Neural Correlates of Social Decision Making and Relationships

A Developmental Perspective

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Social competence, e.g., effective functioning in interpersonal relationships, plays an important role in well being during one's lifetime. Social skills, such as perspective taking and understanding intentionality, develop during childhood and adolescence. We hypothesize that these behavioral changes result from protracted development of brain regions involved in social interactions. We give a brief outline of behavioral and neuroimaging studies on fairness, trust, and reciprocity considerations in social decision making and the development of these considerations. We propose that a better understanding of the mechanisms underlying the developing brain and sociocognitive skills is important for understanding the development of social relationships.

Key words: **social interactions; fairness; trust; development; adolescence; friendship**

Introduction

Social competence is one of the most important determinants of healthy functioning.[1] In broad terms social competence refers to effectiveness in social interactions and functioning in relationships.[2] More specifically social competence has been defined as having social and self-regulatory skills, high sociometric status, and positive relationships with others. Positive social interactions as well as relationships, such as supportive friendships, are known to be related to psychological well being and psychosocial adjustment,[3] fluctuations in daily well being,[4] decreased cancer mortality,[5] and decreased cortisol under stress[6] and are known to have buffering effects on functional decline in old age,[7] health complaints, and depression.[8] Given the significance of social interactions on healthy functioning in many domains, it is essential that we understand the mechanisms behind these associations.

Recent advances in the neuroscience field provide us with opportunities to examine neural mechanisms related to behavior within social interactions. These studies focus on various aspects of social interactions that are important for establishing and maintaining positive and cooperative social relationships, including fairness, trust, and reciprocity. These studies have demonstrated the involvement of several brain regions, such as the medial prefrontal cortex (MPFC), the anterior cingulate cortex (ACC), and the insula, which are important parts of a broader brain network involved in social cognition; these brain regions will be introduced below in more detail.

The brain regions that underlie social cognition are known to change during development.

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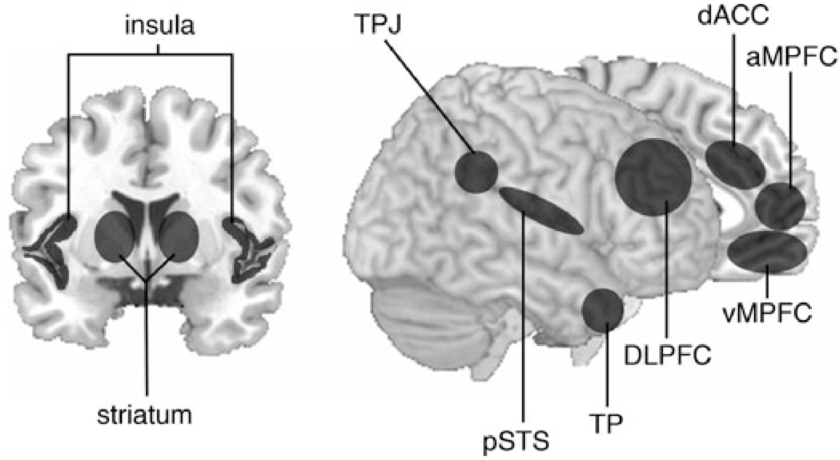

Figure 1. Brain areas involved in social cognition: insula, striatum, temporal parietal junction (TPJ), posterior superior temporal sulcus (pSTS), temporal poles (TP), dorsolateral prefrontal cortex (DLPFC), ventral medial prefrontal cortex (vMPFC), anterior medial prefrontal cortex (aMPFC), and dorsal anterior cingulate cortex (dACC).

It is well established that socially relevant neural functions develop slowly during childhood and adolescents[9] and the most complex forms of social competence are not in place until early adulthood. It is important to understand how the ability to function in basic social interactions occurs as well as the neural mechanisms that support social understanding in childhood and adolescence. The working hypothesis presented here is that the development and reorganization of neural networks during childhood and adolescence underlie developmental changes in social decision making. We will devote special attention to one aspect of social interaction, which is the consideration of intentions of others, and we hypothesize that this ability underlies many developmental changes in social interactions. Specifically we hypothesize that those brain regions that are important in considering intent show a protracted developmental trajectory, which results in developmental differences in the way children and adults operate during social interactions. In this chapter we will outline behavioral and neuroimaging research on the development of social decision making and we will discuss these studies vis-a-vis our hypothesis suggesting that changes in social-cognitive skills are related to the developing brain and underlie the development of social relationships.

Brain Areas Implicated in Social Cognition

Over the past decade the neural correlates of social cognition have been investigated using a wide variety of social paradigms in combination with neuroimaging techniques. Initially these studies focused on tasks involving "mentalizing" or having a theory-of-mind (ToM), i.e., the ability to infer the mental states or intentions of others.[10–12] In general these studies have shown activation of a network of regions, including the MPFC, the posterior cingulate, temporal-parietal junction/superior temporal sulcus (STS), and the temporal poles (see Fig. 1).[13] Among these regions, the MPFC is most reliably activated across different ToM and social perspective-taking tasks as well as in experiments making use of game-theoretical paradigms to study social interaction. The MPFC can be subdivided into three separate regions: the dorsal, anterior/rostral, and ventral MPFC.[14] The anterior MPFC (aMPFC) is thought to be important for mentalizing or integrating the perspectives of self and other,[15] whereas the dorsal MPFC has often been implicated in action and conflict monitoring[16,17] and the ventral MPFC is associated with outcome monitoring and affective learning.[18,19]

In addition to considering the intentions of others, social interactions often require the ability to take into account social norms.[20] In particular the anterior insula (see Fig. 1), often associated with pain and disgust, seems to have a general role in signaling norm violations in social interactions[20,21] as well as in nonsocial settings.[22] Furthermore, areas associated with control or regulatory processes, including the dorsal ACC and the dorsolateral prefrontal cortex (DLPFC), have been consistently engaged when individuals make decisions in which there is conflict between social norms and personal interest[23,24] or when individuals make decisions that may be counter to their own response tendencies.[25,26] It is suggested that, in these cases when there is competiton between social motivations and personal interest, the higher level regulatory processes have a role in modulating the interactions of these lower level biases/processes.[27,28]

Development of the Social Brain

Recently, structural neuroimaging research has demonstrated that there are significant developmental changes in the brain that occur until late adolescence or young adulthood.[29,30] The results of these studies indicate that several cortical regions, including those associated with social cognition, undergo substantial changes in gray and white matter. Furthermore, these cortical regions have different developmental trajectories.[31] As a result, the different areas of the social brain network seem to have different structural developmental patterns.

Although there have been numerous studies that have demonstrated changes in neural mechanisms associated with cognitive control,[9,32,33] only a handful of studies have investigated functional changes in brain processing of social activities during adolescence. In these studies, differences in brain activity between adults and adolescents have been examined using tasks that required mentalizing[34,35] or self-referential thought.[36,37] Although these studies show that the same network of areas is active for adults and adolescents, they have also demonstrated changes in the relative roles of these brain regions with age. In general these studies indicate a shift in dominance from anterior areas, including the aMPFC, to more posterior areas, such as STS and temporal parietal junction (TPJ).[38]

Drawing on these prior studies, our line of research has been influenced by the assumption that brain regions that are important for successful social interaction, including aMPFC, TPJ, the insula, and DLPFC/ACC, undergo changes in function and organization throughout childhood and adolescence. We have started to investigate these changes using straightforward experimental paradigms related to fairness, trust, and reciprocity. Below, we will elaborate on these initial findings and how these may inform our hypotheses regarding changes in social interactions during childhood and adolescence.

A promising way to study intention considerations in relationships is by making use of social interaction paradigms. In cooperative social interactions, which consist of exchange of favors over time, fairness, trust, and reciprocity emerge as significant concepts that play a role in social interactions and also in the formation of relationships. Fairness helps to regulate the balance of self and other regarding interests in interactions with others. Trust is required because cooperative exchanges are often separated in time. Finally, reciprocity, or the repayment of what others have provided us, is important for the maintenance of relationships; if favors are not returned, relationships may be short lived.[39] Over the last several decades, simple economic exchange games have been successfully used to examine individual functioning in social interactions. These exchange games enable us to simulate interactions where individuals have to contrast their self-interest with interests of another person and to understand the intentions of others in making a decision.

Fairness

In prior research, economists and social psychologists have made use of a two-person interaction task, referred to as the ultimatum game (UG), that captures the tendency of individuals to reject unfairness. In the UG, the first player (proposer) is given a sum of money (stake) to share with the second player (responder). If the responder accepts the amount offered by the proposer, the stake is split between the two as proposed. However, if the responder rejects the offer, neither player receives any money. Typically participants propose an equal split offer, which is driven by both their sense of fairness as well as strategic considerations of fear of rejection.[40,41] That is, proposers capitalize on the typical observation that responder decisions are not completely driven by self-interest; if this were the case, responders would accept any offer, no matter how small, because the alternative is receiving nothing. However, responders typically reject offers less than 20% of the stake, suggesting that decisions are based on self–other comparisons, also referred to as "fairness considerations".[42] Prior studies that have examined brain regions that are important for fairness considerations in decision making have demonstrated three important findings. First, receiving fair offers is related to activity brain regions that have previously been associated with reward representation, such as the striatum.[43] Second, receiving unfair offers is related to insula activation, suggesting negative emotional arousal related to unfairness[23] or norm violations.[20] Finally, the DLPFC is important for *rejection* of unfair offers, as demonstrated using repetitive transcranial magnetic stimulation studies.[27,44] Disruption of the right DLPFC was related to increased acceptance of unfair offers, which was interpreted in terms of the executive control that needs to be exerted in order to overwrite acceptance of unfair offers resulting from the default goal of self-interest.

One difficulty with the classic UG paradigm is that it is difficult to dissociate between the intentions of the proposer, that is, whether these are fair or simply strategic. One way to resolve this difficulty is by having participants choose from two fixed distributions of the stake so that it is possible to dissociate between an unfair offer when the alternative was also unfair or an unfair alternative when the alternative was fair.[45] Findings show that responder behavior is intentionality dependent; responders are more likely to reject an unfair offer when the alternative is fair whereas they are more willing to accept an unfair offer when the alternative for the proposer is also unfair.[45,46] In other words, fairness gains meaning in context and the proposer's intentionality plays a crucial role in fairness considerations made by responders (see also Ref. 47).

A recent study from our laboratory has provided further support for this interpretation. Using functional MRI (fMRI), we examined responder behavior in the fixed-alternative UG. Rejection of an unfair offer was related to DLPFC activity independent of the alternative that was offered, supporting the hypothesis that the underlying tendency to accept an offer needs to be controlled as a result of its unfairness. Further, acceptance of unfair offers was related to activity in the subgenual ACC, consistent with the hypothesis that this region is involved in outcome monitoring.[14]

Importantly, the results also revealed that activity in the insula was intention dependent, that is, this region was active when rejecting unfair offers even when the participant did not have a better alternative and was active when accepting unfair offers when the participants could also have offered an equal split. The common factor in these two conditions is that they both occur infrequently (i.e., unfair offers when the proposer had no other alternative are generally accepted and unfair offers when the proposer had a fair alternative are generally accepted) and their occurrence thereby indicates a deviation from the regular pattern of behavior. In this sense, the results support the implications on the role of the insula in social norm violations.[20]

Development of Fairness

Prior studies have demonstrated that children evaluate fairness differently than adults.[48] In a behavioral developmental study we have recently examined the role of intentions in considerations of fairness. We asked 9-, 12-, 15-, and 18-year-old participants to make offers or to evaluate offers in a fixed-version UG. First, we asked participants to make offers when the responder did not have the alternative to reject (referred to as the dictator game[40]). Here, we see that participants choose in a more self-oriented manner than when the responder has the alternative to reject but participants still do not totally maximize their own gains. These results were taken to suggest that proposers value fairness even when there are no strategic intentions (also referred to as inequity aversion, see Ref. 49). Importantly, these offers were similar across age groups, suggesting that the basic evaluation of fairness emerges early in childhood. However, when the responders had the opportunity to reject, proposers made fair offers more often with increasing age, suggesting an increase in strategic fairness evaluation with age. Interestingly, rejection rates of unfair offers reveal age differences related to intentions and fairness considerations. Whereas 9-year-old children reject 60–70% of unfair offers regardless of intentionality of the proposer, 12-year-old children show lower rejection rates of unfair offers if the proposer does not have an alternative. Rejection rates of unfair offers in the no-alternative condition drop to around 30% by age 18. These findings support the hypothesis that the increasing ability to consider intentions of others during adolescence is reflected in decision making related to fairness considerations in social interactions.

To date the neural mechanisms that are important in intention considerations have not yet been studied. Our hypothesis is that brain regions that have previously been identified as important in intention considerations and mentalizing, including the insula, medial PFC, and TPJ, undergo changes during childhood and adolescence. We expect the increasing differentiation between intentions to be related to the development of perspective-taking skills and related neural networks during adolescence. We are currently testing this hypothesis with a group of adolescents.

Trust and Reciprocity

A second paradigm that allows for the study of intentions in social interactions is the two-player trust game (TG) paradigm, which taps into both the trust and reciprocity elements of social interactions.[50] The structure of the TG is as follows: At the beginning of the TG, the first player (trustor) is endowed with a sum of money (e.g., €10). The first player is then presented with two options—he can either directly divide that sum according to a predetermined scheme (e.g., €5 for each player) or he can trust the second player (trustee) and give him the choice to divide the money. The latter option, to trust the other player, potentially leads to a higher pay off for both players because the sum of money is multiplied (typically tripled, in this case to €30). However, if trusted, the second player has two options: (1) reciprocate the trust given by the first player (e.g., €15 for each player) or (2) defect and maximize personal gains (e.g., €30 for the second player and nothing for the first player). As a result, trusting involves a component of risk because the trustee may attain higher personal benefit when not reciprocating.[51] Consequently, trusting may result in a smaller outcome for the first player relative to when he would not have trusted. Thus, the decision to trust involves risk for the trustor and the trustee's decision to reciprocate depends on the offset between maximizing self-interest relative to the appreciation of the trust that was given.

If players in the TG were both completely driven by self-interest they would always defect as trustees and therefore never trust as trustors. However, researchers have demonstrated that even for single anonymous transactions individuals often trust and reciprocate.[50,52] It has therefore been suggested that our motives to trust and reciprocate are not only guided by goals to maximize personal outcomes but also by "other-regarding preferences".[53–56] According to these studies the decision to reciprocate is dependent on evaluating consequences for both self *and* others.

fMRI studies of trust behavior showed that there was greater activity in the aMPFC for trust choices compared to no-trust choices or other control tasks.[52,57] Further, the aMPFC is also more active during defection, that is, when trustees defected relative to when they reciprocated.[58] These results are consistent with the hypothesis that the aMPFC is involved when participants need to make a decision in which they evaluate other and self-related goals.[59–61]

Development of Trust and Reciprocity

Developmental studies using the TG have demonstrated an increase in both trust and reciprocity with increasing age.[62] In a study where the TG was presented to participants of six age groups (8, 12, 16, 22, 32, and 68 years), both trust and reciprocity showed an increase with age, which stabilized around 22 years.[62] Besides an increase in general levels of trust and reciprocity, our findings revealed more subtle developmental changes as well. In our study, which was conducted with four age groups (9, 12, 16, and 25 years), we dissociated between intentions for trust and reciprocity. Specifically, the task was adapted in such a way that the level of risk for the trustor by trusting and the benefit for the trustee by being trusted were manipulated separately. The goal of these manipulations was to examine how the decision to trust or to reciprocate trust was dependent on intentions of the other players. As anticipated, the results demonstrate that developmental changes have different time courses for trust and reciprocity and that the capacity of social perspective taking, or integrating perspectives of the self and the other, develops until late adolescence.

To test the neural correlates of reciprocating behavior during adolescence, we recently performed a neuroimaging study that included adolescents and adults between ages 12 and 22 years. In this study we had participants of three different age groups (12–14 years, 15–17 years, and 18–22 years) play the role of the trustee in the scanner. Importantly, young adolescents showed activation in the same brain regions as mid-adolescents and young adults, but the pattern of activity in the aMPFC was different; there was more activity following reciprocity relative to the older age groups. We have interpreted these results to suggest that young adolescents are less able to dissociate between other and self-regarding goals. Indeed, prior developmental studies using mentalizing paradigms have also reported decreased activity and increased specificity of aMPFC with age.[63]

Taken together, studies of the neural correlates of fairness, trust, and reciprocity reveal several brain regions of the prefrontal cortex, such as the aMPFC, ACC, and DLPFC, as well as subcortical regions, such as the insula and ventral striatum, playing a role in social decision making. A common denominator in the interpretation of the findings lies in the role of understanding intentionality in the psychological processes involved in the decision-making tasks employed in these studies. Developmental changes across adolescence in these brain regions might underlie the observed developmental differences in perspective taking and understanding of intentionality.

From Social Interactions to Relationships

There is still a long way to go on disentangling the role of neural mechanisms with respect to relationships across the life span. Existing research demonstrates that social context is highly important in shaping individual perception and functioning. Neural activity involved in decision making is shown to be different even in the simplest social contexts formed by the mere presence of others than in nonsocial contexts.[64] The majority of neuroimaging studies on social interactions have examined (simulated) exchanges between two strangers, and the results are mostly based on repeated one-shot interactions with multiple anonymous others. As repetitions of these single interactions with strangers build into relationships over time, repeated interactions with the same person allows a closer examination of neural activity involved in relationship patterns. The findings of one study in which participants were provided moral descriptions of their play partners before playing multiple rounds of the TG clearly showed that individuals interpret their interaction partners' behavior differently based on their social knowledge about them.[65] Thus, in real life, individuals interacting with relationship partners are likely to process information (i.e., partner's behavior) differently depending on their prior experiences with and knowledge of the relationship. Over time such information gathered through interactions with specific relationship partners builds into relational schemas.

This idea of differential relational schemas being automatically activated in interactions has recently received support in a priming study on peer relationships in adolescence.[66] Adolescents attributed more hostility toward an unknown protagonist, experienced more anger, and were more likely to retaliate when they were primed by the face of disliked peers than by liked peers. Thus, the spontaneous retrieval of affective person-related information is relationship dependent and guides further social information processing. We hypothesize that the automaticity in social information processing related to different relational schemas is also associated with the activation of the neural networks described above. Such involuntary and spontaneous modulation of social cognition and behavior, in turn, might be related to how existing relationships are maintained.

Another way of approaching the issue of neural mechanisms involved in relationships is by examining brain regions involved in interactions with personally familiar relationship partners. The extent of brain activity related to a particular social interaction might be dependent on the type of relationship that provides the context for the interaction. It is not without reason that the majority of studies have focused on interactions with anonymous others because examination of neural correlates of different relationships are not without challenges. Simulation of multiple trials of social interactions with real relationship partners (e.g., friends, romantic partner, parents) in the scanner is not easy and requires creative study designs. One method that can potentially deal with these challenges is the use of sociometric measurements in identifying dyadic relationships within the peer group. This method provides an efficient way of gathering information on multiple relationship partners (i.e., friends or enemies within the peer group) of individuals. Previously this approach was implemented in a study with adults in examining the neural correlates of friendships.[67] These friendships were more likely to be based on mutual support and prosociality, and the revealed neural mechanisms might differ from friendships that are less likely to be characterized by reciprocity and trust. It is possible to think of other individual characteristics, such as personality, that might also play a crucial role in the development of relationships. Examining the neural basis of behavior within social interactions is showing promise in helping to understand the mechanisms that underlie the development of dyadic relationships, which play an important role in psychological well being throughout life.[68]

Conflicts of Interest

The authors declare no conflicts of interest.

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