

## Social network position, trust behavior, and neural activity in young adolescents

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### ABSTRACT

Our social interactions take place within numerous social networks, in which our relationships with others define our position within these networks. In this study, we examined how the centrality of positions within social networks was associated with trust behavior and neural activity in 49 adolescents ( $M_{\text{age}} = 12.8$  years,  $SD_{\text{age}} = 0.4$  years). The participants played a trust game with a cartoon animation as a partner, which showed adaptive behavior in response to the participant and was generally untrustworthy. Social network positions were obtained in secondary school classrooms where the participants and their classmates reported on who their friends were. Using social network analysis, a score was calculated that indicated the centrality of everyone's position within the friendship network. The results showed that more central social network positions were associated with higher levels of initial trust behavior, although no evidence was found for a relationship between network position and the adaptation of trust behavior. The results of the functional MRI analyses showed that the centrality of the network positions was positively associated with caudate activity when making trust decisions. Furthermore, the adolescents with more central network positions also showed stronger increases of caudate activity when the partner's return was processed compared to the adolescents with less central network positions. The current study provides initial evidence that social network positions in friendship networks relate to socio-cognitive behavior and neural activity in adolescents.

### 1. Introduction

During adolescence, great changes take place in the brain, in socio-cognitive abilities, and in peer relationships. There is ongoing development in brain areas that are involved in socio-cognitive abilities, and these are collectively called the social brain (Blakemore, 2008; Güroğlu, 2021; Kilford et al., 2016). At the same time, adolescents' social world grows in size and complexity, and their peer relationships become increasingly important (Brown and Larson, 2009; Erdley and Day, 2017; Steinberg and Morris, 2001). Being well-connected within social networks can provide opportunities to learn about people's behavior and thereby shape socio-cognitive abilities. A complex form of socio-cognitive behavior is trust behavior, which plays a vital role within social interactions. During social interactions, it is important to show trust behavior toward others but trusting someone who is not trustworthy can be a costly mistake. Research shows that, with age, adolescents become better at differentiating between trustworthy and untrustworthy interaction partners. Compared to young adolescents, mid-adolescents and late adolescents showed stronger increases in trust behavior toward

trustworthy partners and stronger decreases in trust behavior toward untrustworthy partners throughout social interactions (Van den Bos et al., 2012). Also, with age, adolescents showed improved abilities to overcome incorrect prior expectations about their interaction partner and showed improved ability to respond to the actual trustworthiness level that the partner displayed (Lee et al., 2016). Despite the concurrent development of the brain, socio-cognitive abilities, and peer relationships during adolescence, there is little research that has examined the interplay between these domains (Baek et al., 2021; Smith et al., 2020). Therefore, in the current study, we examined how peer relationships, measured by the extent of social embeddedness in secondary school classrooms, are associated with trust behavior and related neural activity in young adolescents. Given the novelty of the research question, we examined these relationships in a group of young adolescents of a narrow age range and did not investigate developmental effects.

Different fields of research have shown the importance and influence of peers on adolescent behavior. For example, being observed by peers promoted adolescent risk-taking behavior and elicited more activity in reward-related brain areas in adolescents compared to adults

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(Chein et al., 2011; Gardner and Steinberg, 2005; Smith et al., 2015). Also, previous research has linked different aspects of social relationships to socio-cognitive abilities. For example, children with higher theory of mind (Caputi et al., 2012 [ages 5–7]) and empathy abilities (Oberle et al., 2010 [ages 9–11]) were more liked by peers, while having friends (as opposed to no friends) (Wentzel et al., 2004 [ages 11–12]) or feeling connected to friends (Padilla-Walker et al., 2015 [mean age 13.3]) are (indirectly) positively related to prosocial behavior. Moreover, the number of close friends and a higher quality of peer relationships are positively associated with mentalizing abilities (Boele et al., 2019; Portt et al., 2020; Stiller and Dunbar, 2007). These studies provide initial evidence that peer relationships are associated with social behavior and socio-cognitive abilities. To fully understand this interrelationship, it is important to consider that our daily social life involves a complicated web of social networks characterized by different patterns of direct and indirect social relationships, and that each individual has a position within these networks. Insight into these complex social interrelationships is particularly relevant during adolescence. This is a period when social life changes rapidly and becomes more complex as adolescents spend more time with peers and move away from the home environment (Brown and Larson, 2009; Lam et al., 2014).

Our social networks, which consists of complicated patterns of direct and indirect relationships, cannot fully be captured by self-report or the assessment of dyadic relationships (e.g., the frequency of being liked or the number of friendships). Social network analysis is a technique that not only takes dyadic relationships into account but characterizes the entire structure of relationships within a community (Everett et al., 2013). For all individuals within a given group, social network analysis maps the presence of specific types of relationships, for example, friendship relationships or those based on social preference, and how these are connected as a network. These relationships can be quantified in different ways, focusing on either the individual's position within the network or the network as a whole. One way to quantify the individual's position is by using the measure of eigencentrality (Bonacich, 1987; Everett et al., 2013). In contrast to a measure representing only dyadic social relationships, the eigencentrality measure considers to who you are connected as it is calculated based on the number of social relationships you have while also considering the social relationships of the people to who you are connected (i.e., the extent of being well connected to well-connected others). In this way, the eigencentrality measure provides information about an individual's embeddedness and degree of influence within the network (Baek et al., 2021; Robins, 2015). So, this means that when using this measure, it is considered that it is important who the people are to whom one is connected. For example, pupils in a school class may perceive and treat person A and person B differently while they both have three friends in class. However, person A is friends with person C, who has many connections, while person B and person C are not friends. The friendship with person C enables person A to easily meet many other peers, and this may positively impact person A's behavior and well-being. Also, classmates may be more reluctant to mistreat person A than person B because person A might receive support from many others (provided by classmate C who has many connections, and these connections are again connected to other classmates) (Baek et al., 2021). Previous research has shown that eigencentrality (based on a social preference network) was positively associated with prosocial behavior (Van den Bos et al., 2018 [mean age 14.8]) and empathy abilities (Wölfer et al., 2012 [mean age 13.7]). These results provide initial evidence that being well embedded within a social network may offer unique opportunities to learn about people's social behavior and their motives, which may contribute to the development of complex socio-cognitive abilities, and these abilities can be employed during social interactions.

Social interactions can be simulated by experimental paradigms such as the trust game (Berg et al., 1995). This game simulates a social interaction based on trust. The trust game can be used as a single round game (i.e., one-round trust game) or it can be expanded to multiple rounds (i.e., multi-round trust game). In a round, the trustor (i.e., participant)

allocates an amount of money (called the investment) between themselves and the interaction partner. The investment is tripled before the partner receives it. The partner chooses an amount (if any) to return to the participant and keeps the remainder to themselves. The investment in a one-round trust game is often used as indication of the level of baseline (i.e., general) trust toward unknown others. In a multi-round trust game, social processes may start to play a role which are not present during a one-round game (e.g., trust decisions are affected by strategic considerations such as protecting one's social reputation). The investment during the first round of a multi-round trust game is often referred to as initial trust behavior. A multi-round trust game also allows for the examination how the trustor adapts their trust behavior throughout the game in response to the partner's trustworthy or untrustworthy behavior. The trust game has been often used in adolescent (Güroğlu et al., 2014; Lee et al., 2016; Van de Groep et al., 2018; Van den Bos et al., 2012; Westhoff et al., 2020) as well as adult samples (amongst other the meta-analyses of Bellucci et al., 2017; and Van den Akker et al., 2020).

Previous studies indicated that there is some evidence that the level of initial trust increases with age (Fett et al., 2014 [ages 13–49]; Van den Bos et al., 2012 [ages 11–21]). The results of these studies also showed increased adaptive trust behavior throughout adolescence and adulthood, which may be explained by a development in mentalizing processes (Fett et al., 2014 [ages 13–49]; Van den Bos et al., 2012 [ages 11–21]). Relatedly, in a cross-sectional study it was found that mentalizing abilities were associated with the extent of adaptive trust behavior, as adolescents with higher scores on a mentalizing task showed more trust behavior toward a trustworthy partner and more malevolent behavior toward an untrustworthy partner than adolescents with lower scores on the mentalizing task (Fett et al., 2014). As previously discussed, these mentalizing abilities, which are important for adaptive trust behavior (Fett et al., 2014), are related to properties of one's social relationships (Boele et al., 2019; Portt et al., 2020; Stiller and Dunbar, 2007). This may suggest that being well embedded in social networks in daily life may promote social learning and socio-cognitive development. However, to our knowledge, few studies have linked social network positions to trust behavior. A recent study in adolescents did not find evidence for a relationship between eigencentrality (based on a social preference network) and initial investments in the trust game (Van den Bos et al., 2018 [mean age 14.8]). This study did not examine the adaptation of trust behavior, though eigencentrality may be related to the adaptation of trust behavior during repeated social interactions. Being well embedded within a social network may provide a unique position to learn about other people's motivations and how these guide their behavior. This may encourage social learning processes about how to adequately respond to differing trustworthiness levels of other people. Preliminary indications that the centrality of network positions are positively associated with trust in multi-round trust games is shown by Buskens (1998), who used a simulated dataset. So, the question if eigencentrality is related to the adaptation of trust behavior is still open. Therefore, we examined the relationship between social network position and both initial trust behavior and the adaptation of trust behavior using a multi-round trust game design.

Similar to the paucity of studies that link social network positions to trust behavior, few studies have linked social network positions to neural activity, while this could provide insights into how our social world is related to the cognitive and neural processes that underlie trust behavior (Baek et al., 2021; Smith et al., 2020). Multiple studies have elucidated the key cognitive and neural processes involved in the trust game itself. Meta-analytic evidence from neuroimaging studies that used the trust game showed that the left ventral striatum and right caudate activity is increased during multi-round trust games (Bellucci et al., 2017). The ventral striatum has been related to social reward processes and reward prediction error processing, while the caudate plays a role in social learning that is based on actions and their consequences (Balleine et al., 2007; Bellucci et al., 2017; Cox and Witten, 2019; Joiner et al., 2017; Knutson and Cooper, 2005; O'Doherty, 2004). These processes enable

the trustor to learn about the trustworthiness of the partner, thereby affecting the trustor's investments and their evaluation of the partner's return in light of their own expectations (Alós-Ferrer and Farolfi, 2019; Krueger and Meyer-Lindenberg, 2019). Additionally, mentalizing processes play a role in the trust game, as they enable the trustor to infer the partner's intentions and thereby anticipate the potential return (Alós-Ferrer and Farolfi, 2019). It is suggested that these mentalizing processes are mediated by the involvement of areas that belong to the so-called social brain. Important areas of the social brain that are known for their role in mentalizing processes are the temporoparietal junction (TPJ) and the medial prefrontal cortex (mPFC) (Crone and Dahl, 2012; Kilford et al., 2016; Van Overwalle, 2009). The involvement of the TPJ and the mPFC in trust interactions has been supported by recent studies using the trust game in adolescents and (young) adults (Fareri et al., 2020 [mean age 21.4]; Feng et al., 2021 [ages 23–26]; Fujino et al., 2020 [mean age 27]; Lemmers-Jansen et al., 2019 [mean age 16.5]). Moreover, cognitive control processes that support goal-directed behavior and decision-making are also involved in trust interactions (Krueger and Meyer-Lindenberg, 2019). A brain area associated with these processes is the dorsolateral prefrontal cortex (dlPFC) (Declerck et al., 2013; Miller and Cohen, 2001), and multiple studies have found increased dlPFC activity in young adults during the trust game (Feng et al., 2021 [ages 23–26]; Fouragnan et al., 2013 [mean age 29.5]; Lemmers-Jansen et al., 2017 [mean age 21.5]). Together, these studies elucidate the underlying cognitive and neural processes involved in social interactions based on trust and provide the basis for investigating trust behavior and the related processes as a function of one's position within a social network. We do note that the association between network position, trust behavior, and related neural activity may be bidirectional. It could also be possible that high levels of trust in other people (and the related neural activity) may enable adolescents to develop stronger social relationships and have more central positions within the social network.

The aim of the current study was to examine how embeddedness within a social network is related to trust behavior and neural activity in young adolescents. Given the novelty of the research question, we examined these relationships in a group of young adolescents of a narrow age range and did not investigate developmental effects. Social network analysis was used to measure the individual's network position. These network positions were quantified using the eigencentrality measure and indicated the degree of social embeddedness and influence within the network. To this end, sociometric data were collected in classrooms with pupils who had just started secondary school. Eigencentrality measures were calculated based on friendship networks because these are, especially for young adolescents in full-time education, meaningful social relationships that are important for their psychological and social functioning (Erdley and Day, 2017; Rubin et al., 2006). In this way, we were able to relate daily life indicators of social network positions to trust behavior and to the neural processes that underlie trust behavior. The participants played a trust game in the MRI scanner in the role of the trustor and were informed that they would play a game with a computer counterpart (displayed as a cartoon animation, see 2.3. Materials). The partner's behavior was modeled using a preprogrammed algorithm that showed adaptive trust behavior in response to the participant's investments. We focused on an untrustworthy partner (as opposed to a trustworthy partner) as the adolescents' social world becomes more complex. During adolescence, social life shifts from the family environment to peers, and adolescents will meet many new people of which some will show untrustworthy behavior. This means that learning to recognize who not to trust and learning how to respond to these untrustworthy others becomes more important. The partner's behavior was preprogrammed in such a way that the partner profited from trust behavior shown by the participant. To maximize their outcome, the participant was better off not increasing (i.e., decreasing or not changing) their investment but, instead, benefited from not trusting the partner.

First, we expected adolescents with more central network positions to show more trust at the start of the interaction (i.e., initial trust behavior) compared to adolescents with less central network positions. Initial trust behavior was measured by the investment during the first round of the multi-round trust game. In general, showing initial trust at the start of an interaction is more prosocial as this increases the chance of a fruitful cooperation. Previous research showed that having friends (Wentzel et al., 2004) or having a central position within a social network (Wölfer et al., 2012) is positively associated with prosocial behavior and empathy. As adolescents with more central network positions are more socially embedded in the network, they might also show more prosocial behavior and be keener on social cooperation and, therefore, show more initial trust compared to adolescents with less central network positions. Second, since the number and quality of peer relationships are positively associated with mentalizing abilities (Boele et al., 2019; Portt et al., 2020; Stiller and Dunbar, 2007), this might suggest that central positions within friendship networks may provide unique opportunities to develop complex socio-cognitive abilities. This suggests that central network positions may enable adolescents to learn about other people's intentions which drive their behavior and, thus, about who can and cannot be trusted. Therefore, we expected the adolescents with more central positions to respond to untrustworthy behavior more adaptively, hence, to show a greater decrease in trust behavior over the course of the interaction compared to adolescents with less central positions. Moreover, using region of interest analyses, we examined if network position is associated with neural activity in the regions reported by a meta-analysis and review studies on the trust game (Alós-Ferrer and Farolfi, 2019; Bellucci et al., 2017; Krueger and Meyer-Lindenberg, 2019). The regions of interest (ROIs) that were selected based on these studies are the ventral striatum, caudate, TPJ, mPFC, and dlPFC. We expected that these brain areas and the cognitive processes to which these areas have been related (i.e., social reward processes, mentalizing processes, and cognitive control processes) are involved in both the investment phase and the feedback phase of the game (King-Casas et al., 2005; Redcay and Schilbach, 2019). We expected activity within these ROIs to be related to social network position; however, given the novelty of the research question (i.e., relating social network positions to neural activity), we did not have prior hypotheses about how neural activity within the ROIs and social network positions were related. Also, whole-brain analyses were conducted to explore the relationship between social network positions and activity outside the ROIs. Furthermore, in line with the behavioral analyses in which the change in trust behavior was studied, we examined exploratory time-related changes in neural activity within the ROIs during the game and tested if social network positions were associated with these activity changes.

## 2. Material and methods

### 2.1. Participants

The participants of the current study took part in both the first wave of the behavioral study and the first wave of the fMRI study of the #SOCONNeCT project (Sijtsma et al., 2021; Van Buuren et al., 2021, 2020). The behavioral study consisted of the administration of multiple questionnaires and tasks, including a different version of the trust game compared to the one administered in the current study (the versions used a different cartoon animation and a different algorithm modeling the partner's behavior). Eight secondary schools participated in the #SOCONNeCT project, and all schools were part of the two higher educational tracks in the Netherlands. During the data collection period, the two higher level educational tracks constituted the top 40% of pupils. When participants and parent(s)/caregiver(s) signed written informed consent for the behavioral study of the #SOCONNeCT project ( $N = 647$ ), they indicated whether they could be contacted for participation in future studies within the #SOCONNeCT project, including the fMRI study. The goal for the fMRI study was to recruit a subsample of about 10% of

the participants in the behavioral study. We reached out to all the participants (370 adolescents) that indicated they could be contacted for participation in future studies. Of these, 159 participants (43%) did not respond or were no longer interested. A further 125 participants (34%) had dental braces, which excluded them from participating. In total, 86 participants (23%) agreed to participation (see also Van Buuren et al., 2021, 2022, 2020). None of the 86 participants had contra-indications for MRI (e.g., metal implants, non-removable medical devices, braces, claustrophobia, or a neurological disorder). Both right- and left-handed participants were included in the analyses. Both the participant and the parent(s)/caregiver(s) signed written informed consent for participation in the fMRI study.

Of the 86 participants, two participants (2%) withdrew from participation because they were too anxious at the beginning of the scanning session and 15 participants (17%) were excluded due to too much movement (>3 mm) during the scanning of the trust game. Furthermore, participants were included in the analyses of the current study if they, next to participation in the first wave of fMRI study of the #SOCONNeCT project, completed the social network questionnaire during the first wave of the behavioral study of the #SOCONNeCT project, and if they were in classes in which at least 70% of the pupils completed this social network questionnaire. A high participation rate within a class (rule of thumb >70%) is recommended to secure reliable social network measures (Cillessen and Marks, 2011; Marks et al., 2013). We excluded 20 participants (23%) who were in classes with a participation rate below 70% and one participant (1%) who was absent during the administration of the social network questionnaire. This resulted in the inclusion of 49 participants (57%) from fourteen classes in the analyses of the current study ( $M_{\text{age}} = 12.8$  years,  $SD_{\text{age}} = 0.4$  years, 18 boys, 11 left-handed). These classes were divided over four schools (four classes were from school 1, four classes were from school 2, three classes were from school 3, and three classes were from school 4).

Per wave, the school received €7.50 per pupil that participated in the behavioral study (for use in class activities). The participants received €20 for participation in the fMRI study. They also received an additional monetary payout based on the average earnings per trial in the game (the maximum payout was €10). The #SOCONNeCT project and its procedures were approved by the Scientific and Ethical Review Board of the Faculty of Behavioural and Movement Sciences of the Vrije Universiteit Amsterdam.

## 2.2. Procedure

The social network questionnaire that was used in the current analyses was administered during the first wave of the behavioral study of the #SOCONNeCT project. Data collection for the behavioral study of the #SOCONNeCT project took place in a classroom setting and was therefore arranged with the relevant school. Data collection was led by researchers and trained research assistants and lasted 90 min in total, including classroom explanations (i.e., what research entails, the rights that participants have, and the aim of the research project) and the administration of materials not analyzed in the current study. All materials were provided by the researchers, completed individually with the tables separated, and were validated prior to the study (see Sijtsma et al., 2021). At the time of the first wave, the participants had just transferred from primary to secondary school, which makes this an important period for the formation of new friendships. In all the participating secondary schools, the pupils followed all courses with the same group of peers for the entire first academic year, which means that the peers in the classroom are an important group to create new friendships. This also implies the pupils had some time to get to know each other before the #SOCONNeCT project started (on average, data collection took place 11 weeks after the start of the academic year).

Similar to the social network questionnaire, the fMRI data that was used in the current analyses was collected during the first wave of #SOCONNeCT project. The participation was in arrangement with the

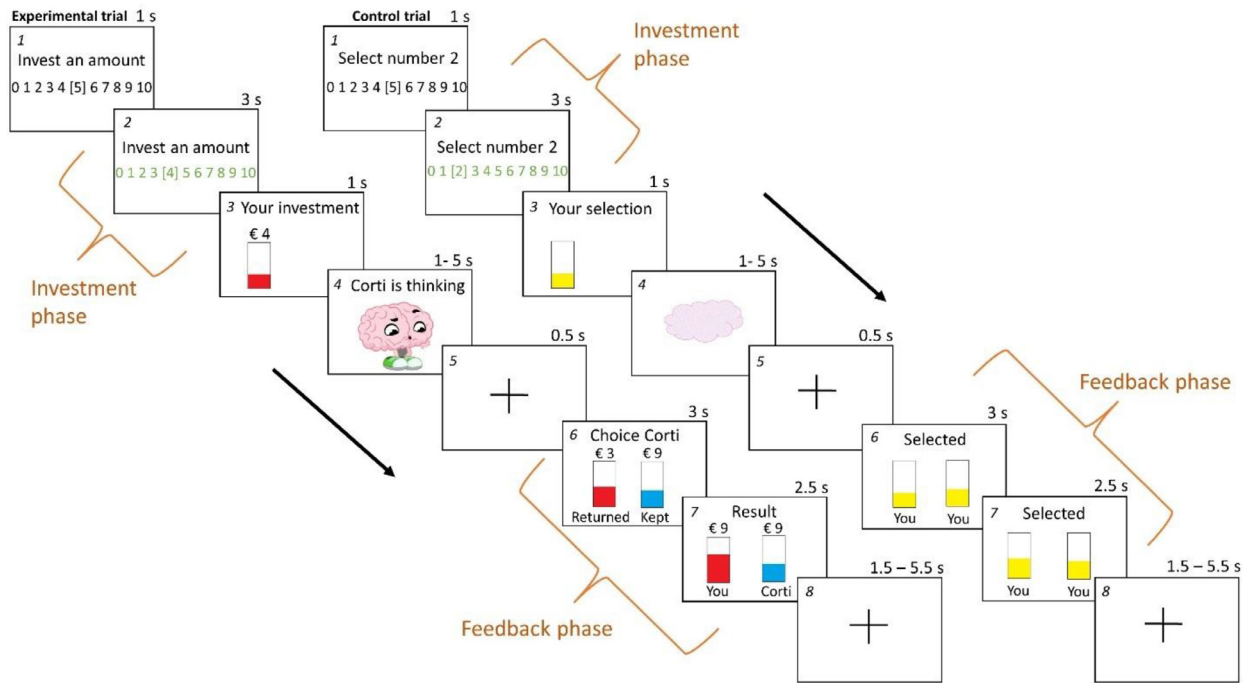
parent(s)/caregiver(s). On average, scanning took place 14.5 weeks after the administration of the social network questionnaire. The participants visited the MRI scanning location together with their parent(s)/caregiver(s). Before entering the MRI scanner, the participants received instructions about the scanning procedure, including an explanation on the trust game. The participants were informed that they would play a game with a computer counterpart (displayed as a cartoon animation named “Corti”). The participants were not given any information about Corti’s trustworthiness. After the instructions, the participants played a practice version of the game in the mock scanner. This was for explanatory purposes only, meaning that the participants made investments but did not receive returns from a partner and, instead, automatically received a return equal to their investment. After the practice version of the game had finished, the participant was placed in the MRI scanner. The MRI procedure started with a resting state period (Van Buuren et al., 2021), followed by a trait judgement task (Van Buuren et al., 2022, 2020), a structural scan, and ended with the trust game. The total scanning session lasted 45 min. After the trust game had finished, the participants completed a questionnaire outside the scanner in which they rated the partner on honesty and trustworthiness (see 2.3. Materials).

## 2.3. Materials

### 2.3.1. Trust game

The trust game consisted of 27 experimental trials and 27 control trials in pseudorandom order. The task was designed to consist of three blocks (each block consisted of nine experimental trials and nine control trials with an 18 second break between the blocks). The number of trials per block was based on a balance between feasibility in terms of concentration and fatigue in the young adolescent participants and obtaining reliable estimates of the fMRI signal. An experimental trial started with a cue (1 second) that indicated the participant could make an investment between €0 and €10 (see screen 1 in Fig. 1). Next, the participant selected an amount to invest (3 s), after which the investment was shown (1 second, see screen 2 and 3 in Fig. 1). The numbers on the screen turned green after the investment was made. The right index and middle finger were used to move the cursor left and right, and the left index finger was used to select the amount. The amount invested was tripled before it was received by the partner. After a waiting period (1 to 5 s, mean jitter 3 s), the participant saw a fixation cross for 0.5 s (see screen 4 and 5 in Fig. 1). Next, a screen was displayed for 3 s that showed the amount of money the partner kept for themselves and the amount the participant received from the partner, followed by a screen that showed the total earnings for that specific trial (2.5 s, see screen 6 and 7 in Fig. 1). An intertrial interval of 1.5 to 5.5 s (mean interval 3.5 s) was presented that displayed a fixation cross before the start of the next trial (see screen 8 in Fig. 1). For the fMRI analyses, we modeled the period in which the participant made the investment and the period in which the participant received the partner’s return.

Similarly to an experimental trial, a control trial started with a cue (1 second) that instructed the participant to select a specified number (a randomly selected number between zero and ten, see screen 1 in Fig. 1). Next, to simulate the act of making an investment as in the experimental trials, the participant moved the cursor to the specified number (3 s, the numbers turned green after pressing, see screen 2 in Fig. 1). Next, the selected number was shown (1 second, see screen 3 in Fig. 1). After a waiting period (1 to 5 s, mean jitter 3 s), a fixation cross was shown (0.5 s, see screen 4 and 5 in Fig. 1). There were no return or total earnings in the control trials. However, similarly to the experimental trials, the fixation cross was followed by a screen that depicted colored bars that displayed the selected number (3 s, see screen 6 in Fig. 1). Similar to the experimental trials, this was followed by a screen for 2.5 s that depicted colored bars with a larger colored section compared to the previous screen (see screen 7 in Fig. 1). An intertrial interval of 1.5 to 5.5 s (mean interval 3.5 s) was presented that displayed a fixation cross before



**Fig. 1.** *The trust game: An experimental trial (left) and a control trial (right).* Note. The seconds above the screens indicate the duration of the screens. The digit in the top left corner indicates the screen number (the screen number was not visible for the participant but corresponds to the text in 2.3.1. *Trust game*). In the experimental trial, the participant shared an investment with the partner, e.g., €4, and kept the remainder for themselves (€6). The investment was multiplied by three (€4 × 3) and received by the partner (€12). The partner then shared a return (€3) and kept the remainder to themselves (€9). The trial ended with the total earnings for the participant (€6 + €3 = €9) and the partner (€9). In this trial, a factor of 0.75 was used ( $0.75 \times €4 = €3$ ). If the participant increases their investment in the next trial, the probability of a smaller return increases (i.e., the factors of 0.5 and 0.75 become 2.5% more probable while the probability of factor 1.0 decreases by 5%). However, if the participant decreases or does not change the investment in the next trial, the probability of the factors determining the partner's return do not change. In the control trial, the participant selected a specified number, which was randomly selected between zero and ten. There were no return or total earnings in the control trials. However, during the feedback phase of the control trial, the first screen showed colored bars that depicted the selected number and the second screen showed bars of which the colored section was increased to mimic the change in the colored bars during the feedback phase of the experimental trials. For the fMRI analyses, we modeled the investment phase and the feedback phase (indicated by the orange arrows) of both types of trials.

the start of the next trial (see screen 8 in Fig. 1). For the fMRI analyses, the period during which the participant selected the number and the period during which the participant viewed the colored bars of the selected number were modeled. In contrast to the experimental trials, the control trials did not include a social component or information related to a social interaction. This design is comparable to the trust game as used in previous fMRI studies (Fett et al., 2014; Hanssen et al., 2021; Lemmers-Jansen et al., 2019, 2017).

We used an untrustworthy partner (as opposed to a trustworthy partner) as previous work showed that this type of behavior triggered adaptive trust behavior in participants (Fett et al., 2014; Van den Bos et al., 2012). Also, the social world becomes more complex during adolescence and, as adolescents will meet new people of which some will show untrustworthy behavior, learning who not to trust becomes more important. A hypothetical partner was used whose behavior was modeled using an algorithm to control the partner's trustworthiness. The algorithm showed adaptive trust behavior in response to the participant's investment. Specifically, it was preprogrammed in such a way that when the participant increased their investment compared to the previous trial, the chance of a lower return increased, meaning that the partner profited from participant's trusting behavior. In other words, participants were better off not increasing (i.e., lowering or not changing) their investments and, instead, benefited from not trusting the partner.

The exact amount that the partner returned was based on the participant's investment multiplied by a predefined factor (0.5, 0.75, or 1.0) and rounded to the nearest 50 cents. During the first trial, there was an equal probability of each factor being selected (i.e.,  $\frac{1}{3}$ ). For the remaining trials, the probability of each factor to be selected changed depend-

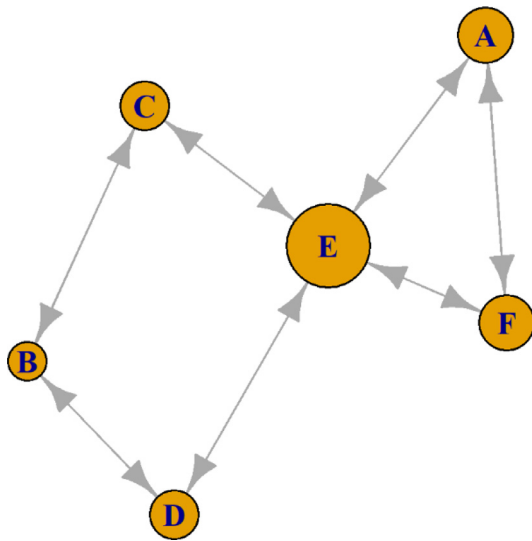
ing on whether the participant changed their investment compared to the previous trial.

When the participant increased their investment compared to the previous trial, the probability of a smaller return increased. As such, the factors of 0.5 and 0.75 became 2.5% more probable while the probability of factor 1.0 decreased by 5%. In other words, trusting behavior by the participant resulted in a greater probability that the partner responded by returning less (though never less than half the investment). In cases where the participant increased their investment over seven trials (not per se consecutively), the probability of factor 0.5 reached 50%, the probability of factor 0.75 reached 50%, and the probability of factor 1.0 reached 0%, after which the factors remained stable for the remaining trials left in the game. When the participant decided to decrease the investment or not change the investment compared to the previous trial, the probability of the factors determining the partner's return did not change.

As the factor determining the partner's return was based on a probability, it could happen occasionally that the partner's return was equal to the investment (in case the factor was of 1.0) or that it increased relative to the investment compared to the previous trial (for example, the factor was 0.75 for the current trial while the factor for the previous trial was 0.5). On average, these two situations occurred in 28% on the trials meaning that, on average, untrustworthy behavior was displayed in 72% of the trials (46%–85%,  $SD = 8\%$ ).

### 2.3.2. Trust game questionnaire

After the trust game was completed, the participants were administered a questionnaire about the trust game outside the scanner. The



**Fig. 2.** An example of a hypothetical social network. Note. This example demonstrates how friendship eigencentrality scores are calculated in which the eigencentrality scores of one's friends is considered. The circles represent individuals, and the double-headed arrows represent reciprocal friendships. The size of the circle is proportional to the eigencentrality of that person. Person A and B both have two reciprocal friendships but person A's eigencentrality is higher (i.e., the circle is larger) than person B's eigencentrality. This is because person A is friends with person E who has four reciprocal friendships and, thus, person E has a very high eigencentrality score which increases person A's eigencentrality. Person B is friends with person C and person D, but as they both have two reciprocal friendships, they have lower eigencentrality scores, and this decreases person B's eigencentrality.

participants rated the partner on a scale of zero to ten on honesty and trustworthiness to verify whether the participants experienced the partner as untrustworthy (higher scores indicated more honest and more trustworthy, see Appendix A).

### 2.3.3. Social network positions

Sociometric data were collected in secondary school classrooms using a peer nomination questionnaire. This questionnaire consisted of nine questions in total. For the current analyses, we used the question "Who on this list are your friends?". A list with the names of all classmates was displayed on an iPad (iPads were provided by the researchers). The participant could select a maximum of fifteen classmates. The answers were used to create a closed network reflecting reciprocal friendship relationships within the class in which everyone occupied a position (see Fig. 2 for a hypothetical network example).

Social network positions were based on the closed friendship network and quantified using the eigencentrality measure which indicated the participant's degree of social embeddedness and influence within their class (Bonacich, 1987; Everett et al., 2013). The eigencentrality measure does not merely count the number of friends one has, but also considers to whom one is befriended. When one is befriended with peers who have many friends, this increases one's eigencentrality score and, similarly, if one is befriended with peers with few friendships, this decreases one's eigencentrality score. In other words, when calculating the eigencentrality score of an individual, the eigencentrality scores of the individual's friends (and their friends etc.) is considered (see Fig. 2). To control for differences in class sizes, we used the normalized eigencentrality measure calculated by UCINET and these were transformed to z-scores (Borgatti et al., 2002). All participants in the current study ( $N = 49$ ) and their 334 classmates reported on their friendships within the class (see 2.2. Procedure). Details on the participation rate per class can be found in Appendix B.

## 2.4. Behavioral data analyses

Mixed models in R (RCoreTeam, 2020 [version 4.1.1]) were used to perform behavioral data analyses (the *lme4* package by Bates et al. (2015) and the *lmerTest* package by Kuznetsova et al. (2017) were used). Mixed models allow the intercept (i.e., initial trust behavior) and the slope (i.e., change in trust behavior) to be fixed or random. A fixed intercept models the mean starting point of the investments, while a random intercept models the individual differences in starting points. Likewise, a fixed slope models the mean change in investments over trials and a random slope models the individual differences in the change in investments. In our design, there are repeated measurements of the same participant over trials and the participants are nested within school classes. The intraclass correlation for the level class is 0.02, which means that 2% of the total observed variability in investment scores was due to differences between classes. Due to this low percentage, we did not include class as a level in the model. This means that the first level of the model is the level of time (i.e., trials) and the second level is participant (see Appendix C for the equations of the multi-level model). First, a null model with a random intercept for the level participant was fitted (without fixed effects). In model 1, the variable age was added to control for possible age effects and kept in the next model if it improved model fit. As the participant's investments are assumed to be influenced by previous partner behavior, we added a variable that captured partner behavior during the previous trial in model 2 (this was operationalized as the predefined factor that determined the partner's return during the previous trial and for trial 1 this was set to one). The fit of model 2 was compared to the fit of model 1. In model 3, the main effect of time (both the linear effect and the quadratic effect) was added as a fixed effect. The quadratic effect was kept in the model if model fit improved compared to only including the linear effect of time. In model 4, the main effect of the honesty rating about the partner and the interaction between the honesty rating and time were added (and kept if this improved model fit compared to model 3). In model 5, the main effect of the trustworthiness rating about the partner and the interaction between the trustworthiness rating and time were added (and kept if this improved model fit compared to model 3). In model 6, a random slope of time was added (and kept if this improved model fit compared to the previous model). In case the random slope of time improved model fit then, in model 7, the variable eigencentrality was added in a two-way interaction with time as a fixed effect (including the fixed main effect of time and the fixed main effect of eigencentrality). In case the random slope of time did not improve model fit (and only the fixed main effect of time was significant), then, in model 7, only the main effect of eigencentrality was added as fixed effect (without the two-way interaction between eigencentrality and time). The investments per trial served as outcome variable. The maximum likelihood estimation method was used to fit the models. Model comparison was done using the likelihood ratio test ( $p < .05$ ). Akaike Information Criterion (AIC) values and Bayesian Information Criterion (BIC) values were provided for completeness (lower values indicated a better model fit).

## 2.5. MRI data acquisition

MRI data were acquired on a 3.0 Tesla Philips Ingenia CX MRI scanner equipped with a 32-channel-phased array head coil (Spinoza centre for Neuroimaging; Philips Medical Systems, Best, the Netherlands). For the trust game, 494 functional images were obtained using a two-dimensional echo planar imaging-sensitivity encoding (EPI-SENSE) sequence (voxel size 3 mm isotropic; repetition time (TR): 2000 ms; echo time (TE): 27.63 ms; flip angle = 76.1°; matrix 80×80; field of view = 240×240×121.8; 37-slice volume with a 0.3 mm gap, slice acquisition ascending sequential order). Furthermore, a T1-weighted structural image was acquired using a three-dimensional

fast field echo sequence (parameters: voxel size 1 mm isotropic, TR = 8.2 ms; TE = 3.7 ms; flip angle = 8°; matrix 240×188; field of view = 240×188×220; 220 slices in total).

## 2.6. ROI definition

ROIs were defined based on a meta-analysis and review studies in the trust game literature combined with trust game studies in adolescents. First, based on the meta-analysis by Bellucci et al. (2017), we included the left ventral striatum ( $x, y, z = -2, 2, -6$ ) and the right caudate ( $x, y, z = 12, 18, -4$ ). Second, we selected the TPJ, mPFC, and dlPFC based on recent review studies (Alós-Ferrer and Farolfi, 2019; Krueger and Meyer-Lindenberg, 2019). Given our focus on adolescence, the coordinates of these regions were based on trust game studies in adolescents (Lemmers-Jansen et al., 2019, 2017) (right TPJ:  $x, y, z = 45, -43, 32$ ; mPFC:  $x, y, z = 0, 42, 6$ ; right dlPFC:  $x, y, z = 51, 18, 30$ ). All coordinates are presented in MNI space. Eight mm spheres were created around the coordinates of the TPJ, mPFC, and dlPFC. Five mm spheres were created around the coordinates of the ventral striatum and caudate, due to the small size of these areas and their proximity to the ventricles. See Fig. 4.A for the resulting ROIs.

## 2.7. Preprocessing fMRI data

Statistical Parametric Mapping 12 was used to perform fMRI analyses. In the first step of preprocessing, the functional images were realigned to the mean reference scan. Next, slice time correction was applied using the middle slice as reference. Next, the structural image was co-registered to the mean functional image obtained with realignment. Then, tissue probability maps matched for the age and sex of the current sample were created using the CerebroMatic toolbox (Wilke et al., 2017) and these maps were used to segment the co-registered structural image (a similar approach was used in Van Buuren et al. (2021); Van Buuren et al. (2022); Van Buuren et al. (2020)). Next, the functional and structural images were normalized to MNI space using the normalization parameters obtained with segmentation and the normalized functional images were smoothed using a 6 mm Gaussian kernel full width at half maximum.

## 2.8. fMRI data analyses

The fMRI analyses were comprised of two parts. First, the main analyses of the fMRI data were univariate analyses based on the average neural activity across all the experimental trials, relative to the control trials, separated for the investment phase and feedback phase of the trust game (see 2.8.1. *Main analyses*). On second level, these average signal changes were investigated using a region of interest approach to probe trust game-related changes in activity and to probe the association between social network position and neural activity within the predefined ROIs. We opted for a region of interest approach to increase sensitivity of our analyses and because prior studies showed involvement of specific regions during the trust game (see 2.6. *ROI definition*). Additionally, we used a whole-brain approach to explore trust game-related activity outside the ROIs and to explore relationships between social network position and neural activity outside the ROIs. Previous work (Bellucci et al., 2017; Krueger and Meyer-Lindenberg, 2019) gives a clear understanding about the ROIs involved in the trust game, but given the novelty of the research question (i.e., relating social network positions to neural activity) we also explored activity outside the ROIs.

Secondly, in line with the behavioral analyses that examined time-related changes in investments, we probed time-related changes in neural activity during the experimental trials, relative to the control trials, within the ROIs (separated for the investment phase and feedback phase) and tested whether social network position is associated with these neural activity changes (see 2.8.2. *Time-analyses*). Trial-to-trial analyses can be applied to the behavioral measurement of trust (i.e.,

the investments), as the investment is a direct measure of each trial. In contrast, the fMRI (BOLD) signal is not a direct measure of neural activity related to one trial and can be better and more reliably estimated when the signal is averaged across trials. Therefore, recent studies that employed the trust game in adolescent samples used trial-to-trial analyses for their behavioral analyses, while the MRI analyses were based on average neural activity across trials (Hanssen et al., 2021; Lemmers-Jansen et al., 2019, 2017). Moreover, one of these studies employed the trust game with a similar design as the design of the current study, and revealed that trial-based beta-estimation resulted in highly variable, unreliable estimates over trials (Hanssen et al., 2021). We examined the stability of the beta-estimates per trial for the current dataset and, similar to Hanssen et al. (2021), the results indicated unreliable estimates over trials that were unsuitable for a trialwise approach (the method of the GLM approach can be found in Appendix D). To allow for time-related analyses, the trust game that was used in the current study was designed to consist of three blocks (see 2.3.1. *Trust game*) and the average neural activity (i.e., fMRI signal) per block was used in the time-related analyses (see 2.8.2. *Time-analyses*).

### 2.8.1. Main analyses

For the first part of the MRI analyses, i.e., the main analyses, normalized and smoothed functional MRI data were submitted into a general linear model (GLM) consisting of four regressors of interest. The first regressor modeled the “investment phase” of the experimental trial and consisted of the period in which the participant made an investment (modeled up until the participant made a response so there was a maximum duration of 3 s, see Fig. 1). A second regressor modeled the “feedback phase” of the experimental trial and contained the period that the participant viewed the colored bars of the partner’s return and viewed the total earnings of the specific experimental trial (duration of 5.5 s, see Fig. 1). The third regressor modeled the “investment phase” of the control trial and contained the period in which the participant selected the number (modeled up until the participant made a response so there was a maximum duration of 3 s, see Fig. 1). A fourth regressor modeled the “feedback phase” of the control trial and contained the period that the participant viewed the two screens that displayed the colored bars of the selected number (duration of 5.5 s, see Fig. 1). A regressor of no interest was included that consisted of the time that covered the cue to invest and the cue to select (screen 1 in Fig. 1) and the time that covered the waiting periods of the experimental trials and the control trials (screen 4 in Fig. 1). All regressors were modeled by convolving a box-car function with a canonical hemodynamic response function (Friston et al., 1995). Six motion parameters obtained with realignment were added as regressors of no interest to remove effects of motion and a high-pass filter was included to remove low frequencies not of interest (cut-off 128 s). Subsequently, two contrast images were created for each subject that contrasted the investment phase and the feedback phase of the experimental trials to the equivalent phase of the control trials.

For second-level analyses, average contrast values were extracted for each ROI and each subject using the MarsBar version 0.44 toolbox (<http://marsbar.sourceforge.net>). First, to examine trust game-related activity, a one-sample t-test for each contrast was used to test which ROIs showed increased activity during the investment phase and the feedback phase of the experimental trials compared to the equivalent phase of the control trials. Per phase (i.e., the investment phase and feedback phase), the analyses were corrected for multiple comparisons using a Bonferroni correction (the adjusted significance cut-off was 0.05/5 ROIs = 0.01). Second, per ROI, a regression analysis was conducted to examine the relationship between social network position and neural activity. The extracted ROI contrast values served as outcome variable and the eigencentality scores as predictor variable. This was done separately for the investment phase and the feedback phase and by using a separate model per ROI. Per phase (i.e., the investment phase and feedback phase), the analyses were corrected for multiple comparisons us-

ing a Bonferroni correction (the adjusted significance cut-off was 0.05/5 ROIs = 0.01).

Additionally, whole-brain analyses were performed to explore trust game-related activity outside the ROIs. This was done by using one-sample t-tests for both the investment phase and the feedback phase of the experimental trials relative to the equivalent phase of the control trials. Also, whole-brain analyses during the investment phase and the feedback phase were performed to explore associations between eigencentrality and neural activity outside the ROIs. This was done by using one-sample t-tests for both the investment phase and the feedback phase of the experimental trials relative to the equivalent phase of the control trials with eigencentrality (centered) as covariate. Whole-brain analyses were cluster-corrected using a cluster defining threshold of  $p < .001$ , and a cluster-probability of  $p < .05$ , family-wise error corrected.

### 2.8.2. Time-analyses

In the second part of the MRI analyses, time-related changes in neural activity within the ROIs were examined. The three time blocks (each block consisted of nine experimental trials and nine control trials) were used. Similar to the GLM for the main analyses (see 2.8.1. Main analyses), each time block consisted of the four regressors of interest which modeled the investment phase and feedback phase of the experimental trials and the equivalent phases of the control trials. One regressor of no interest was included that consisted of the time that covered the cue to invest and the cue to select (screen 1 in Fig. 1) and the time that covered the waiting periods of the experimental trials and the control trials (screen 4 in Fig. 1). Six motion parameters were included as regressor of no interest to remove head motion. A high-pass filter (128 s) was applied to remove low-frequencies. For each time block, contrast images were created that compared the investment phase and the feedback phase of experimental trials relative to the equivalent phase of the control trials, which resulted in six contrasts (3 blocks  $\times$  2 contrast images = 6 contrasts).

Next, average contrast estimates were extracted for each of the six contrasts and for each ROI and subject using the MarsBar toolbox. Mixed-model regression analyses were performed for each ROI and each phase separately to examine the main effect of time block (3 levels) and the interaction between eigencentrality and time block on neural activity within each ROI. This resulted in five models per phase (i.e., the investment phase and feedback phase). Each model was fitted according to the same procedure, which was as follows. Level 1 of each model was time and level 2 was participant and, therefore, a random intercept for participant was included in each model. In each model, a fixed effect two-way interaction between eigencentrality and time block was included, as well as the main effects of eigencentrality and time block. In each model, the extracted ROI contrast values per time block served as outcome variable. Per phase (i.e., the investment phase and feedback phase), the analyses were corrected for multiple comparisons using a Bonferroni correction (the adjusted significance cut-off was 0.05/5 ROIs = 0.01).

## 3. Results

### 3.1. Behavioral results

#### 3.1.1. Manipulation checks

To verify that the participants experienced the partner as predominantly untrustworthy, a trust game questionnaire was administered after the game. On a scale of zero to ten (higher scores indicated more honest and more trustworthy), the average rating of the partner's honesty was 2.94 ( $SD_{\text{honesty}} = 2.54$ ) and the average rating of the partner's trustworthiness was 2.88 ( $SD_{\text{trustworthiness}} = 2.81$ ), which suggested the partner was perceived as untrustworthy. The mean investment during the game was 4.02 ( $SD = 2.8$ ). The mean reaction time of the experimental trials was 1.82 s ( $SD = 0.36$ ) and the mean reaction time of

the control trials was 1.81 s ( $SD = 0.34$ ) (no significant difference between the reaction times of both types of trials was found:  $t(48) = -0.33$ ,  $p = .74$ ). Descriptive results of the investments per trial can be found in Appendix E.

#### 3.1.2. Behavioral results

The aim of the current study was to examine if social network position was related to trust behavior and to neural activity. Mixed-model analyses showed the best model fit for model 7, which included the factor determining the partner's behavior during the previous trial, the linear main effect of time, the main effect of eigencentrality, and the interaction between eigencentrality and the linear effect of time as fixed effects, and the random slope of time as random effect (i.e., this model did not include age, a quadratic main effect of time, the interaction between eigencentrality and the quadratic effect of time, the main effects of the honesty and trustworthiness ratings, and the interaction between the honesty rating and time and between the trustworthiness rating and time because these did not contribute significantly). The results of the log-likelihood test when model 7 was compared to model 6 were:  $\chi^2(2) = 14.79$ ,  $p < .001$ . The explained variance of model 7 is 0.29 meaning that the overall model (including both the fixed and random effects parts) explains 29% of the variance in investments. The results of model 7 showed a significant, negative linear effect of time on the participants' investments, indicating that the participants' levels of trust significantly decreased over time. Furthermore, the significant, positive effect of eigencentrality on investments indicated that participants with higher eigencentrality scores showed higher investments, including a higher initial investment, compared to participants with lower eigencentrality scores (see Fig. 3). The interaction between eigencentrality and the linear effect of time was not significant, indicating there is no evidence that adolescents with more central network positions responded to the partner behavior more adaptively compared to adolescents with less central network positions. The AIC and BIC values of all models are presented in Table 1. The description of model 7 is presented in Table 2. In line with the three-block MRI approach, the behavioral analyses were repeated using a three-block approach. The results showed similar results when using the three-block behavioral approach compared to when using a trial-based behavioral approach.

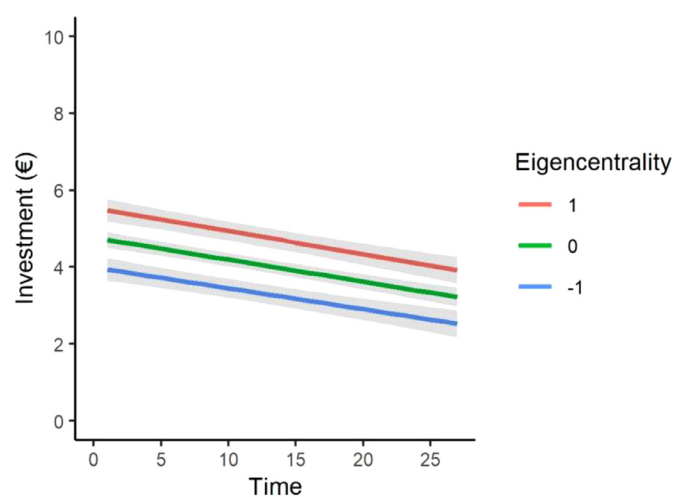


Fig. 3. A significant main effect of eigencentrality on investments. Note. Time (i.e., trials in the trust game) is displayed on the x-axis. Investment (in euros) is displayed on the y-axis. Eigencentrality scores were transformed into z-scores and analyzed as a continuous variable but, for visual purposes, only the values 1, 0, and -1 are displayed in this figure. The lines in the figure represent the model-implied time-related linear decrease in investments for different values of eigencentrality scores.



**Table 1**  
Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values of the model building procedure.

Null model		Model 1		Model 2		Model 3		Model 4		Model 5		Model 6		Model 7	
AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC
6229	6245	6229	6249	6196	6216	6174	6200	6176	6213	6176	6213	6169	6205	<b>6158</b>	<b>6205</b>

Note. The final model is printed in bold.

**Table 2**  
The results model fit 7.

	Beta coefficient	Standard deviation/ Standard error	t-value (p-value)	95% CI*	
				Lower	Upper
<i>Random effects</i>					
Intercept subjects		1.23		0.78	1.58
Slope time		0.05		0.02	0.07
Residual		2.35		2.26	2.45
<i>Fixed effects</i>					
Intercept	3.18	0.29	11.09 (< 0.001)	2.65	3.74
Partner's return	1.29	0.34	3.74 (< 0.001)	0.67	1.93
Time linear	-12.67	3.23	-3.92 (< 0.001)	-18.85	-6.76
Eigencentality	0.73	0.18	4.11 (< 0.001)	0.39	1.08
Eigencentality × time linear	-0.61	3.09	-0.2 (0.84)	-6.62	5.59

Note. Results of the fit of model 7 reporting beta coefficients, standard deviations of the random effects, standard errors of the fixed effects, t-values, p-values, and the 95% confidence intervals (CI).

\* The 95% CI for the random effect is on the standard deviation of the effect as the *lmerTest* package does not report beta coefficients and p-values for random effects. The 95% CI for the fixed effects is on the beta coefficient.

### 3.1.3. Post-hoc analyses

The results discussed above did not show evidence for a relationship between the subjective ratings of the partner and the adaptation of trust behavior, nor for a relationship between eigencentality and the adaptation of trust behavior. Post-hoc, we analyzed if eigencentality was related to the subjective ratings of the partner. First, the results showed that eigencentality scores did not correlate significantly with the honesty and trustworthiness ratings (honesty:  $r(47) = 0.06$ ,  $p = .68$ ; trustworthiness:  $r(47) = 0.03$ ,  $p = .85$ ). Also, there was no evidence that the relationship between the subjective ratings and trust behavior depended on one's social network position (honesty:  $t(49) = -0.8$ ,  $p = .43$ ; trustworthiness:  $t(49) = 1.3$ ,  $p = .2$ ). Furthermore, the results of post-hoc analyses indicated no evidence that participants with higher eigencentality scores showed a stronger decrease in their investments if they rated the partner as increasingly dishonest/untrustworthy (honesty:  $t(49) = 1.26$ ,  $p = .21$ ; trustworthiness:  $t(49) = 1.03$ ,  $p = .31$ ). Furthermore, in line with the approach of Xiang et al. (2012) and Koshelev et al. (2010) we additionally explored the effect of previous partner behavior and the effect of the participant's previous trusting behavior up to three trials back on the current investment (the first three trials were not included in these analyses). The results showed that the effect of the factor determining the partner's behavior during *trial-1* was significant ( $t(1127) = 3.97$ ,  $p < .001$ ), as well as the factor determining the partner's behavior during *trial-3* ( $t(1127) = 2.89$ ,  $p = .004$ ). The effect of the factor determining the partner's behavior during *trial-2* was not significant ( $t(1126) = 1.57$ ,  $p = .12$ ). Concerning the effects of the participant's previous trusting behavior on the current investment, only the effect of the investment during *trial-1* was significant ( $t(1175) = 3.19$ ,  $p = .001$ ), while the effect of the investment during *trial-2* ( $t(1171) = 0.5$ ,  $p = .61$ ) and during *trial-3* ( $t(1176) = 0.49$ ,  $p = .63$ ) was not significant.

## 3.2. fMRI results

### 3.2.1. Main analyses

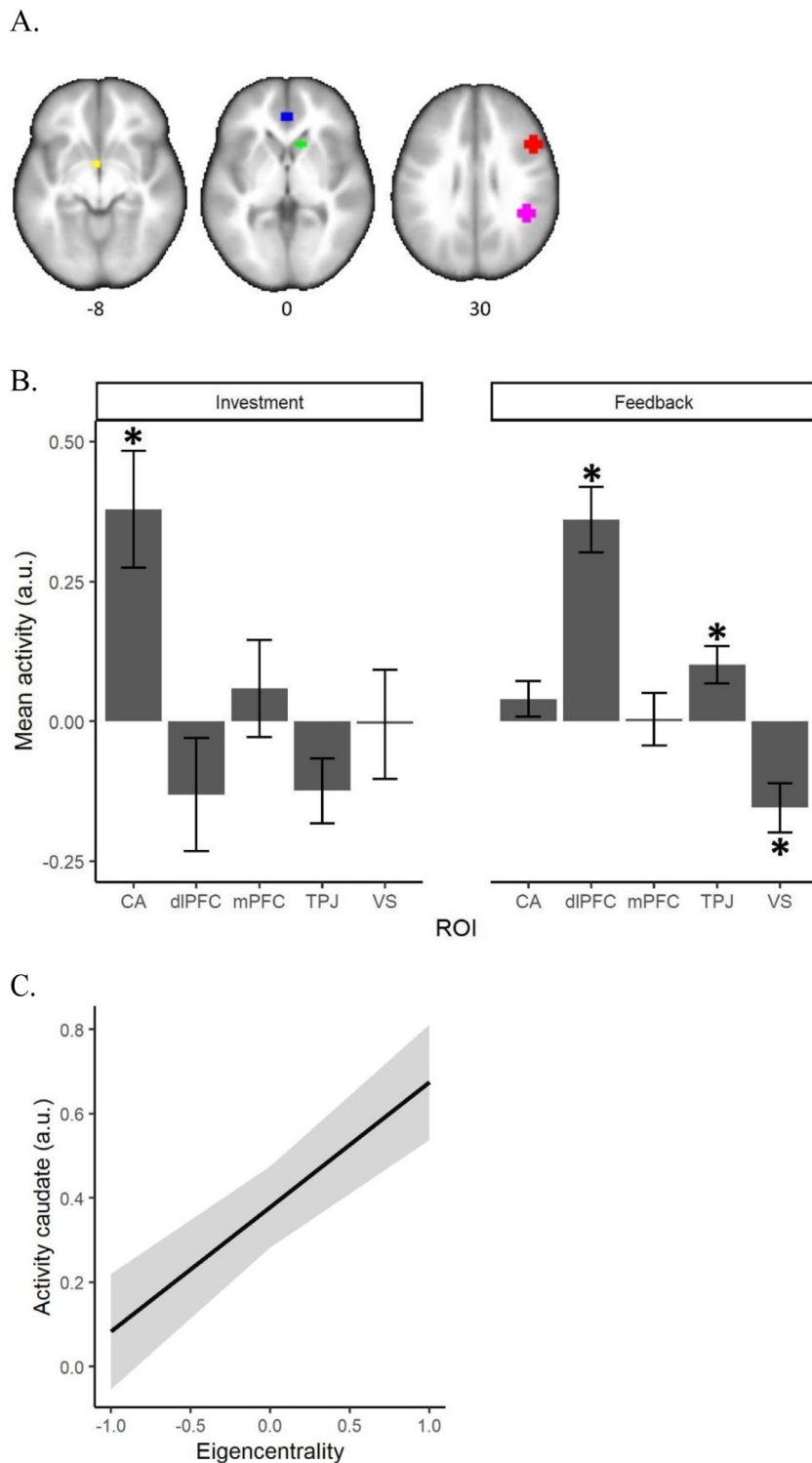
The main fMRI analyses were based on the average neural activity across all the experimental trials, relative to the control trials, sepa-

rated for the investment phase and feedback phase. We first examined trust game-related activity during the investment phase and the feedback phase of the experimental trials (compared to the equivalent phase of the control trials). Second, the relationship between social network position and neural activity was examined (Bonferroni correction was applied separately per phase and the adjusted significance cut-off was 0.05/5 ROIs = 0.01).

First, the results of the ROI analyses showed significantly increased activity in the caudate ( $t(48) = 3.62$ ,  $p < .001$ ) during the investment phase of the experimental trials when compared to the equivalent phase of the control trials (see Fig. 4.B and Appendix F). During the feedback phase of the experimental trials (relative to the equivalent phase of the control trials) significantly increased activity was observed within the dlPFC ( $t(48) = 6.12$ ,  $p < .001$ ) and the TPJ ( $t(48) = 3.04$ ,  $p = .004$ ), while the ventral striatum ( $t(48) = -3.53$ ,  $p < .001$ ) showed significantly decreased activity (see Fig. 4.B and Appendix F). Activity in the mPFC was not significantly increased or decreased during any of the two phases (see Appendix F). These results indicate that during the investment phase, there is evidence for increased activity in the caudate and, during the feedback phase, there is support for increased activity in the dlPFC and the TPJ, while the ventral striatum shows decreased activity.

Second, regression analyses showed that during the investment phase of the experimental trials (relative to the equivalent phase of the control trials), eigencentality was significantly positively associated with activity in the caudate ( $t(49) = 3.05$ ,  $p = .004$ , beta coefficient = 0.3, standard error = 0.1) but not significantly associated with activity in other ROIs (see Fig. 4.C and Appendix F). Furthermore, eigencentality was not significantly associated with activity within any of the ROIs during the feedback phase of the experimental trials (relative to the equivalent phase of the control trials, see Appendix F). These results indicate that the higher someone's eigencentality score, i.e., the more central one's position within a friendship network, the more caudate activity someone showed during the investment phase of the task.

Additional whole-brain analyses were conducted. First, we explored trust game-related activity outside the ROIs. The results of the whole-brain analyses were in line with the ROI results. During the investment phase, the whole-brain results revealed activity within the bilateral cau-



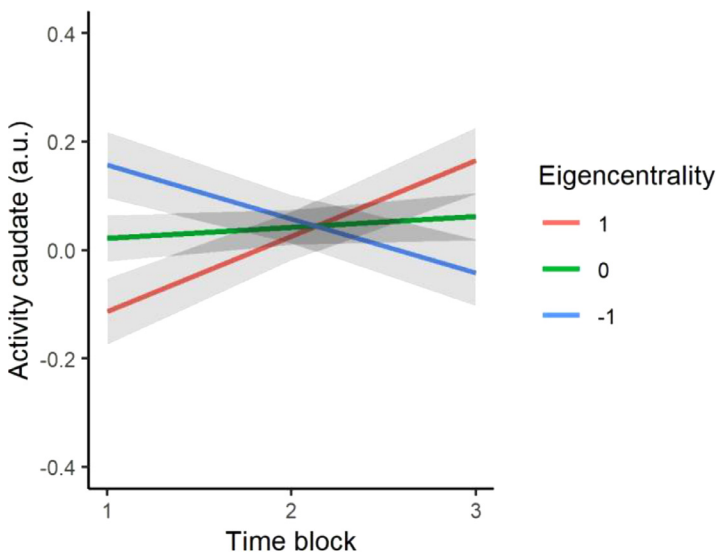
**Fig. 4.** A: Regions of interest. B: The results of the analyses on trust game-related activity within the ROIs. C: A positive association between eigencentality and caudate activity during the investment phase. Note. Fig. 4.A: Yellow = ventral striatum, blue = mPFC, green = caudate, red = dlPFC, pink = TPJ. The numbers in the figure represent z-coordinates. Fig. 4.B: ROIs are displayed on the x-axis. CA = caudate, dlPFC = dorsolateral prefrontal cortex, mPFC = medial prefrontal cortex, TPJ = temporoparietal junction, VS = ventral striatum. Mean activity (in arbitrary units) is displayed on the y-axis. Error bars depict the standard error of the mean. Left panel: Signal changes in the ROIs during the investment phase. The asterisk indicates significant activity changes in the caudate. Right panel: Signal changes in the ROIs during the feedback phase. The asterisk indicates significant activity changes in the dlPFC, TPJ, and ventral striatum. Fig. 4.C: Eigencentality (in z-scores) is displayed on the x-axis. Caudate activity (in arbitrary units) is displayed on the y-axis. The line in the figure represents the model-implied linear increase in caudate activity when eigencentality scores increase.

date (extending into the ventral striatum), the dorsal medial prefrontal cortex, right precuneus, and bilateral occipital areas (see Appendix G). During the feedback phase, increased activity was observed within the bilateral occipital lobe, the dorsal medial prefrontal cortex, dorsal lateral prefrontal cortex, bilateral caudate, bilateral insula, bilateral superior parietal gyri, and bilateral angular gyri (extending into the TPJ, see Appendix G). Second, the results of the whole-brain analyses to examine associations between eigencentality and neural activity outside the

ROIs indicated no significant associations during both the investment phase and the feedback phase.

### 3.2.2. Time-analyses

The three blocks of the trust game (each block consisted of nine experimental trials and nine control trials) were used in the analyses probing time-related changes in neural activity within the ROIs. Multilevel analyses were performed for each ROI and each phase separately to ex-



**Fig. 5.** A significant interaction between eigencentrality and time block on the activity within the caudate during the feedback phase. Note. Each time block consisted of nine experimental trials and nine control trials and are displayed on the x-axis. Caudate activity (in arbitrary units) is displayed on the y-axis. Eigencentrality scores were transformed into z-scores and analyzed as a continuous variable but, for visual purposes, only the values 1, 0, and -1 are displayed in this figure. The lines in the figure represent the model-implied time-related linear increase in caudate activity for different values of eigencentrality scores.

amine the effect of time block and the interaction between eigencentrality and time block on neural activity within each ROI (Bonferroni correction was applied per phase and the adjusted significance cut-off was 0.05/5 ROIs = 0.01).

The results of the ROI analyses showed no significant main effect of time block and no significant interaction between eigencentrality and time block within any of the ROIs during the investment phase (see Appendix H). During the feedback phase, the ROI results showed a significant interaction between eigencentrality and time block within the caudate ( $t(98) = 4.03, p < .001$ , beta coefficient = 1.18, std. error = 0.29, see Fig. 5). There was no significant main effect of time block and no significant interaction between eigencentrality and time block on neural activity in any of the other ROIs during the feedback phase (see Appendix H). In conclusion, only during the feedback phase, results indicated that the higher a person's eigencentrality, the stronger the increase of caudate activity over time.

#### 4. Discussion

In the current study, the association between embeddedness in a social network, trust behavior, and neural activity was examined in young adolescents. We used social network analysis to compute the social network position of each individual in their secondary school classroom. In this way, we captured the complicated web of direct and indirect friendships relationships in daily life, and we did not rely solely on self-report or on the assessment of dyadic relationships. The results showed that more central social network positions were significantly associated with higher levels of initial trust behavior, but no evidence was found for a significant relationship between eigencentrality and the change in investments. Furthermore, the neuroimaging findings showed that neural activity patterns during the game were in line with findings of previous studies that used the trust game (Bellucci et al., 2017; Delgado et al., 2005; Fett et al., 2014; Lemmers-Jansen et al., 2019, 2017; Van den Bos et al., 2011). More importantly, eigencentrality was positively associated with caudate activity when making an investment. Additionally, the results of the time-analyses showed a positive interaction between eigencentrality and time block on caudate activity during the feedback phase.

The results of the behavioral analyses showed a significant positive association between eigencentrality and investments, indicating that the more central the social network position is, the higher the investment at each trial was. In line with our hypotheses, this means that adolescents with more central network positions showed higher levels of initial

trust behavior than adolescents with less central positions. This suggests that the extent of embeddedness within a social network that someone is familiar with, in this case the embeddedness of adolescents within their classroom, may be related to the extent of initial trust behavior in social interactions with unknown others. In line with this, using another setup, Welch et al. (2007) showed that the degree of connectedness within a social network and the degree of trust in acquaintances are both positively associated with the degree of trust in strangers. An explanation for the positive association between eigencentrality and initial trust behavior may be that more central adolescents have higher levels of self-esteem and social skills due to their position in the network. Research has shown that social relationships are positively related to self-esteem through receiving positive appraisal from peers (Harris and Orth, 2020), and that these relationships also enable one to develop socio-cognitive abilities (e.g., prosocial behavior) (Oberle et al., 2010; Padilla-Walker et al., 2015; Wentzel et al., 2004; Wölfer et al., 2012). So, a central position within a network of peers may provide feelings of self-esteem and increased developed socio-cognitive abilities, which may give someone feelings of confidence to take the risk to show initial trust during social interactions with unfamiliar others outside one's network. In contrast to our findings, Van den Bos et al. (2018) did not find a relationship between eigencentrality and initial trust behavior. This might be explained by the differences in the trust game design that was used. In the trust game used by Van den Bos et al. (2018), the participants were informed that they would play each trial with a different partner, while in our design the participants were aware that they would interact with the same partner for the entire interaction. This means the participants in the current study knew they were going to build a social relationship with the partner, and this may have had a stimulating effect on the initial trust that was shown. However, when interpreting the current findings, it is important to note that the effects that were found can be bidirectional, where more central network positions lead to more initial and average trust behavior but where more trust behavior may also lead to more central network positions. Also, we should note that the results of the final model showed that for every standard deviation increase in eigencentrality (which were analyzed as z-scores), the initial investment would only increase by €0.74 (on a scale from €0 to €10), which suggests this is a small effect.

The results showed that, on average, adolescents decreased their investments over time, indicating they noticed the partner's predominantly untrustworthy behavior. In contrast to our hypothesis, we did not find evidence for a relationship between eigencentrality and the decrease in trust behavior during the task. We hypothesized that, com-

pared to adolescents with less central network positions, adolescents with more central network positions would respond to the untrustworthy behavior more adaptively leading to a greater decrease in their trust behavior. The absence of a relationship between eigencentality and the adaptation of trust behavior is remarkable and shows a clear discrepancy with the finding that adolescents with higher eigencentality scores showed a stronger increase of caudate activity throughout the game than adolescents with lower eigencentality scores. These results show the additional value of functional MRI scanning as these results tentatively show the involvement of cognitive processes and brain activity that are not indicated by behavioral analyses alone.

Interestingly, on a neural level, the ROI results showed a positive association between eigencentality and caudate activity during the investment phase. Given the novelty of this study aim, we did not have hypotheses about the relationship between eigencentality and brain activity within the ROIs. A post-hoc suggestion for the positive association between eigencentality and caudate activity may be related to the untrustworthy nature of the partner, which may have been experienced as unexpected. Previous trust game studies suggested that the caudate is involved in feedback learning and the anticipation and the reception of rewards, in addition to the processing of unexpected outcomes (Delgado et al., 2005; Fouragnan et al., 2013; King-Casas et al., 2005; Smith-Collins et al., 2013). We speculate that the increased caudate activity in adolescents with more central network positions might indicate that the partner's untrustworthy behavior may have been experienced as a greater violation of their expectations compared to adolescents with less central positions. In line, the results showed that the participants with more central network positions showed higher levels of initial trust behavior themselves, and this may tentatively suggest that the untrustworthy nature of the partner may have been more unexpected for them than it was for less central adolescents, hence, the increased caudate activity. Furthermore, previous work has suggested that caudate activity and related cognitive processes are involved in both the investment phase as well as the feedback phase of the game (King-Casas et al., 2005). In line, the results of the time-analyses at the neural level showed a positive interaction between eigencentality and time on caudate activity during the feedback phase of the game. These results indicate that the higher a person's eigencentality, the stronger the increase of caudate activity over time. This might tentatively suggest a continuation of expectancy violations regarding the partner's behavior, perhaps suggesting that during the game, the adolescents with more central positions did not update their expectations of the partner's behavior as much as adolescents with less central positions. Together, the current results indicate that, compared to adolescents with less central positions, adolescents with more central positions approach a social interaction with more trust and show more caudate activity during this interaction, possibly indicating the processing of unexpected behavior during social interactions. However, this interpretation is speculative and requires further research.

The unique contribution of the current study is that we related friendships in social networks in daily life to trust behavior and underlying neural activity. As discussed above, the results showed a positive association between eigencentality and caudate activity. However, the results of the current study did not show evidence for an association between eigencentality and activity in any other ROIs apart from the caudate. Also, the results of the whole-brain analyses did not indicate support of significant associations between eigencentality and neural activity during both the investment and feedback phase. There are only a few studies in which data from social networks in daily life are related to neural activity (see, for example, Zerubavel et al. (2015) and Parkinson et al. (2017)). Together, the current findings and the findings of previous studies give a first indication that there are differential associations between features of social networks and neural correlates of social cognition, but future research is required to replicate these findings. Furthermore, the results showed that the task itself elicited neural activity patterns in line with findings of previous trust game

studies (Bellucci et al., 2017; Delgado et al., 2005; Fett et al., 2014; Lemmers-Jansen et al., 2019, 2017; Van den Bos et al., 2011). The trust game-related whole-brain results showed increased activity in the left caudate, precuneus, and the dorsal medial prefrontal cortex during the investment phase, and increased activity in the dorsal medial prefrontal cortex, bilateral superior parietal gyri, bilateral angular gyri, and bilateral caudate during the feedback phase. The trust game-related region of interest results showed increased activity in the caudate during the investment phase, and increased activity in the dlPFC and the TPJ during the feedback phase. In contrast, the ventral striatum showed decreased activity during the feedback phase. Interestingly, activity in the mPFC was not significantly increased or decreased during both phases of the game. Although some studies showed significant mPFC activity during the trust game (Krueger and Meyer-Lindenberg, 2019), meta-analytic results (Bellucci et al., 2017) did not show support for the mPFC being significantly activated during the trust game.

A number of considerations should be kept in mind when interpreting the current results. First, the participants in the current study were selected from schools that participated in the #SOCONNeCT project. The Dutch educational system is divided into three educational tracks based on academic performance. The schools that were included in the #SOCONNeCT project were part of the two higher educational tracks and this may have led to a selection bias which limits the generalizability of the results to relatively well-educated adolescents. In addition, within this pool of participants in the #SOCONNeCT project, there was a further selection of participants who were willing to participate in the fMRI study. This set-up also means that it may have occurred that the participants of the current study talked to each other about the study at school as there were no explicit instructions they were not allowed to do so. Second, the social network positions were examined in the specific context of the classroom. This means that we did not capture the adolescent's entire social life and thus could only examine associations between social network positions inside the classroom environment, trust behavior, and brain activity. Nevertheless, we believe the network positions that were used in the current study are a good reflection of the adolescent's social embeddedness because the classroom is an important environment where young adolescents spend much time. Third, on average, MRI scanning took place 14.5 weeks after the administration of the social network questionnaire which means that some changes might have taken place in the composition of the social network. Furthermore, the sample size of the current study was relatively small to detect individual differences related to social network positions and, furthermore, we have only focused on friendship relationships. Future studies may examine differences in the interplay between social embeddedness, social behavior, and neural activity for a broader set of social network settings and different types of social relationships in bigger samples. Another limitation is that participants were aware that the partner in the trust game was a computer counterpart (displayed as a cartoon animation), which may have made the social interaction less realistic (Johnson and Mislin, 2011). Nevertheless, the cartoon animation was considered appropriate for this age group given that adolescents are accustomed to interacting with virtual characters in video games (Adachi and Willoughby, 2013), and because computer counterparts elicit similar (but weaker) responses compared to human counterparts (Decety et al., 2004; Kircher et al., 2009; Rilling et al., 2004; Van 't Wout et al., 2006). The advantage of informing participants that they were playing with computer counterparts is that everyone had a similar understanding of their confederate. After the trust game was finished, the participants reported that they experienced the cartoon animation as dishonest and untrustworthy. Future research could benefit from administering more questions tapping into how participants perceive a cartoon animation as partner and the motivations for their investment choices. Fifth, the current results are correlational findings and do not tell us whether the network position is a cause or a consequence (or both) of the increased initial trust behavior and the caudate activity. Moreover, the control trials of the trust game did not include (non-social)

risk-taking and reward processes. Therefore, the findings of the current study may also be influenced by risk-taking processes based on monetary rewards. Last, a low number of trials per block were used in the analyses testing the effects of time. However, the trust game comprised a total of 27 experimental and 27 control trials and was designed in a similar fashion as the task design employed in previous studies, which indicated significant neural activity during the game (Fett et al., 2014; Lemmers-Jansen et al., 2019).

In conclusion, the current study contributes to the literature by incorporating indicators of daily life social relationships when examining socio-cognitive behavior and the related cognitive processes in adolescents. Importantly, we found eigencentality to be positively associated with initial trust behavior and with caudate activity during both phases of the trust game, while no evidence was found for an association between eigencentality and the adaptation of trust behavior. We tentatively suggest that, at a young age when social life is drastically changing and growing more complex, human behavior and the brain are affected by the social networks around us and vice versa.

## 5. Credit author statement

Conceptualization: H.S., M.B., and L.K.; methodology: H.S., M.B., and B.B.; software: H.S., M.B., M.H., R.W.; formal analysis: H.S., M.B.; investigation: H.S., M.B., M.H., R.W., N.L.; data curation: H.S., M.B., M.H., N.L., and L.K.; writing—original draft preparation: H.S. and M.B.; writing—review and editing: M.H., R.W., N.L., B.B., and L.K.; supervision: M.B., L.K.; project administration: H.S., M.B., M.H., N.L., and L.K.; funding acquisition: L.K. All authors have read and agreed to the published version of the manuscript.

## Declaration of Competing Interest

None.

## Data availability

Data will be made available on request.

## Ethics statement

The study was approved by the Scientific and Ethical Review Board of the Faculty of Behavioral and Movement Sciences of the Vrije Universiteit Amsterdam. All participants and parent(s)/caregiver(s) signed informed consent.

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## Appendix A

After the trust game was completed, the participants were administered a questionnaire about the trust game outside the scanner. The participants rated the partner on a scale of zero to ten on honesty and trustworthiness. These questions were administered in Dutch. The English translation can be found in brackets:

- 1) Vond je de andere speler eerlijk? (Did you think the other player was honest?)
- 2) Vond je de ander speler betrouwbaar? (Did you think the other player was trustworthy?)

## Appendix B

**Table B.1**

Number of participants and pupils per class.

Class	Number of participants per class	Number of pupils per class	Participation per class (in percentages)
1	24	28	0.86
2	24	28	0.86
3	25	29	0.86
4	24	26	0.88
5	25	27	0.93
6	22	24	0.92
7	23	26	0.88
8	21	23	0.91
9	25	30	0.83
10	27	30	0.9
11	27	30	0.9
12	29	32	0.91
13	16	20	0.8
14	22	28	0.79

## Appendix C

Multi-level analyses were used to examine the change of trust behavior throughout the game. Mixed models allow the intercept (i.e., initial trust behavior) and the slope (i.e., change in trust behavior) to be fixed or random. A fixed intercept models the mean starting point of the investments, while a random intercept models the individual differences in starting points. Likewise, a fixed slope models the mean change in investments over trials and a random slope models individual differences in the change in investments. In our design, there are repeated measurements of the same participant over trials. Therefore, the first level of the model is the level of time (i.e., trials) and the second level is participant. Below are the equations of the multi-level model, separated per level (these equations and their explanations are based on Bauer and Curran (2020) and Curran et al. (2012)).

### Level 1

$$y_{ij} = \beta_{0j} + \beta_{1j}x_{ij} + r_{ij}$$

### Level 2

$$\beta_{0j} = \gamma_{00} + u_{0j}$$

$$\beta_{1j} = \gamma_{10} + u_{1j}$$

### Reduced form:

$$y_{ij} = (\gamma_{00} + \gamma_{10}x_{ij}) + (u_{0j} + u_{1j}x_{ij} + r_{ij})$$

The explanation of the symbols, level 1:

$y_{ij}$  indicates the investment at trial  $i$  for participant  $j$ .

$\beta_{0j}$  indicates the intercept of participant's  $j$  trajectory (i.e., the investment during the first trial).

$\beta_{1j}$  indicates the slope in investments per unit of trial for participant  $j$ 's trajectory (i.e., the rate of change in investments).

$x_{ij}$  indicates the value of the predictor trial at observation point  $i$  for participant  $j$ .

$r_{ij}$  indicates the residual between the observed investment and the investment that is expected based on the participant's trajectory at trial  $i$  for participant  $j$ .

The explanation of the symbols, level 2:

$\beta_{0j}$  indicates the intercept of participant's  $j$  trajectory (i.e., the investment during the first trial).

$\gamma_{00}$  indicates the mean of the individual intercepts (i.e., the investment during the first trial) pooling over all participants.

$u_{0j}$  indicates the difference between the participant’s intercept (i.e., the investment during the first trial) and the mean intercept (i.e., the mean investment during the first trial).

$\beta_{1j}$  indicates the slope in investments per unit of trial for participant  $j$ ’s trajectory (i.e., the rate of change in investments).

$\gamma_{10}$  indicates the mean of the individual slopes (i.e., the mean rate of change in investments) pooling over all participants.

$u_{1j}$  indicates the difference between the participant’s slope (i.e., the rate of change in investments) and the mean slope (i.e., the mean rate of change in investments).

**Appendix D**

Following Hanssen et al. (2021), we examined the stability of the beta-estimates per trial to verify whether a trialwise approach was appropriate for the current dataset. The results indicated, similar to Hanssen et al. (2021), unreliable estimates over trials which were unsuitable for a trialwise approach. The method of these analyses is explained below.

Based on Mumford et al. (2012), we conducted a trialwise approach in which a separate GLM per trial was created. Specifically, a separate GLM was created per trial and per phase (i.e., the investment phase and feedback phase) comprising a regressor modeling the specific trial and the specific phase (e.g., the investment phase for trial 1), and a regressor of no-interest modeling the other phase of the specific trial (e.g., the feedback phase for trial 1) and both phases of all other trials (e.g., the investment phase and the feedback phase for trial 2 through 27). Additionally, the six realignment parameters were included to remove effects of motion and a high-pass filter was included to remove low frequencies not of interest (cut-off 128 s). This resulted in 27 models for the investment phase of the experimental trials, 27 models for the investment phase of the control trials, 27 models for the feedback phase of the experimental trials, and 27 models for the feedback phase of the control trials. Next, for each phase and trial, we extracted the average beta-estimate within each ROI and, per phase, contrasted the beta-estimate of the experimental trial to the respective control trial. Thus, for example, the beta-estimate within each ROI of the investment phase of the first experimental trial was contrasted to the investment phase of the first control trial. This resulted in a contrast value for each ROI and each participant per trial for the investment phase (experimental trial–control trial) and for the feedback phase (experimental trial–control trial).

**Appendix E**

**Table E.1**  
Mean (M) and standard deviation (SD) of the investments per trial.

Trial number	$M_{investment}$	$SD_{investment}$
1	4.94	2.32
2	4.92	2.58
3	4.88	2.61
4	5.39	2.93
5	4.12	2.24
6	4.51	2.78
7	4.37	2.6
8	4	2.54
9	3.78	3.04
10	4.2	2.92

(continued on next page)

**Table E.1 (continued)**

Trial number	$M_{investment}$	$SD_{investment}$
11	3.98	2.63
12	3.76	2.82
13	3.9	2.97
14	4.35	3.17
15	4.22	3.22
16	3.71	3.12
17	3.84	2.96
18	3.39	2.86
19	3.84	2.58
20	3.67	2.44
21	4.12	2.76
22	3.61	2.64
23	3.22	2.5
24	3.45	2.69
25	3.61	2.83
26	3.31	3.12
27	3.47	2.85

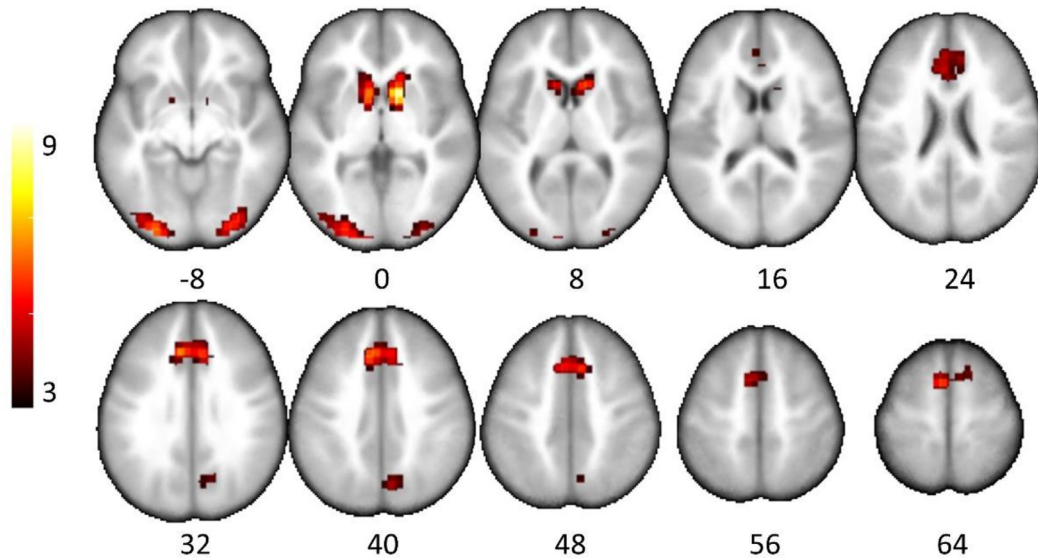
**Appendix F**

**Table F.1**  
The results of the ROI main analyses.

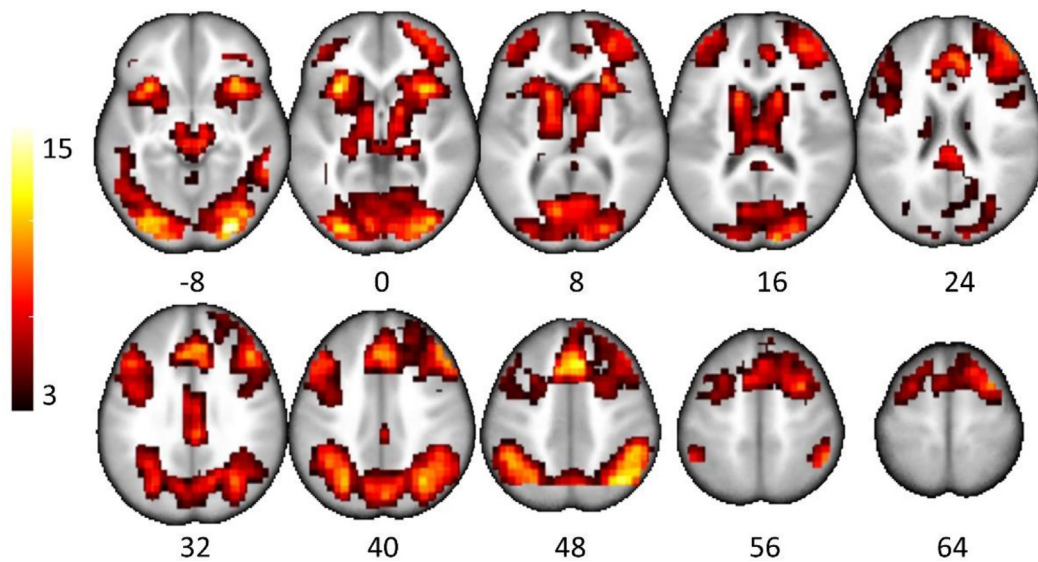
ROI	t-value (p-value)
<b>Investment phase, trust game-related activity</b>	
Ventral striatum	-0.06 (.96)
Caudate	3.62 (< .001)*
TPJ	-2.14 (.04)
mPFC	0.68 (.5)
dIPFC	-1.3 (.2)
<b>Feedback phase, trust game-related activity</b>	
Ventral striatum	-3.53 (< .001)*
Caudate	1.24 (.22)
TPJ	3.04 (.004)*
mPFC	0.08 (.94)
dIPFC	6.17 (< .001)*
<b>Investment phase, relationship eigencentality</b>	
Ventral striatum	1.42 (.16)
Caudate	3.05 (.004)*
TPJ	0.51 (.64)
mPFC	0.41 (.68)
dIPFC	1.17 (.25)
<b>Feedback phase, relationship eigencentality</b>	
Ventral striatum	1.20 (.24)
Caudate	-0.57 (.56)
TPJ	-1.53 (.13)
mPFC	-0.04 (.97)
dIPFC	0.22 (.83)

Note. For all analyses, the investment phase and feedback phase of the experimental trials were contrasted with the equivalent phase of the control trials. The first two parts of the table show the results of a one-sample t-test per phase and per ROI to examine trust game-related activity. The asterisk indicates significance at the Bonferroni corrected significance cut-off of 0.01 (corrected per phase). The last two parts of the table indicate the results of the regression analyses per phase and per ROI to examine the relationship between social network position and neural activity. The asterisk indicates significance at the Bonferroni corrected significance cut-off of 0.01 (corrected per phase).

Appendix G



**Fig. G.1.** *Whole-brain analyses: Investment phase.* Note. The results of the whole-brain analyses contrasting the investment phase of the experimental trials versus the equivalent phase of the control trials (cluster defining threshold of  $p < .001$ , cluster probability of  $p < .05$ , family-wise error corrected). Activity changes are overlaid on an average anatomical brain obtained with the CerebroMatic toolbox, matched for the age and sex of the current sample. The numbers in the figure represent z-coordinates. The color bar indicates  $t$ -values.



**Fig. G.2.** *Whole-brain analyses: Feedback phase.* Note. The results of the whole-brain analyses contrasting the feedback phase of the experimental trials versus the equivalent phase of the control trials (cluster defining threshold of  $p < .001$ , cluster probability of  $p < .05$ , family-wise error corrected). Activity changes are overlaid on an average anatomical brain obtained with the CerebroMatic toolbox, matched for the age and sex of the current sample. The numbers in the figure represent z-coordinates. The color bar indicates  $t$ -values.

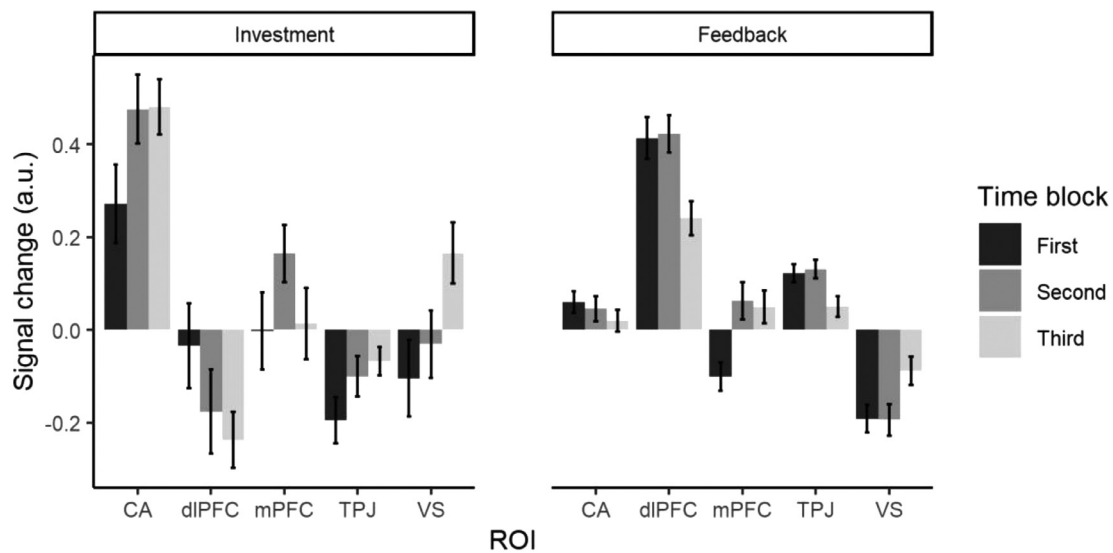
**Table G.1**

The results of the whole-brain analyses of the investment phase and the feedback phase of the experimental trials (versus the equivalent phase of the control trials).

ROI	MNI coordinates			Z-value	Cluster size
	X	Y	Z		
<b>Investment phase</b>					
R caudate	12	12	0	6.7	185
L caudate	-9	18	6	5.82	142
L middle occipital gyrus	-27	-93	-3	5.55	256
L superior frontal gyrus	-9	30	33	5.44	652
R inferior occipital gyrus	36	-87	-9	4.94	152
R precuneus	9	-69	39	4.04	81
<b>Feedback phase</b>					
R inferior occipital gyrus	30	-87	-9	Inf	19790

*Note.* The table shows the significant clusters of voxels. Peak voxels are represented by MNI coordinates (cluster defining threshold of  $p < .001$ , cluster probability of  $p < .05$ , family-wise error corrected). L = left. R = right.

**Appendix H**



**Fig. H.1.** The results of ROI time-analyses. *Note.* ROIs are displayed on the x-axis. CA = caudate, dlPFC = dorsolateral prefrontal cortex, mPFC = medial prefrontal cortex, TPJ = temporoparietal junction, VS = ventral striatum. Mean activity (in arbitrary units) is displayed on the y-axis. Error bars depict the standard error of the mean. Left panel: Signal changes in the ROIs during the investment phase of the first time block (black), during the investment phase of the second time block (dark gray), and during the investment phase of the third time block (light gray), all relative to the equivalent phase of the control trials. Right panel: Signal changes in the ROIs during the feedback phase of the first time block (black), during the feedback phase of the second time block (dark gray), and during the feedback phase of the third time block (light gray), all relative to the equivalent phase of the control trials.



**Table H.1**  
The results of the ROI time-analyses.

ROI	Main effect time block <i>t</i> -value ( <i>p</i> -value)	Main effect eigencentality <i>t</i> -value ( <i>p</i> -value)	Interaction eigencentality and time block <i>t</i> -value ( <i>p</i> -value)
<b>Investment phase</b>			
Ventral striatum	-1.37 (.17)	1.8 (.08)	-0.26 (.8)
Caudate	-1.16 (.25)	3.42 (.001)*	1.7 (.09)
TPJ	-1.22 (.23)	0.53 (.6)	1.33 (.19)
mPFC	-0.08 (.94)	0.17 (.87)	0.09 (.93)
dIPFC	0.92 (.36)	1.29 (.2)	1.09 (.28)
<b>Feedback phase</b>			
Ventral striatum	-1.36 (.18)	1.36 (.18)	-1.43 (.15)
Caudate	0.68 (.5)	-0.5 (.62)	4.03 (< .001)*
TPJ	1.67 (.1)	-1.56 (.12)	1.46 (.15)
mPFC	-1.64 (.1)	-0.01 (.99)	0.11 (.91)
dIPFC	1.77 (.08)	0.19 (.85)	0.57 (.57)

*Note.* For all analyses, the investment phase and feedback phase of the experimental trials were contrasted with the equivalent phase of the control trials. A mixed-model regression analysis was performed for each phase and for each ROI separately. The asterisk indicates significance at the Bonferroni corrected significance cut-off of 0.01 (corrected per phase).

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