingulate and precuneus, supporting the behavioral change of increased trust and reciprocity with age. Furthermore, age-related reductions in activation were present in the reward-related orbitofrontal cortex and caudate during interactions with a trustworthy, cooperative partner, possibly reflecting stronger expectations of trustworthiness and a reduced prediction error signaling. The authors suggest that during unfair interactions, age-related increases in anterior cingulate (ACC) activation, an area implicated in conflict monitoring, could mirror the necessity to inhibit higher pro-social tendencies in the face of the partner's actual levels of cooperation (Fett et al., 2014b). Age-related increases of activation of the TPJ and the right dorsolateral prefrontal cortex (dlPFC) have been found when receiving trust from others as a trustee. Activity in the anterior medial prefrontal cortex (amPFC), a region associated with self-oriented processing and mentalizing, in contrast was found to be higher in younger individuals (van den Bos et al., 2011). In sum, these studies suggest, like in adult samples (Declerck et al., 2013; Rilling et al., 2007; Krueger, 2008; Delgado et al., 2005; King-Casas et al., 2008), that differential neural activation patterns in brain areas involved in mentalizing, reward learning and cognitive control are associated with age-related changes in trust and reciprocity towards others.

1.3. Gender differences in the development of trust and social reciprocity

It is often believed that women are superior at mentalizing and therefore more trusting, pro-social and cooperative than men. It is possible that higher trust, pro-sociality and social reciprocity become increasingly apparent in developing females compared to males as a consequence of differential developmental trajectories or societal demands (De Bellis et al., 2001; Lenroot and Giedd, 2010; Neufang et al., 2009; Beutel and Johnson, 2004). Research, however, shows that even though women frequently outperform men on mentalizing tasks (Baron-Cohen et al., 2001; Rutherford et al., 2012), this does not necessarily translate into higher trust, prosociality or social reciprocity. Evidence indicates that men are more trusting than women, both in single (Croson and Gneezy, 2009; Buchan et al., 2008) and repeated social interactions in the trust game (Croson and Gneezy, 2009; Balliet et al., 2011). However, when trust is violated, females are more likely to stay trusting and restore trust, possibly motivated by wanting to maintain relationships (Haselhuhn et al., 2015). When thinking about mentalizing as underlying factor of social behavior, it is also important to consider that mentalizing abilities do not necessarily drive pro-other oriented behavior, but can also be used to manipulate others for the own advantage (Derks et al., 2015).

Only little is known about gender differences in trust and social reciprocity during late adolescence and early adulthood. One early study on trust in adolescence reported no gender differences in trust (van den Bos et al., 2010), while a more recent study found that boys show higher trust towards others than girls (Derks et al., 2014), as often reported in adults. According to social role theory, the male gender role promotes agentic, instrumental, and outcome-based behavior, while females are thought to adopt a more communal and interpersonal facilitative behavior (Derks et al., 2015; Balliet et al., 2011; Andreoni and Vesterlund, 2001; Eagly, 2009). Research has shown that the relationship between expected returns and trusting behavior is stronger among men, suggesting that they might approach interactions more strategically, so that they are mainly beneficial to themselves, looking to maximize the own outcome. In line with this, Declerck and colleagues propose that the motivation to cooperate (or not), is modulated by the cognitive control system (centered on the lateral prefrontal cortex, e.g. the dlPFC) and regions of the social brain including the TPJ, the mPFC, and the amygdala that process social signals (Declerck et al., 2013). They postulated that self-regarding individuals (who are more likely to adopt an economically rational strategy) are more likely to rely on cognitive control to make decisions, whereas other-regarding individuals (who are more likely to adopt a socially rational strategy) are more likely to recruit areas of the social brain system during decision-making. Thus if males were indeed more strategic, and females more inclined to establish cooperation and to interpersonal facilitative behavior, gender differences in trust and social reciprocity should vary between the genders as a function of the trustworthiness of the interaction partner. That is, in the trust game the contrast in behavior between males and females should be less prominent during cooperative interactions compared to interactions with an unfair partner because cooperation can be economically valuable and driven by concern for the own gain, as well as by concerns for the others' outcomes and socially rewarding cooperation. However, an approach that is mainly beneficial to the self and economically driven should lead to lowering investments in the case of unfair returns. Neuroimaging can shed light on differential decision-making strategies, beyond behavioral investigations. To our knowledge gender differences in the neural correlates of the development of trust and reciprocity in late adolescence and early adulthood have not yet been investigated.

1.4. The current study

This study set out to investigate gender differences in the development of trust and reciprocity and their underlying neural mechanisms. The sample included individuals in late adolescence and young adults from 16 to 27 years to capture the period of late developmental social changes. We used two multi-round continuous trust games, one with a pre-programmed cooperative and one with an unfair partner. Participants played the role of the investor. We hypothesized an age-related increase in the first investment (i.e. basic trust). In addition, we expected that with age trust would increase during cooperative interactions, and that trust during unfair interactions would decrease. Based on the literature, we hypothesized that the change in trusting behavior would be moderated by gender, whereby males and females would show similar investments during cooperative interactions and where men would show lower investments during unfair interactions than females, in line with a more economic approach as opposed to a behavioral approach that aims to re-establish cooperation.

At the neural level we hypothesized to find age-related increases in brain activation in mentalizing related brain regions (TPJ and amPFC), as a reflection of an increased propensity to take others perspective into account during decision making (Fett et al., 2014a; van den Bos et al., 2011; Blakemore, 2008) To support this reasoning we also measured mentalizing with the Reading the Mind in the Eyes task. In line with a decision making strategy driven by social motives (other regarding) in females as suggested by Declerck and colleagues (Declerck et al., 2013) we hypothesized to see stronger activation of the brain areas associated with social behavior during interactions with both game partners in females (e.g. TPJ, amPFC). In line with the proposition of a more economic reasoning strategy in males we expected to see greater activation in the brain areas associated with cognitive control (dlPFC and ACC) during decision making in both trust game conditions in males. To support this reasoning, other-regarding and self-regarding preferences were assessed using the social value orientation measure (Van Lange et al., 1997). The caudate is involved in learning mechanisms, including computations of the probability of rewarding outcomes and prediction error signaling, but also during reward consumption (Grahn et al., 2008; Hare et al., 2008; Knutson et al., 2001; Knutson and Cooper, 2005; Lutz and Widmer, 2014; Delgado et al., 2004; Delgado, 2007; Haruno et al., 2004; Walter et al., 2005). Some previous trust game studies have linked caudate activity primarily to reward (Fett et al., 2014b; Gromann et al., 2013, 2014) or learning signals (Delgado et al., 2005; King-Casas et al., 2005; Baumgartner et al., 2008) during cooperation (van den Bos et al., 2011), as compared to defection. If caudate activity would exclusively signal the rewarding value of cooperation it should be activated more strongly in the cooperative condition, as compared to the unfair condition. If the caudate signal would reflect feedback learning during social interactions, activation should show in both cooperative and unfair interactions. Fett and colleagues found an age-related decrease in caudate activation (Fett et al., 2014b). Here we investigate to what extent we can replicate this finding.

2. Methods

2.1. Participants

Fifty-three healthy individuals in late adolescence and young adults, aged 16–27, were recruited at schools, or through snowball sampling in the wider Amsterdam area. Inclusion criteria were age between 16 and 30 and a sufficient command of the Dutch language. Exclusion criteria were a personal or family history of psychiatric disorders, and any contraindications for MRI scanning. Two participants could not be scanned due to metal implants and anxiety before scanning. Seven participants were excluded from analyses due to bad data quality, a neurological disorder, a family history of bipolar disorder and failing to understand the task. The remaining 43 subjects (21 female, $M_{age} = 21.51$ $SD = 2.65$; 22 male, $M_{age} = 20.64$, $SD = 2.87$) did not differ in age ($F(1, 41) = 1.05$, $p = 0.31$) or educational level ($\chi^2(2, N = 43) = 0.57$, $p = 0.75$) between genders. Differences in the vocabulary subscale of the Wechsler Adult Intelligence Scale (WAIS (Wechsler, 1997)) were found ($F(1, 41) = 5.20$, $\beta = 0.38$, $p = 0.03$) and therefore controlled in all analyses. For further group characteristics, see Supplementary Table S1. All participants gave written informed consent. When under the age of 18, both the participant and at least one parent consented. This research was approved by the Ethical Committee of the VU Medical Center Amsterdam.

2.2. Measures

2.2.1. Trust game

Two multi-round trust games were used. Participants played the role of investor, believing that their anonymous counterpart, the trustee, was connected to them via the Internet. In reality, they played against a computer, with two algorithms programmed to respond always in a cooperative and always in an unfair way. The algorithm was programmed in a probabilistic way: The amount returned depended on the previous investment. In the cooperative condition, the first repayment was either 100%, 150% or 200% of the amount invested, each occurring with a probability of 33%. Subsequent repayments increased if the investment reflected an increase in trust relative to the previous investment, but remained stable in all other situations. With each increase in trust from the investor, the chance of a repayment of 200% increased with 10%. In the unfair condition, the first repayment was 50%, 75% or 100% of the amount invested, each occurring with a probability of 33%. Subsequent repayments decreased if the current investment reflected an increase in trust relative to the previous investment, but remained stable in all other situations. With each increase in trust from the investor, the chance of a repayment of 50% invested increased with 10% (Fett et al., 2014b; Gromann et al., 2013; Fett et al., 2016). The two games were presented in counterbalanced order. Each game consisted of 20 experimental and 20 control trials. At the beginning of each experimental trial, participants started with €10. Any amount between €0 and €10 could be invested. The invested money was tripled and the trustee (i.e. computer) then made a repayment. Control trials were included as baseline condition for the fMRI analysis. The design and duration of the control trials were equal to the experimental trials, but without the element of investment. In the control trials participants had to move the cursor to a number between 0 and 10, which was indicated by a red arrow. Every trial started with an investment cue (2 s); the investment period where participants made their choice followed, where a number line appeared, with the cursor always in the mid-

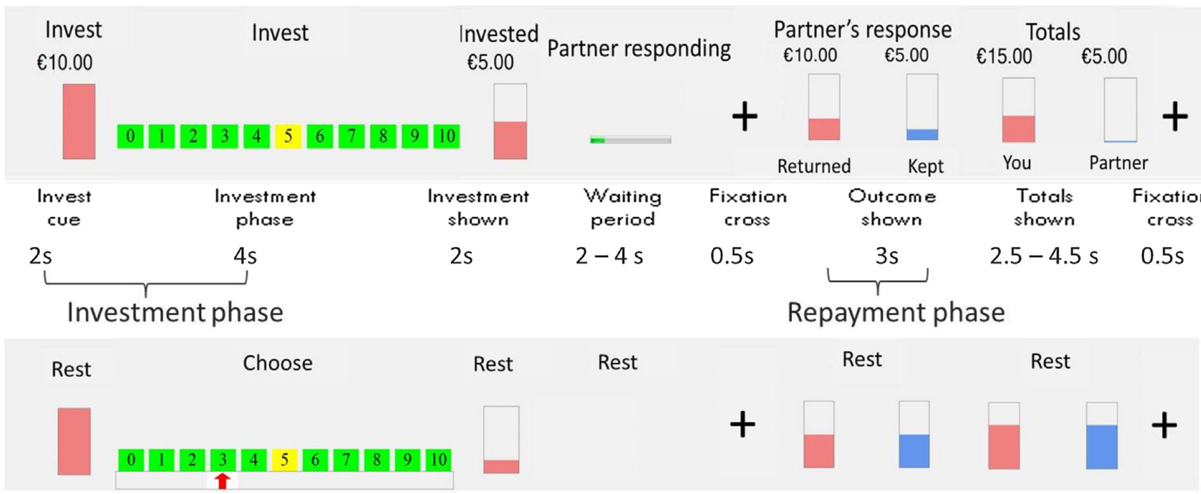

Fig. 1. Graphical Overview of the Trust Game.
Note: Top row represents the visual stimuli in the game trials; middle row are the separate phases including durations of the trust game; bottom row represents the visual stimuli in the control trials

Table 1
Investments made in the trust game.

	Male $N=22$ Mean (*SD*)	Female $N=21$ Mean (*SD*)	Overall $N=43$ Mean (*SD*)
First investment, basic trust	7.68 (1.84)*	6.33 (1.53)	7.02 (1.81)
Mean investment Cooperative	8.05 (2.70)	7.39 (2.66)	7.73 (2.70)
Mean investment Unfair	3.55 (3.15)	3.44 (2.80)	3.50 (2.98)

* $p = 0.013$.

dle, on the 5 (4 s, regardless of reaction times); the invested amount was shown (2 s), followed by a waiting period (jittered, 2–4 s), and a fixation cross (500 ms). Finally, the returned amount (3 s) and the final totals of both players (jittered, 2.5–4.5 s) were displayed, followed by a fixation cross (500 ms). Every trial lasted 18.5 s in total. For a graphical representation of the set-up of the trust game, see Fig. 1.

2.2.2. Other measures

The trust game was followed by a questionnaire to investigate participants' opinions on the behavior of their counterpart, and to check if they believed that they were playing a real person (see Supplementary Questionnaire S-Q1). Four participants did not believe the manipulation. Additional questionnaires and tasks were administered to provide explanations for trust game behavior. Specifically we assessed mentalizing (Reading the Mind in the Eyes task; Eyes task (Baron-Cohen et al., 2001)), Social Value Orientation (SVO (Van Lange et al., 1997)), and general cognitive ability (WAIS vocabulary subscale, see Supplementary Table S1).

2.3. Procedure

After signing the consent form, participants completed several tasks and questionnaires, followed by two further, computer-administered tasks: the Eyes task and SVO. Immediately prior to scanning, the trust game was explained and several practice trials were played. When necessary, participants were provided with additional oral feedback to maximize their comprehension of the task. Subsequently participants were scanned for 65 min, starting with the trust game, followed by the structural scan and another task.

After the testing session participants received an image of their brain, €25 for participation, and a reimbursement of travel expenses.

2.4. fMRI data acquisition

fMRI data were obtained at the Spinoza Center Amsterdam, using a 3.0 T Philips Achieva whole body scanner (Philips Healthcare, Best, The Netherlands) equipped with a 32 channel head coil. A T2* EPI sequence (TR = 2.31, TE = 27.63, FA = 76.1°, FOV 240 mm, voxel size $2.5 \times 2.5 \times 2.5$, 40 slices, 0.3 mm gap) was used, which resulted in 325 images per condition. A T1-weighted scan was obtained for anatomical reference (TR = 8.2, TE = 3.8, FA = 8°, FOV 240*188 mm, voxel size 1×1 x 1, 220 slices).

2.5. Data analysis

2.5.1. Behavioral data

Demographic and behavioral data were analyzed using Stata 13 (StataCorp, 2013) with regression analyses and chi square tests. We analyzed associations of gender and age with the first investment (basic trust), mean investments and with the development of investments (changes in trust) across repeated interactions (indicated by trial number) and by condition (cooperative and unfair). We used multilevel random regression analyses (XTREG), to account for multiple observations [investments (level 1); within participants (level 2)]. All analyses were performed controlling for WAIS vocabulary score, which has been used as an indicator of general IQ. Associations of trust with behavioral parameters SVO and Eyes task performance were investigated.

2.5.2. Imaging data

Imaging data were analyzed using Statistical Parametric Mapping 8 (SPM, 2009). Functional images for each participant were preprocessed using the following steps: realign and unwarp, coregistration with individual structural images, segmented for normalization to an MNI template and smoothing with a 6 mm Gaussian kernel (FWHM). At first-level, a general linear model (GLM) was used to construct individual time courses for the investment and repayment phase per condition. We used an event-related design. For each trial we defined the investment as the period of stimulus onset to the moment of investment, and the repayment phase as the period the partner's return was displayed

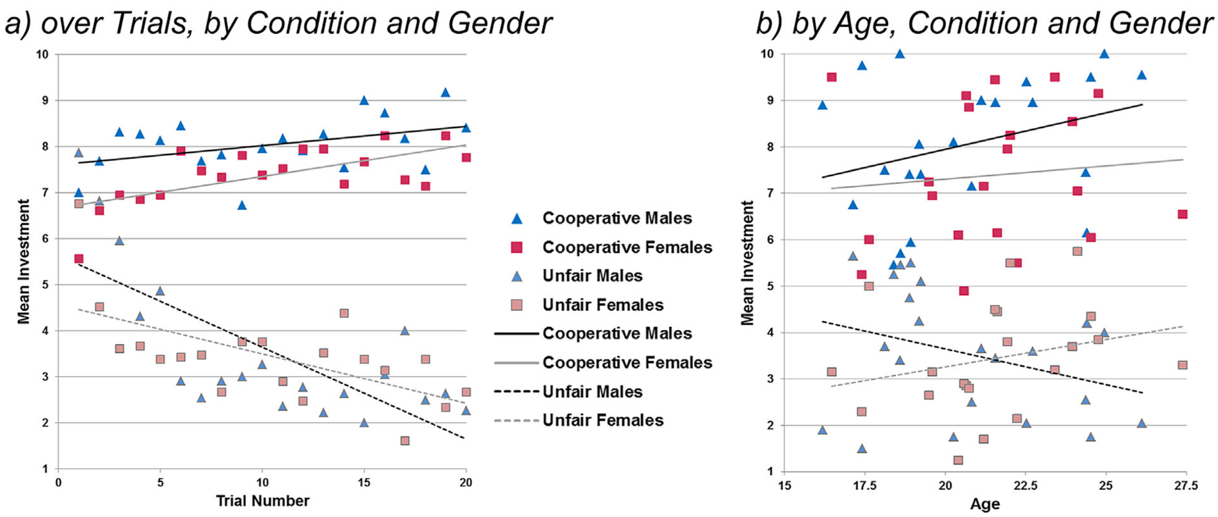

Fig. 2. Mean Investments. (a) over Trials, by Condition and Gender (b) by Age, Condition and Gender

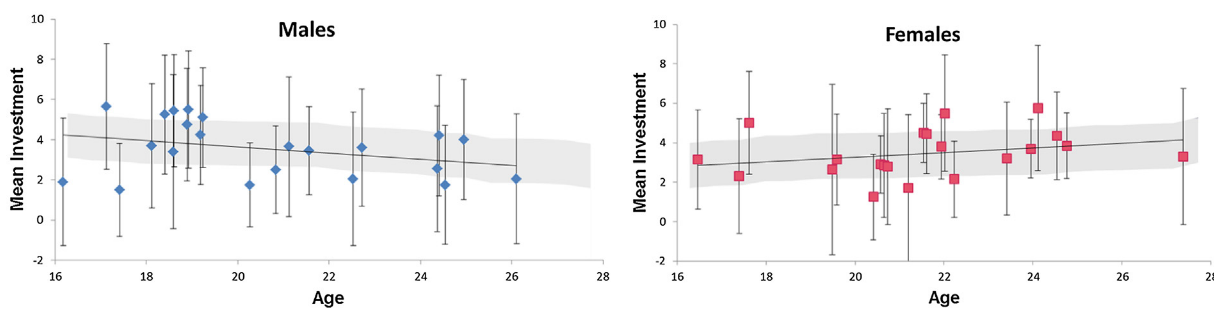

Fig. 3. Changes in Trust in the Unfair Condition by Age per Gender.
Note: Mean investments are shown, with 1 standard deviation of varianc, with and error band of 1SE around the regression line

(see Fig. 1). Trials from both the cooperative and unfair conditions were contrasted with control trials. All analyses were controlled for the WAIS vocabulary score. To control for financial aspects that could explain any group differences in reward signals, investment was added as a regressor to the analyses.

A priori ROI analyses were performed. ROIs were derived from two seminal studies investigating trust and reciprocity in the trust game in adolescent samples (12–22 and 18–22 years). The right TPJ (MNI coordinates: 45, −43, 32), right dlPFC (51, 18, 30), right insula (36, 24, 0) and the ACC (-3, 27, 33) (van den Bos et al., 2011) were complemented with left TPJ (−44, −46, 29), ventral striatum (VS; 14, 12, −5) and amPFC (0, 42, 6) (van den Bos et al., 2009). We also included bilateral caudate ROI's (right: 6, 11, 5; left: −7, 12, −4), based on a review on social decision making (Rilling and Sanfey, 2011). The caudate is reliably activated by the trust game (van den Bos et al., 2011; Fett et al., 2014b; Gromann et al., 2013, 2014; King-Casas et al., 2005; Bellucci et al., 2017). With these ROIs we covered important areas for trust development, reward learning, social cognition and cognitive control. All ROIs were defined as a sphere of 10 mm around the given coordinates, except for VS and caudate, where a 5 mm sphere was used.

We investigated associations of ROI activation with age and gender and their interaction using MarsBaR (version0.43; http://marsbar.sourceforge.net). Adjusted p-values were calculated, taking the correlation between the β-values into account by using the Simple Interactive Statistical Analysis Bonferroni tool (http://www.quantitativeskills.com/sisa/calculations/bonfer.htm), resulting in different p-values per condition (Li et al., 2014; Woudstra et al., 2013). We analyzed brain activation during both the investment and the repayment phase of the game, where mentalizing and reward (learning) mechanisms are represented in both phases, and differences between the two conditions. Several recent studies suggested that functional brain changes during adolescence may not necessarily be linear (Blakemore, 2012; Crone and Dahl, 2012; Blakemore and Choudhury, 2006; Achterberg et al., 2016). We therefore tested linear and quadratic associations in all our analyses. Of all significant ROIs, associations of beta-values with the behavioral parameters SVO and Eyes task were investigated (see Table S1).

An additional, exploratory whole-brain analysis was performed to examine group wise differences in regions outside the a priori defined ROIs. The results are presented in the Supplementary Material (Tables S2–S4).

3. Results

3.1. Behavioral analyses

Direct comparisons of cooperative and unfair interactions were first investigated in a full model including age, gender, trial number and condition. The four-way interaction was not significant. Deleting this interaction from the model, analysis revealed significant interactions of age-by-gender-by-condition on investment ($b = 0.37$, $p < 0.001$ 95%CI = 0.19/.56), showing that the age-by-gender interaction differed between conditions. The interaction trial number-by-condition on investment was significant ($b = -0.21$, $p < 0.001$ 95%CI = −0.25/−0.17). No significant associations of first and mean investment were found with any of the

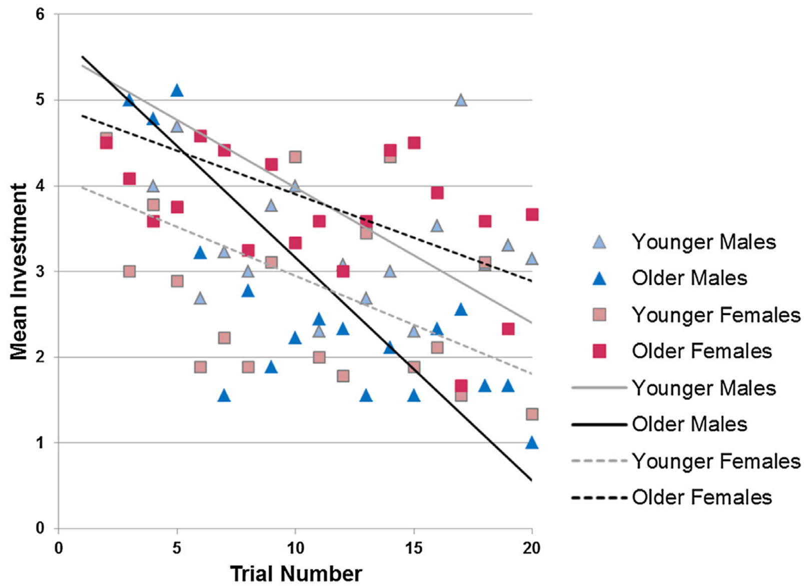

Fig. 4. Changes in Trust in the Unfair Condition, by Gender and Age (Median split).
Note: For better interpretation of the results, a median split of age (Median age = 20.83) was performed.

behavioral parameters (see Table S1). Analyses by condition are reported below.

Table 1 shows the first investment (basic trust) and the mean investments by gender and condition. Males made significantly higher first investments than females ($F(2, 40) = 4.06$, $\beta = 0.32$, $p = 0.043$). There was no significant age-by-gender interaction in relation to first investments and no association between age and first investment was found (both $p > 0.7$).

In the *cooperative condition* no age-by-gender-by trial number interaction, no age-by-gender interaction, and no main effects of age and gender were found on investments. Non-significant interactions were removed from the model. There was a significant association between trial number and investments ($b = 0.05$, $p < 0.001$ 95%CI = 0.03/.08) showing that over time all participants became more trusting in response to a cooperative other.

In the *unfair condition*, there was no age-by-gender-by-trial number interaction. After deleting the 3-way interaction from the model, significant interactions were present between gender and trial number ($b = 0.10$, $p = 0.001$ 95%CI = 0.04/.16, see Fig. 2a) and gender and age ($b = 0.28$, $p < 0.04$, 95%CI = 0.01/.55, see Fig. 2b). Separate analyses by gender showed a marginally significant age-by-trial number interaction in males ($b = -0.01$, $p = 0.06$, 95%CI = −0.03/.001). With increasing age males showed a stronger decrease in investments towards the unfair other (see Fig. 3). In females there was no significant age-by-trial number interaction, i.e. the behavior towards the unfair partner did not change with increasing age, but a significant main effect of trial number ($b = -0.11$ $p < 0.001$, 95%CI = −0.15/−0.06) indicated that females were adapting to the unfair nature of the other over time (see Fig. 2a). Fig. 4 shows the interaction of trial number-by-age, per gender, for which a median split for age was performed to visualize the effect.

3.2. fMRI ROI analyses

ROI analysis of associations between brain activation and age revealed several significant linear age-related increases in brain activity in the cooperative investment phase and linear age-related increases in the caudate in both repayment phases. Associations between brain activation patterns and gender only became apparent in the cooperative repayment phase (see Table 2). There were no quadratic or negative associations between age and ROI activation and no significant associations of ROI activation and any of the behavioral parameters (see Table S1) were found.

Table 2
ROI analyses outcome, by condition of the trust game.

Condition Association	ROI	p	t
Cooperative investment*			
Increasing with age	Right TPJ	0.021	2.10
	Right dlPFC	0.028	1.97
Cooperative repayment**			
Increasing with age	Right caudate	0.023	2.06
Males > females	Right TPJ	0.025	2.02
Females > males	Right caudate	0.014	2.29
Unfair repayment***			
Increasing with age	Right caudate	0.025#	2.03
Cooperative > Unfair investment****			
Increasing with age	Right TPJ	0.014	2.26
	Right dlPFC	0.029	1.95

Note: All ROIs were defined as a 10 mm sphere (except right caudate: 5 mm) around the following MNI coordinates: right temporo-parietal junction (TPJ): 45, −43, 32; right dorso-lateral prefrontal cortex (dlPFC): 51, 18, 30; right caudate: 6, 11, 5.
* Adjusted threshold p = 0.040.
** Adjusted threshold p = 0.031.
*** Adjusted threshold p = 0.024.
**** Adjusted threshold p = 0.039.
\# = Bordering the adjusted *p*-value.

3.2.1. Cooperative interactions

3.2.1.1. Associations between ROI activation and age. With increasing age, investing in a cooperative partner was associated with increased activation in the right TPJ and dlPFC (see Fig. 5). In the repayment phase right caudate activation was also positively associated with age. When comparing investment in the cooperative and unfair condition directly, age was associated with a stronger increase in activation of the right TPJ and dlPFC in the cooperative condition than in the unfair condition.

3.2.1.2. Associations between ROI activation and gender. There were no significant associations between ROI activation and gender in the investment phase. In the repayment phase males activated the

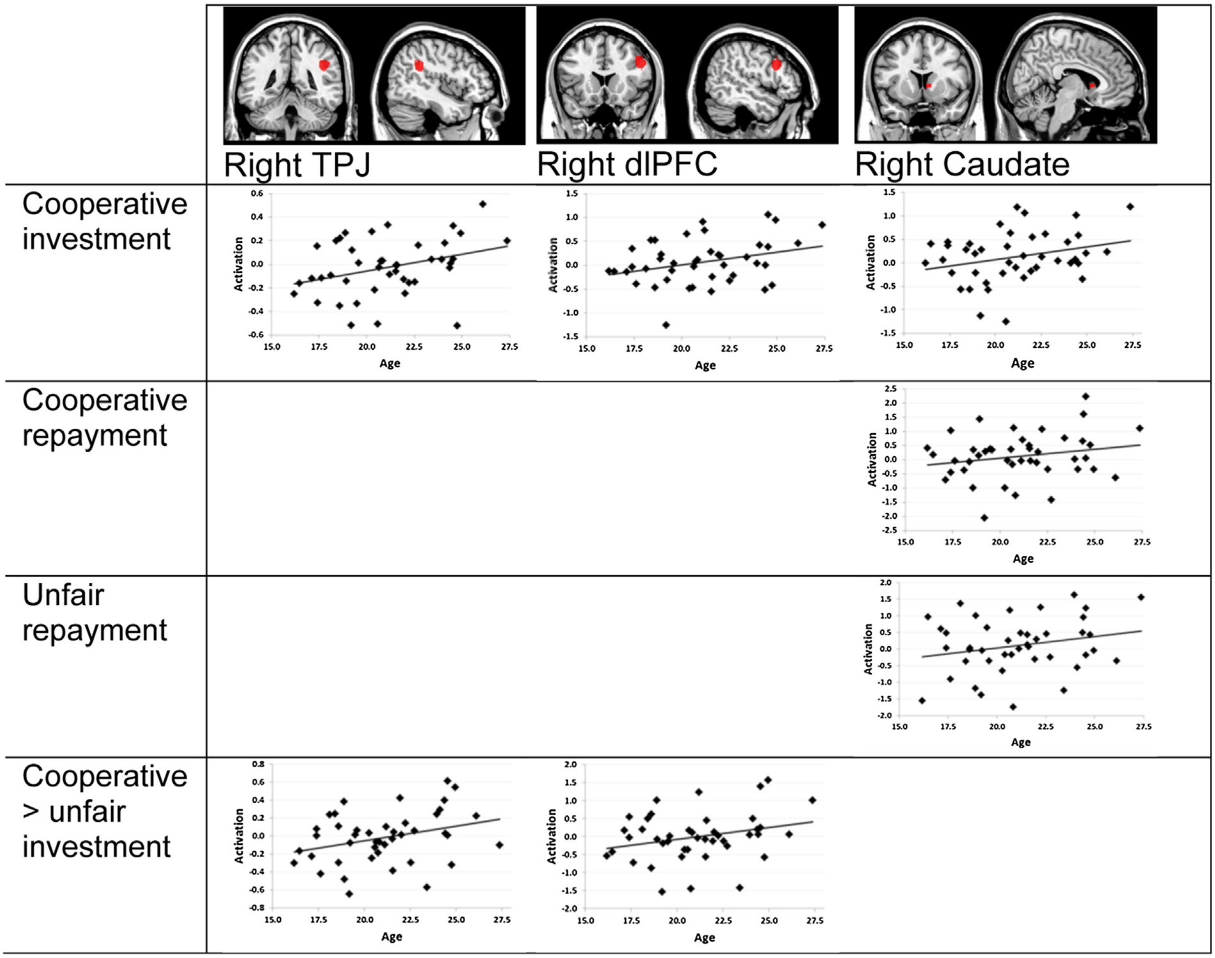

Fig. 5. Activation Beta Values during Cooperative Investment by Age.

TPJ more than females and females activated the caudate more than males (see Fig. 6).

3.2.1.3. Age-by-gender interactions. There were no significant age-by-gender interactions in the investment or repayment phase of the cooperative condition.

3.2.2. Unfair interactions

3.2.2.1. Associations between ROI activation and age. In the investment phase no associations between ROI activation and age were found. When receiving the repayment of an unfair partner, right caudate activity increased significantly with age (see Fig. 5).

3.2.2.2. Associations between ROI activation and gender. There were no significant associations between gender and brain activation during the investment or repayment phase in unfair interactions.

3.2.2.3. Age-by-gender interactions. There were no significant age-by-gender interactions in the investment or repayment phase of the unfair condition.

3.2.3. Whole-brain results

Exploratory whole-brain analyses were performed to investigate associations between brain activation and age and differences between genders in brain activation in regions outside the a-priori defined ROIs. For exploratory purposes, results are described at a more lenient threshold of $p = 0.001$ uncorrected. All clusters equal to and larger than 10 voxels with FWE-cluster corrected p-values are reported. Based on recent simulation data, the results should be interpreted with caution (Eklund et al., 2016). The results are presented in the Supplementary Material (Tables S2–S4).

4. Discussion

The aim of this study was to investigate the development of trust and social reciprocity and their underlying neural mechanisms from late adolescence into early adulthood taking into account possible gender differences. The current study showed gender specific changes in trust in unfair interactions, whereby males adapted their behavior more strongly towards an unfair partner than females. Behavioral differences in response to an unfair partner became more pronounced between the genders with age. Largely similar neural activation patterns in males and females and few age effects suggest that similar, mature cognitive strategies are employed during social interactions.

4.1. Behavioral findings

4.1.1. Basic trust

Contrary to our expectations, we did not find significant age-related increases in basic trust, operationalized as the first investment in the trust game. This is in contrast with the existing literature (Fett et al., 2014b; Sutter and Kocher, 2007; van den Bos et al., 2010, 2012) which reported linear increases of the first investment with age. An explanation could be that the sample was significantly older than samples in previous research, and that

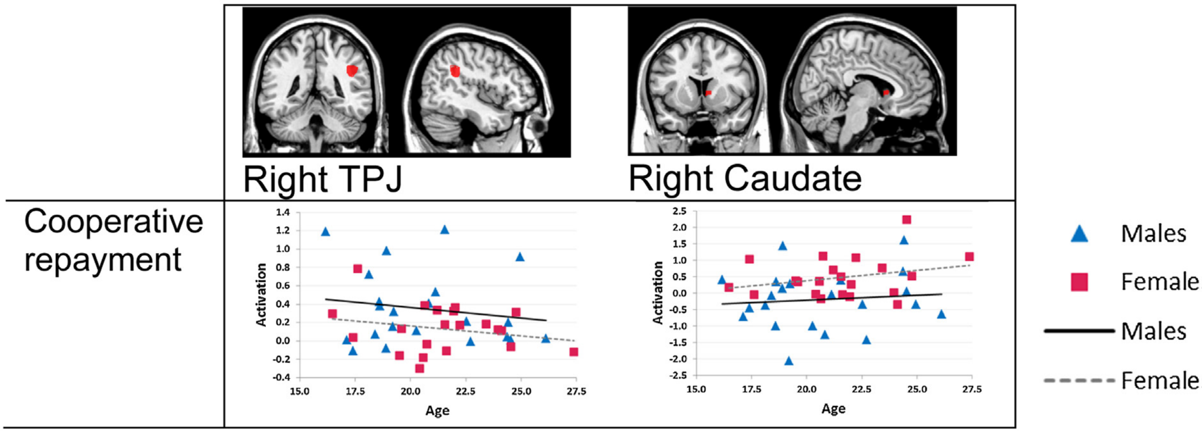

Fig. 6. Activation Beta Values during Cooperative Investment by Gender.

major changes in trusting behavior might occur earlier in development. Basic trust was higher in males than females. To date there has been very little research on gender differences in trust and reciprocity in late adolescence and early adulthood. Our findings regarding basic trust point into the same direction as the majority of the trust game results in adults, which show that males generally trust more than females (Sutter and Kocher, 2007; Croson and Gneezy, 2009; Buchan et al., 2008) and also corroborate the recent findings in an adolescent sample (Derks et al., 2014). Many possible motivations may underlie differences in basic trust. Lower trust in females than males could reflect higher risk aversion in the former (Eckel and Grossman, 2008), but could also indicate a strategic awareness of males that higher initial investments are more likely to set-off mutual cooperation (Killingback and Doebeli, 2002; Fehr et al., 2002). Future studies should employ additional measures to further investigate the reasons that drive gender differences in basic trust. Based on the fact that participants might not always be consciously aware of their motives, direct and indirect measures such as social value orientation can shed a light on underlying motives. However, here no associations between basic trust and SVO were found.

4.1.2. *Trust in cooperative interactions*

We also did not find age-related increases in trust over repeated interactions in the cooperative condition. This result is not in line with previous findings by Van den Bos and colleagues (van den Bos et al., 2010, 2012), who found age-related increases of trust. As discussed above with regard to basic trust, the absent age effect could be due to the restricted age range of the current sample. In cooperative interactions Fett and colleagues (Fett et al., 2014b) for example found age-related increases in trust that were mainly driven by differences between the youngest and the oldest individuals in the sample, which ranged from 13 to 49 years of age. In our sample the age range was smaller and the youngest participants already older and possibly more mature than in the other studies (16 years compared to 9 and 13 respectively). In sum, this evidence suggests that major changes in trust and reciprocity may take place in late childhood and early adolescence. Clearly, more research is needed to replicate the current findings. Furthermore, the results showed that gender differences in trust are no longer present during repeated interactions with the cooperative counterpart. If risk aversion indeed played a role in gender differences in basic trust towards an unknown counterpart, females' fear of betrayal may no longer play a role in the face of reliable positive reciprocity by the interaction partner.

Both males and females adapted their behavior to the positive feedback of the counterpart by increasing their trust, showing successful learning about the nature of the counterpart over repeated trials. The absence of age-related changes suggests that in cooperative interactions both males and females reach a relatively mature social processes in their mid-teens.

4.1.3. *Trust in unfair interactions*

There was a differential pattern of trust during unfair interactions in males and females, with males showing a steeper decline in trust towards the unfair partner compared to females. These gender differences in dealing with unfair behavior became increasingly pronounced with age; with age, only males decreased investments more strongly. No such trend was present in females. Thus, behavioral gender differences in late adolescence and early adulthood become increasingly apparent under unfair treatment. While speculative, males' increasingly sharper decline in investment could reflect different mechanisms such as an increasingly strategic approach that repays unfair behavior tit-for-tat and protects the own outcome, or a greater inclination for retaliation (Balliet et al., 2011). While females also lower their trust in response to unfairness, their overall higher investments could reflect coaxing attempts to re-establish cooperation. In contrast to basic trust, in repeated unfair interactions, risk mechanisms are unlikely to play a role. As suggested by previous research, females are more likely to stay trusting and restore trust when trust is violated, possibly motivated by wanting to maintain relationships (Haselhuhn et al., 2015). However, there are of course other possible explanations for the gender differences in trusting behavior that should also be considered.

4.2. *Neuroimaging findings*

Cooperative investments were associated with age-related increases in activation in the right TPJ and dlPFC. These findings are in line with earlier trust game findings, where age-increased neural activation was found in absence of behavioral change, in a slightly younger sample (van den Bos et al., 2011). A similar finding has been reported by Blakemore and colleagues (Blakemore et al., 2007) in a study on mentalizing in adolescents and adults, which showed more posterior (temporal) activation with increasing age, in absence of behavioral changes. In addition to changes in cognitive strategies this effect could be due to continued brain development (van den Bos et al., 2011).

In the cooperative repayment phase, males showed more TPJ activation than females, whereas females showed more caudate activity than males. In combination with the behavioral results, which did not reveal gender differences, the imaging results suggest that males and females adopt slightly different cognitive strategies in response to processing the repayments (Cahill, 2006). However, these do not seem to be primarily pro-self-oriented, as indicated by our analyses including the SVO (see Supplementary material, S-Q1 and Table S1). Previous research in adolescents has linked a higher propensity for perspective taking to higher levels of trust during cooperation and steeper declines of trust in unfair interactions (Fett et al., 2014a). In light of these findings, behavioral patterns of males, could thus suggest more mentalizing in males, however, TPJ activity did not show a significant association with the Eyes task. Clearly, the Eyes task taps into different aspects of mentalizing than the task employed by Fett and colleagues (Fett et al., 2014a) which measures the propensity to take the perspective of another person. Future studies should include other mentalizing tasks to investigate how different aspects of mentalizing relate to trust game behavior and the underlying neural mechanisms.

With increasing age, the dlPFC was activated increasingly in both males and females when investing in a cooperative partner. The dlPFC is part of the cognitive control network (Declerck et al., 2013) and previous research has shown that it is involved in rule-based selection of responses and in updating the expectation of reward (Ridderinkhof et al., 2004; Barraclough et al., 2004; Paulus et al., 2002; Jiang and Kanwisher, 2003), thus enhancing goal-directed behavior and optimizing decision making (Riedl et al., 2010). An explanation for our finding could be that individuals increasingly consider higher order social rules when making decisions. However, our behavioral questionnaire data, such as SVO and questions regarding the use of strategies cannot provide evidence for this explanation.

The utilized trust game employed an iterative design, that required continuous social learning (Haruno et al., 2004). The age-related increase in caudate activation contrasts with the hypothesis of a *hyper-responsive* reward system in adolescence (Galvan, 2010), and with a previous developmental study, that showed age-related decrease of caudate activity which has been proposed to be due to reduced prediction error signaling (Fett et al., 2014b). If caudate activity would exclusively signal the rewarding value of social cooperation it should be activated more strongly in the cooperative condition, as compared to the unfair condition. However, caudate activation during both cooperative and unfair repayment phases suggests that social reward learning mechanisms are changing with age (Grahn et al., 2008; Hare et al., 2008; Knutson and Cooper, 2005; Walter et al., 2005; Bellucci et al., 2017; Haber and Knutson, 2010). Moreover, females activated the caudate more than males during cooperative repayment, which in the context of behavioral differences in basic trust may be explained as increased learning, due to the lower start-off at base-line.

4.3. Limitations

Several limitations of the current research should be considered. First, the current sample size was modest. The results were similar to what others found in comparable samples (Belli et al., 2012; Sutter and Kocher, 2007), however replication is needed. The modest sample size may have resulted in a lack of power to detect subtle age effects and age-by-gender interactions in the trust game paradigm. In addition, future research should also aim include younger adolescents in a larger sample to study the development of trust and gender differences before late adolescence, where effects might be the largest. Second, four participants did not believe they were playing against a human counterpart. This might have influenced their behavior. However, analyses without these participants did not change the results. Higher investments in the cooperative condition and lower investments in the unfair condition showed that overall the experimental manipulation of the counterpart (unfair and cooperative) was effective. Third, participants were not paid based on performance. There is some evidence that real payment has a different effect on decisions and related brain activity than hypothetical payment (Vlaev, 2012; Hertwig and Ortmann, 2001). However, hypothetical payment may influence the strength, but not the direction of the effect (Derks, 2015). This point might be an issue when comparing the current findings to findings from other studies. Others however have found no differences in outcome between real and hypothetical payment (Locey et al., 2011; Madden et al., 2003). In addition, participants were instructed to maximize their own gain, which could have influenced their behavior. The instruction could have diminished age or gender related differences in pro-self and pro-other strategies on the game, and therefore could impact comparability with other studies' results that used different instructions (Liberman et al., 2004). Last, the trust game is a paradigm that involves complex cognitive processes. Here we show few differential behavioral and neural mechanisms in males and females under cooperative and unfair treatment. fMRI can shed a light on neural mechanisms associated with cognitive processes and strategies, yet it needs to be noted that involvement of various brain regions as identified using fMRI does not allow for an inference of cognitive strategies (so-called reverse inference) (Poldrack, 2006). Suggestions made regarding possible mechanisms are therefore speculative, even when supported by previous research. Future research should set out to employ detailed experimental and questionnaire measures to investigate individual motives for the displayed trust behavior that could shed a light on underlying mechanisms.

5. Conclusions

The current study adds to the emerging literature investigating the development of social decision making and its underlying neural mechanisms, and provides initial insights on gender specific social decision making processes in mid-adolescence and early adulthood. The results show mostly stable patterns of trust and social reciprocity from mid-adolescence to early adulthood. Gender differences were present in basic trust and dependent on the nature of the counterpart during repeated interactions. Males reacted stronger to unfair treatment by the other than females by investing less and this effect became more pronounced with age. Our neuroimaging findings show few age-related changes in brain activation between mid-adolescence and early adulthood and do not support a distinction of a decision making strategy relying on social brain areas in females and cognitive control related areas in males.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.dcn.2017.02.001.

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