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Keywords

development, social brain, self, perspective taking, society, contributions

Abstract

Research has demonstrated that adolescence is an important time for self- and other-oriented development that underlies many skills vital for becoming a contributing member of society with healthy intergroup relations. It is often assumed that these two processes, thinking about self and thinking about others, are pitted against each other when adolescents engage in social decision making such as giving or sharing. Recent evidence from social neuroscience, however, does not support this notion of conflicting motives, suggesting instead that thinking about self and others relies on a common network of social-affective brain regions, with the medial prefrontal cortex playing a central role in the integration of perspectives related to self and others. Here, we argue that self- and other-oriented thinking are intertwined processes that rely on an overlapping neural network. Adolescents' motivation to contribute to society can be fostered most when self- and other-oriented motives align.

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1. INTRODUCTION

Our society is based on principles of contribution and reciprocity in order to develop and maintain social networks (Dunbar 2018). Contributing involves multiple actions of doing good to others, such as helping friends and family (in-group contributions); spending time, money, or cognitive effort—volunteering, helping, and investing in charity—to unknown others in need (out-group contributions); and contributing to goals and norms in education, work, and rules of society (societal contributions). One of the main challenges of each human community is to understand how young people develop social motives and can make a valuable contribution to society, balancing between self-oriented and other-oriented goals and needs. Fitting in and being a contributing member of the social world can be considered one of the most fundamental tasks of the adolescent period (Fuligni 2019).

1.1. Adolescence as an Important Time for Contribution to Society

Adolescence is a critical period in development for acquiring societal contribution values, because it involves the transition between childhood—characterized by strong dependency on parents and caregivers—to adulthood, in which one is expected to function as a mature, independent individual (e.g., politically, financially, and socially) and to commit to social norms (Crone & Dahl 2012, Duell et al. 2016). Although historical and cultural differences exist in its definition, adolescence can be defined as the period between 10 and 24 years of age (Sawyer et al. 2018), starting with the biological onset of puberty. Pubertal development involves extensive changes in hormone levels that affect physical appearance as well as brain and behavioral development, and it is thought to trigger social-affective sensitivities (Blakemore et al. 2010). The end phase of adolescence is often

Reciprocity:

responding positively to the positive actions of others, rewarding kind actions

described as the time when the individual adopts mature social and societal norms that focus on social responsibility and contribution to the larger society. Even though participating in the social world is important also earlier in childhood, the growing maturity and skills developed during adolescence increasingly move the responsibility for this task from parents, schools, and communities to the adolescents themselves. In recent years, possibly because of increasingly complex societies, researchers have described a prolonged period of adolescent development, also referred to as emerging adulthood, during which individuals show further advancement in academic and social development, with longer dependency on parents (Arnett 2000). This review describes the processes that help us understand how and when adolescents become contributing members of society.

1.2. Self- and Other-Oriented Development as Intertwined Processes

We argue that the key feature of psychological development during adolescence is the development of a set of social cognitive skills that serve as building blocks to the integration of self with others, and that taken together predict how young people will contribute to society. First, these include processes identified by research on self-development, such as identity, self-concept, and the monitoring of selfish impulses, although others play an important role in each of these domains (e.g., developing a reflected self, which refers to the integration of self attributes from the perspective of others). Second, these processes involve social perspective taking, mentalizing, and valuing outcomes for others, although many of the existing studies have acknowledged the intertwined development of these processes and self-related ones (e.g., mentalizing about others relative to self).

This distinction between self- and other-related processes has sometimes led to the assumption that these are separable processes pitted against each other. New insights from the field of social neuroscience hold the promise for fundamentally new insights that will help to understand how youth make the integration between self- and other-oriented perspectives and balance between these perspectives when contributing to society. Neuroscience research in the domain of self-development has consistently demonstrated that self-development includes elements of others, through social comparison, social influence, or cultural social identity (Pfeifer & Peake 2012). Neuroscience research that has focused on how individuals engage within the social world consistently demonstrated that many of the processes that are important for engagement, such as social group membership, educational commitment, or community participation, involve elements of the self, such as intrinsic motivation or self-identification with the group (Blakemore & Mills 2014).

As will become evident in the review, these processes involve a common neural network including the medial prefrontal cortex (medial PFC) as an important convergence zone at the intersection of cognition, social processing, and affect. The medial PFC connects input from the subcortical ventral striatum, the cortical lateral prefrontal cortex (lateral PFC), and the social brain network, including the temporal parietal junction (TPJ) and temporal cortex, all regions that are important for the various building blocks involved in developing self- and other-related processes, making it likely that these processes develop in an intertwined fashion (**Figure 1**). The medial PFC has a protracted developmental trajectory, with continuing reduction of gray matter volume until the early twenties (Mills et al. 2014). Moreover, functional connectivity between the ventral medial PFC and the ventral striatum is strongest in childhood and decreases during adolescence until early adulthood (van Duijvenvoorde et al. 2016). We will describe the general developmental trajectories of the medial PFC, the ventral striatum, and associated brain regions (TPJ, precuneus, and temporal cortex) in relation to three core processes that are important for contribution to society: developing self, thinking about others, and balancing between goals of self and others. As will become evident in this review, the medial PFC serves as a hub region for the

Mentalizing: the ability to understand one's own and other people's minds

Medial PFC: medial prefrontal cortex

Lateral PFC: lateral prefrontal cortex

TPJ: temporal parietal junction

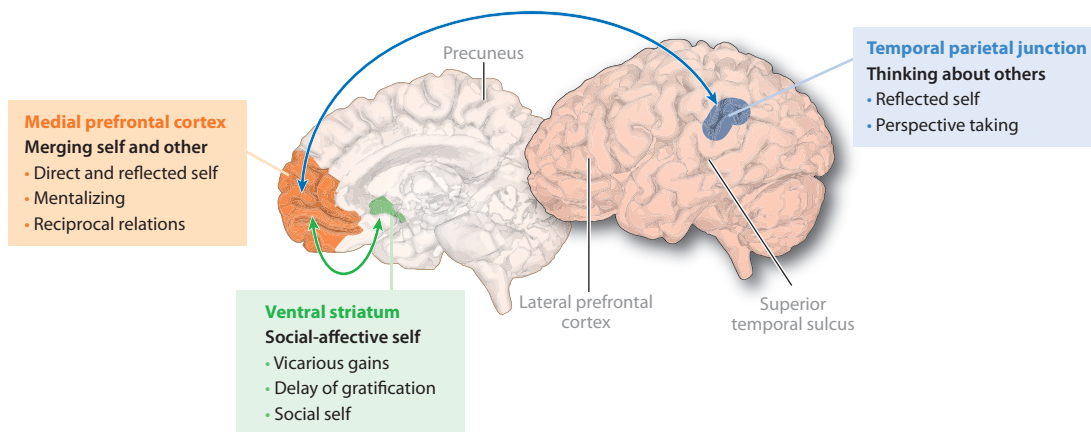


Figure 1

Contributing to society (educational commitment, interpersonal relations, commitment to societal goals). Display of brain regions involved in self- and other-related processing in adolescence. The medial prefrontal cortex (medial PFC) is involved in the intertwined development of self- and other-related processing, suggesting an important hub function for communication with other networks. The first network is important for cognitive perspective taking (*blue area and arrow*): The medial PFC is active together with the temporal parietal junction when thinking about self from the perspective of others (e.g., reflected self, understanding intentions). The second network is important for the social-affective self (*green area and arrow*): The medial PFC is active together with the ventral striatum when gaining for others (friends, family), delaying gratification, and evaluating the social self. The merging of both networks may lead to the intertwined development of self and others. Additional regions that are described in various paradigms as involved in these processes are the lateral prefrontal cortex, the precuneus, and the superior temporal sulcus. Illustration copyright Robert van Sluis; reproduced with permission.

integration of several of the neural systems that underlie these social processes, making it a strong candidate for the integration and coordination of self with others.

A hypothesis discussed in this review is that the social integration of self- and other-related processes is important for how young people engage in societal contributions. Contributing to society is an umbrella term for many processes that can be differentiated into multiple dynamic and interacting behaviors. These processes have mainly been captured in research on prosocial behavior (Blakemore & Mills 2014, Penner et al. 2005), but this research has often neglected the importance of balancing between multiple goals in adolescence, including self-oriented goals and other-oriented goals. Here, we take the perspective that societal contributions emerge from the integration of self- and other-related processes in multiple contexts and from the balancing between these processes in case the goals do not align.

This review describes new insights from the perspective of social neuroscience research on the ways neural and self- and other-oriented development affect how young people get engaged in societal contributions. We describe behavioral, functional, and structural neuroimaging studies that appeared in the last 5–10 years and focused on three fundamental processes that are important for the integration of self with others: developing self, thinking about others, and giving/sharing, which involves balancing between goals of self and others. We also place these findings in the context of contemporary youth, who engage in larger social networks than previous generations due to access to online social networks.

Prosocial behavior:
actions intended to
benefit others

2. SELF-ORIENTED DEVELOPMENTS

Self-oriented goals can be described at multiple levels, such as developing a stable identity with commitments toward educational and interpersonal goals, developing stable self-concepts, and

balancing between needs for self now and in the future. As shown below, the medial PFC plays an important role in integrating these different types of self-views.

2.1. Identity Development

Self-perspectives are critically involved in identity development. Identity development is often described as the search for self-defined values and commitments to various domains of life (education, work, social relationships) (Becht et al. 2017a). Self-concept clarity, an indication of self-certainty, is predictive for identity development (Schwartz et al. 2012). Moreover, higher self-concept clarity is important for social relations, as it predicts fewer negative interactions with parents over time (Becht et al. 2017b).

Definitions of self-concept clarity are often based on stability versus variability over time. Research on this topic has especially benefited from daily assessments, which provide a much richer and more reliable assessment of self-concepts compared to longitudinal assessments over longer time intervals. Prior longitudinal research including daily assessment of identity processes (reconsideration of goals, exploration in depth, and commitment to goals) showed that a subgroup of adolescents (approximately 50%) develops an identity crisis in either the educational or interpersonal domains (higher reconsideration with relatively low or vague commitments), with dips in commitment around ages 15–17 (Becht et al. 2016). [Crocetti et al. (2016) find a similar dip in self-concept clarity around ages 17–18.] A study on evaluation of self-traits reported that adolescents show a reduction in positive self-descriptions in the academic domain around ages 14–16 (van der Crujssen et al. 2018). These findings underscore the important transitions in self-concept clarity and identity development in adolescence, which can affect adolescents' functioning in several domains. It is not surprising that this dip occurs mainly in the academic domain, given that this is a social environment in which there is a stronger focus on social comparison as well as expectations from parents and others. Experiencing an identity crisis in the educational domain affects not only school anxiety but also perceived support from peers, suggesting that this crisis has more general effects on the well-being of adolescents (Becht et al. 2016). There is currently little understanding of why some adolescents develop a stable self-concept whereas others experience an identity crisis. Neuroscience can provide more insights into these individual differences, although very few studies to date have examined the relation between neural development and identity formation.

A novel recent perspective examined the relation between individual differences in identity development and structural brain development. This study focused on the ventral striatum and prefrontal cortex, regions that are also implicated in self-referential processing (pursuing self-defined goals) and delay of gratification (controlling immediate impulses for long-term goals) (Becht et al. 2018). Various neuroscience studies have revealed that there are continuous changes in brain structure and connectivity during the whole period of adolescence and extending into early adulthood. These changes are observed in the prefrontal cortex, which is part of the evolutionary younger areas that are important for the capacity to focus on goals in the face of distractors and obstacles and for understanding intentions of self and others (Tammes et al. 2017). Changes are also observed in the ventral striatum, particularly the nucleus accumbens, which is part of the evolutionary older regions of the brain that are involved in the processing of motivational and affective signals (Wierenga et al. 2018). This led researchers to ask whether the trajectories of development of the lateral PFC and the ventral striatum differ depending on levels of identity development.

The study by Becht et al. (2018) examined the trajectories of structural brain development and identity development in a longitudinal design. Both the nucleus accumbens and the lateral PFC showed a decrease in volume across three time points between ages 12–22, consistent with prior

Identity

development: the process of developing a sense of oneself in terms of personality and social connections

Self-concept clarity:

The extent to which people have clear images of who they are, with confident beliefs

Delay of

gratification: resisting a smaller, immediate reward in order to obtain a larger, delayed reward

research (Herting et al. 2018, Tamnes et al. 2017). Identity development was examined in three processes: reconsideration of goals, exploration in depth, and commitment to goals. The study showed that nucleus accumbens volume was negatively related to reconsideration and positively related to commitment, and that the slope of nucleus accumbens decrease was positively correlated with exploration in depth. Furthermore, the volume of lateral PFC was positively correlated with exploration. These findings were interpreted to suggest that the delayed maturation of prefrontal cortex and nucleus accumbens (measured as higher volumes relative to peers) is associated with more stable identity development (Becht et al. 2018). No studies have related daily fluctuations in identity development to brain development, and it will be important for future research to examine reconsideration and commitment fluctuations as well as certainty about identity development across multiple days.

2.2. Self-Concept Development

The relation between structural brain development and identity development provides important insight into the potential differential trajectories of brain development, but experimental measures of self-concept are necessary to understand neural responses when thinking about self. There is a long tradition in developmental psychology that focuses on the development of self-evaluations, defined as the cognitive and affective evaluations of self. Self-report and experimental studies demonstrated that self-evaluations are relatively positive early in childhood (referred to as the positivity bias) and become more negative, or more realistic, in early adolescence, when they are based more on social comparisons (van der Aar et al. 2018). In addition, adolescence is an important period for the development of a more differentiated view of self, which is evident from more diverse self-descriptions depending on the specific context (Harter 2012). Finally, it is well documented that commitments, examined in terms of self-concept clarity, become more stable over the course of adolescence (Kroger et al. 2010, Meeus 2011). Possibly, these processes of self-differentiation are related to maturation and to a stronger integration between the regions that are involved in self-evaluation and identity development.

Recently, research on self-evaluations has been enriched by new developments in social neuroscience research, specifically of studies making use of functional magnetic resonance imaging (fMRI) while evaluating traits of self. These studies have shown that descriptions of self (relative to descriptions of traits in general or descriptions of others) consistently recruit the medial PFC and associated brain areas (Denny et al. 2012). The medial PFC is often involved in self-referential thoughts, in comparing self to others, and in thinking about self in the present, past, and future (Pfeifer & Peake 2012). This fits well with recent findings showing that the medial PFC develops relatively late in evolution (Dunbar 2018) and has a protracted structural development, with changes in gray matter volume until the early twenties (Mills et al. 2014). Thinking about self is inherently social in adolescence, given that self-evaluations emerge from socially comparing self to others. Therefore, it is not surprising that thinking about self and others relies on overlapping brain regions, with a strong involvement of the medial PFC (Denny et al. 2012, Schurz et al. 2014). A prior study showed that simply being observed by others already resulted in more activity in the medial PFC in mid adolescence, which correlated with self-conscious emotions (Somerville et al. 2013).

To examine the neural signature of self-concept development, fMRI studies including children, adolescents, and adults demonstrated that recruitment of the medial PFC differs depending on age. Specifically, it was shown that the medial PFC is more strongly engaged during self-descriptions (relative to descriptions of a fictional character) in early adolescents (ages 9–11) compared to adults (Pfeifer et al. 2007). Follow-up studies that included participants across the

whole range of adolescence showed that the medial PFC was recruited in all age groups, but activity in the medial PFC became more differentiated across adolescence depending on the domain (social, physical, or academic) (van der Cruijnsen et al. 2018). In addition to the medial PFC, important developmental differences were also observed in the TPJ, a region often implicated in switching between self- and other-oriented perspectives (Carter & Huettel 2013, Schurz et al. 2014), and the ventral striatum, a region implicated in affective reward processes (Haber & Knutson 2010, Tamir & Hughes 2018). For the TPJ, it was observed that this region is more strongly involved in adolescence (ages 11–14) when describing self from a reflected perspective, especially when the other person is important for the specific domain (e.g., mothers for educational descriptions and friends for social descriptions) (Pfeifer et al. 2009). Activity in the ventral striatum was less pronounced for positive traits in mid adolescents describing themselves (ages 14–16) compared to children and adults (van der Cruijnsen et al. 2018), but striatum activity is also dependent on the domain and perspective. One study demonstrated that ventral striatum activity was heightened in adolescence (ages 11–14) when describing social self-traits from the perspective of others (Jankowski et al. 2014). Taken together, neuroscience studies consistently show that the medial PFC is involved in evaluating self but works closely together with the TPJ and the ventral striatum. These regions show an increase in specificity to domain and valence when adolescents grow up, marking adolescence as an important transition phase for self-concept development.

The way self-traits are evaluated has important implications for the way adolescents contribute to society. This relation is most consistently shown for academic traits. A previous self-evaluation study showed that mid adolescents (ages 14–16), compared to children (ages 10–13) and older adolescents (ages 17–21), rated themselves less positively on academic traits compared to physical appearance and prosocial traits (van der Cruijnsen et al. 2018). In addition, relatively more positive academic self-evaluations were correlated to commitment to academic goals, and this relation was mediated by activity in a separate mid-line area, the precuneus (van der Aar et al. 2019), which is often coactivated with the medial PFC and is important for perspective taking through mental imagery (e.g., imaging oneself in multiple contexts) (Schurz et al. 2014). These findings suggest that self-concept development is an important factor for youth's capacity to stay committed to goals that are important for their future self, such as being committed to education.

2.3. Inhibiting Selfish Impulses

When making future-oriented decisions, many choices often involve a trade-off between direct or immediate gratification and long-term outcomes (also referred to as delay of gratification). Working toward long-term outcomes puts demands on the impulse to obtain immediate selfish rewards. These demands have been well captured in several behavioral paradigms that require a balance between affective drives and control of actions (Davidow et al. 2018). These findings may partly explain individual differences in how youth contribute to society. Prior longitudinal studies have shown that better delay of gratification is predictive for many outcomes that are important for society, such as commitment to work, health (e.g., refraining from smoking, healthy eating), and financial independence (Ayduk et al. 2000, Moffitt et al. 2011).

The delay of gratification task is a well-known paradigm to assess the balance between preferring short- versus long-term outcomes. In this task, individuals make choices between two options: One involves an immediate smaller reward (e.g., \$2 now) and the second involves a larger reward in the future (e.g., \$10 in two weeks). By providing individuals with multiple choices in which the rewards and the time difference are manipulated, it is possible to calculate an indifference point: a value for which there is no difference between immediate and delayed rewards. This value is indicative of individual differences in delay of gratification. Multiple

developmental studies have demonstrated that delay of gratification increases during adolescence. Children are generally most impatient and prefer options with an immediate reward, whereas in late adolescence and early adulthood individuals are willing to wait longer for a reward (Mischel et al. 1989, Olson et al. 2007, Peper et al. 2018). Delay of gratification tasks typically involve two brain systems: Immediate-reward choices are accompanied by increased activity in the subcortical ventral striatum, whereas delayed-reward choices result in activity in the cortical lateral PFC (McClure et al. 2004). Developmental MRI and fMRI studies including adolescents and adults showed that functional and structural connectivity between the ventral striatum and the medial and lateral PFC continues to mature in adolescence and is predictive for delay of gratification performance (Achterberg et al. 2016, Christakou et al. 2011, Luerssen et al. 2015).

2.4. Summary

Together, these findings suggest that adolescence is characterized by an increased self-focus, a higher value placed on immediate outcomes compared to future ones, and, for a subgroup of adolescents, a crisis in identity development with implications for school anxiety and perceived peer support. All these processes are relying on a similar neural network including the medial PFC, ventral striatum, and lateral PFC, suggesting important interplays between these processes (Figure 2). The abilities to view oneself from multiple perspectives, develop future orientation, and develop educational and interpersonal commitments are important predictors for the way youth contribute to society, including investing in education and work as well as focusing on the needs of others.

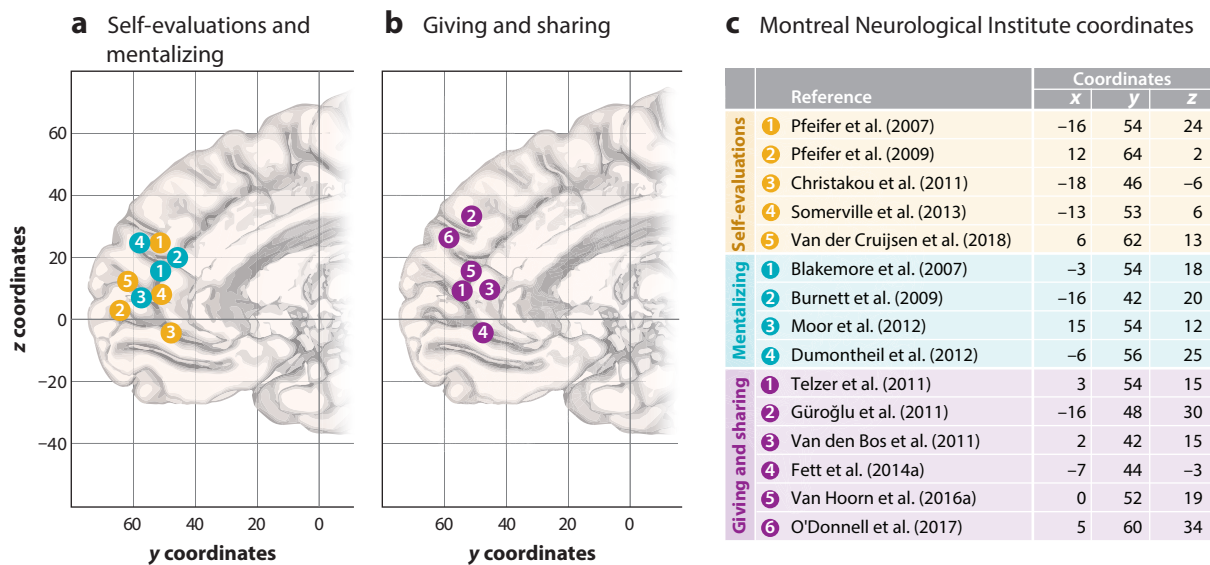


Figure 2

Overview of fMRI studies discussed in the text that report developmental differences in medial prefrontal cortex (medial PFC) activity. Panel *a* shows studies that report developmental differences in medial PFC activity in paradigms of self-evaluations (*orange*) and mentalizing (*teal*), based on *y* and *z* coordinates [*x* coordinates are not shown because all activations are displayed on the midline ($x = -20$ to $x = 20$)]. Panel *b* shows studies that report developmental differences in medial PFC in economic games of giving, fairness, trust, and reciprocity (*purple*). Panel *c* shows a table of displayed studies, including the *x*, *y*, *z* coordinates of regions in the medial PFC for which developmental task differences were reported. Illustration copyright Robert van Sluis; reproduced with permission.

A recent study reported a dynamic interaction between self-certainty and prosocial behavior (Crocetti et al. 2016). In a longitudinal study in which adolescents made the transition from adolescence to early adulthood (ages 16–23, with yearly assessments), it was observed that adolescents who were more self-certain, as assessed through higher self-concept clarity, engaged in more prosocial behavior in the next measurement wave. These findings were interpreted as suggesting that adolescents who are more self-certain are possibly more flexible in responding to the needs of individuals in their environment. Interestingly, the reversed relation was also observed: Those adolescents who engaged more in prosocial behavior were more self-certain at the next measurement wave. Together, these findings suggest a dynamic interplay whereby self- and other-oriented perspectives reinforce each other over time, which may be driven by contribution behaviors and changes in overlapping neural networks. In the next section, we turn to how adolescents develop processes that are important for thinking about others.

Vicarious gaining:

experiencing rewarding feelings when receiving rewards for others

STS: superior temporal sulcus

3. OTHER-ORIENTED DEVELOPMENTS

Contributing to society often involves responding to the needs and perspectives of others. Humans have a fundamental need to be part of a social group, and belonging to a group requires understanding the minds of others (Dunbar 2018). It is now well known that a basic form of perspective taking is present early in life (Scott et al. 2012). Large improvements in perspective taking emerge between 3 and 5 years of age (Carlson et al. 2013), but improvements continue after childhood. The ability to take the perspectives of others develops gradually during adolescence, as observed in both self-report (Blankenstein et al. 2019) and experimental tasks such as the director game, in which participants make decisions about moving objects from the perspective of another person (Dumontheil et al. 2010). Two important processes underlie understanding the needs and perspectives of others: mentalizing about thoughts and actions of others (i.e., theory of mind) and empathic feelings toward others, defined here as valuing outcomes of others (i.e., vicarious gaining). Both processes have been examined extensively in developmental neuroscience research and provide new building blocks for understanding multiple processes that are involved in contributions to society.

Taking the perspectives of others is important when developing close relationships, such as with friends and family (in-group). However, in order to connect to larger networks, taking the perspectives of strangers is also an important way to connect to new individuals (out-group). The study of how individuals distinguish between these groups is informative for understanding how youth develop in-group and out-group distinctions. These processes have been investigated in the domains of both mentalizing and vicarious gaining.

3.1. Mentalizing About Others

Understanding the minds of others, or mentalizing, has been extensively studied in adults and was found to rely on a common set of brain regions, including the medial PFC, the TPJ, and the superior temporal sulcus (STS) (for a meta-analysis, see Schurz et al. 2014). Together, these brain regions have been referred to as the social brain. Mentalizing tasks can take many forms, but they often involve some aspect of thinking about the thoughts of others. For example, studies have reported increased medial PFC activity in adults reading stories that require inferences of the thought and actions of others, including intentional and unintentional harm (Bas-Hoogendam et al. 2017), shame (Michl et al. 2014), and guilt (Morey et al. 2012). A meta-analysis that compared self-referential and mentalizing studies showed that both processes result in overlapping activity in the medial PFC. However, mentalizing about others more strongly recruited the dorsal medial

Director task:

an experimental task in which participants follow instructions to move objects from the perspective of another person (i.e., the director)

PFC, whereas self-referential processing more strongly activated the ventral medial PFC (Denny et al. 2012). The ventral region of the medial PFC has functional and structural connections to the ventral striatum (van Duijvenvoorde et al. 2016) and may therefore be more involved in affective or personally relevant mentalizing (D'Argembeau 2013).

Interestingly, the neural activity patterns in subregions of the medial PFC are sensitive to cultural differences. A meta-analysis of 35 studies examining individuals from Western cultures and East Asian cultures during social cognitive processes showed that individuals from Western cultures more strongly recruited ventral medial PFC, whereas East Asian participants more strongly recruited dorsal medial PFC (Han & Ma 2014). These findings implicate that the neural activity patterns are dependent on experiences and culture and may be most adaptive during adolescent development, when self- and other-oriented views are developing.

The developmental patterns of mentalizing have been well established in behavioral and fMRI studies. A recent longitudinal study including participants aged 8–18 demonstrated that recursive thinking (i.e., thinking about thinking) continues to develop until late adolescence (Van den Bos et al. 2016). These findings fit well with fMRI studies demonstrating that mentalizing is accompanied by continued changes in the medial PFC and TPJ (Blakemore & Mills 2014). Interestingly, several studies demonstrated that younger adolescents recruit the medial PFC more strongly than older adolescents when reading about guilt (Burnett et al. 2009) or social intentions (Blakemore et al. 2007) and when mentalizing about the thoughts of others (Moor et al. 2012). It has been suggested that adolescents may over-recruit the medial PFC when interpreting social situations, whereas they may use more cognitive strategies to perform social tasks when developing into adulthood, which was suggested by stronger lateral PFC activity in adults versus adolescents when performing the director task (Dumontheil et al. 2012). Alternatively, adolescents may engage more strongly in the integration of self- and other-oriented processes when mentalizing, which may account for the stronger activity of the medial PFC, which serves as a hub for social information integration. Other studies have observed that adults recruit the TPJ more strongly than adolescents when performing mentalizing tasks (Blakemore et al. 2007), which may also suggest other strategies used by adults compared to adolescents.

3.2. Vicarious Gaining

In addition to perspective taking (also sometimes referred to as cognitive empathy), other-oriented development involves affective empathy, which is an emotional response to the needs of others. Here we describe affective empathy in the context of experiencing rewarding feelings from the gains of others (vicarious gaining). Research on this topic is based on prior studies showing that adolescence is a period of heightened emotional reactivity, which has often been observed in the context of taking risks and gaining rewards. Several cross-sectional and longitudinal studies revealed elevations in reward sensitivity in the ventral striatum when gaining rewards, with peaks at ages 15–17 (Schreuders et al. 2018a, Silverman et al. 2015). The increase in reward sensitivity has been related to a rise in pubertal development and to hormonal changes such as testosterone rises (Braams et al. 2015, Op de Macks et al. 2016). However, personality factors such as differences in reward drive are also related to individual differences in reward-related activity in the ventral striatum (Braams et al. 2015). The relative decrease in reward-related activity in young adults has been correlated to a relative decrease in self-reported winning pleasure (Schreuders et al. 2018a), suggesting that ventral striatum activity reflects the direct hedonic pleasures of gaining rewards.

Vicarious rewards (i.e., rewards gained for others) may provide important insights into the way individuals enjoy gaining for others, which has been referred to as prosocial reward

(Lockwood et al. 2016). A meta-analysis in adults revealed that the ventral striatum activity when gaining for others depends on the closeness of the target (Morelli et al. 2015). For example, an empirical study including adults who could gain for self, friends, or unknown others (in this study manipulated as strangers who made a bad financial offer) showed that vicarious gaining was observed for the friend but not for the unknown other. This effect scaled with self-report ratings of winning pleasure, which were lower for unknown others (Braams et al. 2014a). A different study showed that individuals who displayed more vicarious reward activity in the ventral striatum when gaining for friends were more likely to act prosocially in daily life (Morelli et al. 2018). Finally, a study in adults examined vicarious gaining for a self-chosen charity. The rationale was that charities may be rated as important and individuals may feel connected to the goals of the charity without being personally connected to the target. Here, it was found that adults showed elevated ventral striatum activity when they gained rewards for themselves and when rewards were gained for both themselves and the charity, but not when gaining solely for the charity. An individual differences analysis revealed that only individuals who reported more empathic traits showed more reward-related activity in the ventral striatum when gaining for the charity (Spaans et al. 2019). Together, these findings show that there are individual differences in ventral striatum activity when gaining for friends and strangers, which correlate with empathy and prosocial behavior in daily life.

Vicarious gains have also been examined across adolescent development. First, it was observed that adolescents show ventral striatum activity not only when gaining for themselves but also when gaining for their best friends. There was some evidence that in girls this effect was larger for participants who reported higher friendship quality with their best friends (Braams et al. 2014b). No such effect was observed when they were gaining for unknown others. The finding that vicarious reward activity in the ventral striatum was observed for close others was confirmed by a study that focused on family members. This study demonstrated that adolescents also show elevated activity in the ventral striatum when they gain rewards for their mothers. Interestingly, this response was elevated in mid adolescence, similar to gaining for self (Braams & Crone 2017). These findings may indicate that rewards for mothers are experienced similarly to rewards for self, possibly indicating close relationships. A subsample of the mothers also participated in an fMRI study in which they could gain vicarious rewards for their children. Gaining rewards for children was also associated with ventral striatum activity (Spaans et al. 2018). In this exploratory study, the sample was too small to relate mother and child responses to each other, but this approach may prove valuable for examining dyadic family relationships (see also Lee et al. 2017).

Given that adolescents take part in larger social networks, an important question concerns whether there are differences between adolescents who are more popular within their social networks, as previous research revealed that popular adolescents respond more to the needs of others. One study showed that adolescents who were more accepted by their peers, as confirmed through more likes in sociometric analyses, showed similar reward-related activity in the ventral striatum when gaining for self and friends, whereas adolescents who were less accepted showed stronger activity for self-gains relative to gaining for friends (Meuwese et al. 2018). These findings may tentatively suggest that adolescents with more intensive social experiences (popular adolescents) more strongly align goals for self and others. Taken together, vicarious gaining provides important information on how adolescents value gains for others. There is some evidence that these effects are more pronounced for individuals with whom adolescents have more intimate social relationships. Also, there is evidence that this reward activity may be more strongly present in adolescence for close family members, suggesting in-group preference.

Economic games:

two- or multiple-player decision games where stakes for self and other are pitted against each other (e.g., dictator game, ultimatum game, trust game, public goods game)

DG: dictator game

3.3. Summary

Perspective taking develops throughout the developmental period of adolescence, and different processes contribute to changes in this domain. Mentalizing research shows that the medial PFC, in particular, is more active in adolescents compared to adults, which may indicate that this region—which has close connections to both the subcortical ventral striatum and the cortical lateral PFC, TPJ, and STS—may play an important role in driving different actions in adolescence (**Figure 2**). In addition, affective processing of vicarious rewards in the ventral striatum correlates with prosocial behavior and is elevated for close family members in mid adolescence. The next section focuses on balancing self-oriented and other-oriented decision making in adolescence.

4. GIVING AND SHARING IN THE CONTEXT OF SOCIETAL CONTRIBUTIONS

Balancing between the needs of self and others is an important process that contributes to youth's behavior toward others in terms of sharing, giving, and reciprocity. In childhood, many of these processes are rule based—for example, judging divisions of goods by norms of equality or equity (Fehr et al. 2008). In adolescence, there is a transition to more advanced ways of reasoning about divisions, such as understanding the perspectives of others when proposing a division (Güroğlu et al. 2009) and distinguishing between in-group and out-group members (Güroğlu et al. 2014a). These behaviors are of great importance when contributing to society and can result in feelings of personal satisfaction (the so-called warm glow) and of respect and admiration from others (Yeager et al. 2018). Whereas the ability to impute the mental states of others has been the subject of many neuroimaging studies, which showed activity in a robust network of medial PFC, TPJ, and STS (Cutler & Campbell-Meiklejohn 2019, Schurz et al. 2014), only recently researchers have developed behavioral tasks that reliably assess different subprocesses of other-oriented behavior (Cutler & Campbell-Meiklejohn 2019). Here, we describe studies that focused on sharing and giving in relation to the target, strategic motives, cooperation and reciprocal relations, and social influence. As shown above, the medial PFC is an important convergence zone connecting these multidimensional processes (**Figure 2**).

4.1. Sharing and Giving Depends on Who the Target Is

Sharing has been examined in a variety of economic games that include a distribution of goods between self and others. A well-known example is the dictator game (DG), in which a proposer can decide how to share a stake (e.g., 10 valuable tokens) between self and an unknown other player. In the standard version, the transition is typically anonymous and does not involve multiple transactions; therefore, there is no involvement of reputation effects. Behavioral research shows that individuals are willing to share some part of their tokens with unknown others, suggesting a general level of prosociality toward out-group individuals (Güroğlu et al. 2009). This sharing response is present already in young children and does not change dramatically during adolescence, although some studies suggest decreases during adolescence in giving to out-group members (Güroğlu et al. 2014a). The neural correlates of this sharing response have been examined using experimental manipulations of the dictator game, and research in adults has showed that costly sharing was associated with increased neural activity in the medial PFC and the ventral striatum (Güroğlu et al. 2014b), suggesting that processes that are involved in vicarious gaining and mentalizing are also involved in giving to anonymous others.

Giving behavior, however, is strongly dependent on the identity of the interaction partner. For example, adults gave more to friends than to strangers in a two-choice dictator game

(Schreuders et al. 2018b). In addition, the putamen, a brain region closely connected to the ventral striatum, was more strongly active when making prosocial choices to benefit friends (Schreuders et al. 2018b), consistent with the literature on vicarious gaining (Braams et al. 2014a). A different study that used a two-choice donating task that involved personal noncostly rewards or costly choices that benefited family members showed that individuals with higher family obligation values showed stronger connectivity between the ventral striatum and the medial PFC (Telzer et al. 2011). Cultural differences were also observed, such that neural activity associated to costly giving to family was more pronounced for youth with a Latino background compared to White youth (Telzer et al. 2010). Finally, youth who showed stronger neural response in the ventral striatum when costly giving to family showed a reduction in depressive symptoms one year later (Telzer et al. 2014).

4.2. Sharing and Giving Depends on Perspective Taking

Giving can also be strategic because of the expected response of the receiver. For example, behavior can get punished when not benefiting the other person. This behavior has been examined using the ultimatum game (UG), a variation to the DG in which the second player has the possibility to refuse the offer, in which case neither party receives anything. Giving behavior is significantly greater in the UG compared to the DG, suggesting that individuals are sensitive to strategic motivations and are taking the perspective of others when making their offer. The difference between UG and DG behavior increases during adolescence, suggesting that strategic understanding also changes during childhood and adolescence (Güroğlu et al. 2009, Steinbeis et al. 2012). This hypothesis was supported by an fMRI study that examined behaviors of second players (recipients) in the UG. Players in this game refused a low offer in two different context conditions. In the first condition, the first player had no other option than to make a low offer (no-choice condition), and in the second condition the first player preferred a low offer above an equal split of goods. The no-choice condition required perspective taking of the participants to understand the motives of the first player. Here, it was found that the refusal of no-choice low offers decreased during adolescence, suggesting that older adolescents understood that the other player had no other option than to make a low offer (Güroğlu et al. 2009). This behavior was accompanied by stronger activity in the medial PFC and TPJ when evaluating the no-choice offers (Güroğlu et al. 2011). Finally, a study that included younger children compared UG and DG neural activity in younger children and adults. This study observed that strategic versus nonstrategic giving was correlated with behavioral control and activity in the lateral PFC, a region often implicated in cognitive control (Steinbeis et al. 2012). Together, these findings suggest that the neural processes involved in mentalizing (medial PFC, TPJ) and cognitive control (lateral PFC) contribute to strategic giving changes during childhood and adolescence.

4.3. Cooperation and Reciprocal Relations

Another form of giving and sharing that involves both perspective taking and interpersonal relations is trust and reciprocity. Trust shares similarities with cooperation because it involves an act in which the giver expects to be reciprocated. Trust is often examined with the trust game, in which a first player has the possibility to share a certain stake of tokens or to give (a share of) the tokens to a second player, in which case these tokens are doubled or tripled. The second player can then decide how to share the tokens with the first player. The second player can reciprocate the trust, in which case part of the stakes are returned to the first player, or defect the trust, in which case the second player keeps most of the stake and exploits the trust received for personal gain. Whereas there is some initial evidence that trust and reciprocity increase in childhood

(van den Bos et al. 2010), the behavioral effects in adolescence are less consistent. Overall, trust decisions stay relatively stable, although trust is sensitive to context factors, such as the risk of trusting (van de Groep et al. 2018). Trust is also sensitive to the interaction partner (Fett et al. 2014a). A behavioral study that examined trust decisions toward friends, disliked others, and strangers showed that with increasing age, adolescents trusted friends more than disliked others and strangers (Güroğlu et al. 2014a). An fMRI study with a trust game paradigm in which the other player was either trustworthy or untrustworthy showed that with increasing age, adolescents adjusted their behaviors to the behavior of the interaction partner (i.e., more trust choices toward the trustworthy partner and less toward the untrustworthy partner). This behavioral change was accompanied by increased activity in the medial PFC and TPJ and less activity in the ventral striatum (Fett et al. 2014a). This was interpreted to suggest that with trustworthy partners, the older adolescents build up the expectation that trust will be reciprocated and thereby rely more on mentalizing regions.

Reciprocity in the trust game is an important index of prosocial behavior, as there are no strategic behaviors involved. Therefore, reciprocity in the trust game shares similarities with giving behavior in the DG. Reciprocity in the trust game increases in childhood, but the patterns of reciprocity behavior in adolescence are inconsistent between studies. Studies reported increases (van den Bos et al. 2010), no age-related changes (Fett et al. 2014b), and decreases (van de Groep et al. 2018) in reciprocity behavior between 10 and 20 years of age. These findings suggest that reciprocity in adolescence is strongly dependent on contextual factors. Some evidence for specific effects in early adolescence comes from fMRI studies on reciprocity in the trust game. A prior study examining early adolescence (ages 12–14), midadolescence (ages 15–17), and young adults (ages 18–25) revealed that the medial PFC is more active when defecting trust than when reciprocating trust (van den Bos et al. 2011). Interestingly, the youngest age group showed stronger neural activity in the medial PFC specifically for reciprocity, despite similar performance. These findings are consistent with research on self-referential processing and mentalizing about thoughts and actions of others, which showed relatively stronger activity in the medial PFC for younger adolescents (Burnett et al. 2011). These findings highlight the intertwined development of other- and self-related processes. The finding that the medial PFC is especially more active in early adolescence may indicate that this is a period in life with increased sensitivity to social and self-related experiences.

4.4. Social Influence

In the previous sections, we showed that several processes, such as distinguishing between in-group and out-group, perspective taking, and reciprocal relations, are central to how adolescents balance between self- and other-oriented goals when sharing and giving to others. When making decisions that involve self and others, individuals are also strongly influenced by the opinions and behaviors of peers. These social influence effects are particularly strong in adolescence, an important period for social orientation toward peers. Traditionally, social influence has been examined from the perspective of peer influence on risky decision making (i.e., how the presence of peers influences risk-taking behavior). In experimental designs, adolescents (ages 14–18) made more risky choices compared to adults in a driving game in the presence of peers (Chein et al. 2011), and younger adolescents (ages 12–14) followed norms from peers more strongly than norms from adults (Knoll et al. 2015). Adolescents (ages 14–19) also showed stronger activity in the ventral striatum in the presence of peers (Smith et al. 2015), whereas adults (ages 24–29) recruited the lateral PFC more strongly (Chein et al. 2011). A question that was addressed in several studies was whether adolescents are also more sensitive to the opinions of peers in the domains of giving and sharing.

The question of peer influence was examined in the context of a public goods game. This game asks participants, divided in groups of four, to share their tokens with the group. The number of tokens shared is tripled, so that the greatest benefit for the entire group occurs when all individuals contribute. However, at the individual level, personal gain is highest when others contribute more than the participant. It was previously found that adolescents aged 15–17 donate similar amounts when alone than they do when observed by others. However, they donate more when peers give likes after prosocial choices, whereas they donate less when peers give likes after selfish choices (Van Hoorn et al. 2016b). These findings show that adolescents are similarly influenced by both prosocial and antisocial peers. A subsequent fMRI study included participants of two age groups: younger (ages 12–13) and older (ages 15–16) adolescents. The younger adolescents donated most to the group, and both age groups were sensitive to prosocial peer influence (there was no antisocial peer influence in this study). Also, both groups recruited the medial PFC, TPJ, and STS more strongly when peers were observing and judging their choices compared to when they were donating without being observed. The difference in activation in the medial PFC between being observed and not being observed, however, was significantly larger for the younger adolescents compared to the older adolescents, consistent with the notion that the medial PFC is more malleable in early adolescence (Van Hoorn et al. 2016a).

5. DIGITAL SOCIETY AND CULTURAL VALUES

The studies described above focus on general sensitivities to self- and other-oriented processes in adolescence, but some of these sensitivities take specific forms in the context of the current generation. Contemporary youth grow up in increasingly more complex societies compared to previous generations; they cannot imagine a society without the Internet (Baek et al. 2017, Crone & Konijn 2018). Adolescents are constantly connected to their peers and have access to information from sources all over the world. This new development brings challenges, such as problems with the regulation of privacy, addiction, cyberbullying, and public shaming (Odgers 2018, Pingault & Schoeler 2017). There are, however, also many opportunities. Compared to previous generations, contemporary youth have more possibilities to connect to others and to influence society directly through social media communication (i.e., to contribute) (Dahl et al. 2018). Youth report that they experience social media positively (Odgers 2018), and they have multiple opportunities for developing larger social networks. Whereas many of the previous social neuroscience studies focused on experiences and decision making in dyads, much less is known about brain development in the context of larger social networks, such as peer groups or societies. This perspective is, however, highly important because social networks influence individual development and vice versa (Falk & Bassett 2017, Lamblin et al. 2017). Also, ideas can spread more easily through social networks and can have a large impact on society, for example, through networks to spread political ideas, make a change for the environment, or help peers in developing countries.

Sharing ideas is associated with activity in the ventral striatum and the ventral medial PFC, a common valuation network presumed to be involved because people prefer sharing ideas when they assume that others will like them (Baek et al. 2017). It was previously found that disclosing information about the self resulted in activity in the ventral striatum and the medial PFC, which was interpreted to suggest that self-disclosure is intrinsically rewarding (Tamir & Mitchell 2012).

Receiving messages from others may also result in individuals updating their beliefs and adjusting their behaviors to the ideas of others (Tamir & Hughes 2018). Prior studies in adults revealed a common network including the anterior cingulate cortex and the insula, two regions that are often involved in error monitoring and that respond to peer feedback that deviates from one's own opinions, for example, when rating art, T-shirts, or attractive faces (Berns et al. 2010,

Campbell-Meiklejohn et al. 2010). Moreover, stronger activity in the anterior cingulate cortex correlated with more behavioral adjustment. Similar effects have been observed in adolescents in the domain of rating music and bikini models (van der Meulen et al. 2017). Together, these findings show that the brain is wired to adjust to the opinions of groups, even when these are unknown others. These findings underscore the crucial influence of social media communication on youth, given that they spend large numbers of hours online.

Recently, it was found that social integration also influences brain development. Several studies showed that social network size is correlated with brain regions that have the most protracted developmental trajectories, particularly regions involved in mentalizing (Bickart et al. 2012, Kanai et al. 2012, Powell et al. 2012). A recent fMRI study further emphasized the role of the medial PFC in explaining individual differences in how adolescents connect to their larger social world. This study showed that adolescents aged 16–17 who had more opportunities to consult unknown others within a social network recruited the medial PFC during information sharing more than adolescents with fewer connections to unknown others (O'Donnell et al. 2017). These findings were interpreted to suggest that a larger social network size gives opportunities to consult a more diverse range of opinions. Many of these findings are based on correlational effects, but it is likely that individual characteristics and social environment are mutually influencing systems. These findings provide important first steps toward a better understanding of how social networks with known and unknown others can affect how young people contribute to society (family, friends, and unknown others).

6. CONCLUSION

The goal of this review was to provide an integrative perspective on self- and other-related processes that may help understand how, when, and under which circumstances youth contribute to society. We showed that the decomposition of such processes in terms of their behavioral profiles, variability, and neural signatures provides insights into adolescent-specific sensitivities (Tamir & Hughes 2018). We argued that self- and other-related processes, which involve multiple processes that develop in an interrelated fashion, are important to understand how youth become motivated to contribute to society. The way young people balance between self- and other-oriented motives may ultimately be the best predictor of how and when they contribute to society.

A long-term contribution to society is to complete education, find a job, and stay committed to work. For adolescents, investing in education requires several interrelated self-processes, including identity development, future orientation, and inhibition of immediate impulses. We showed that these processes rely on a common network in the medial PFC that is particularly involved when thinking about self traits, and that works closely together with the ventral striatum, TPJ, and lateral PFC. Previous studies suggested that individuals who are better able to inhibit impulses and work toward long-term goals are more likely to succeed in multiple domains in life, including work and education (Moffitt et al. 2011), which is possibly linked to the development of structural and functional connections between the ventral striatum and the PFC (Achterberg et al. 2016). How can adolescents be motivated to contribute by staying committed to education and work? These values may be dependent on values within the family and on goals that provide feelings of commitment, purpose, and meaning (Dahl et al. 2018, Fuligni 2019).

A second important development for contributing to society involves the development of healthy intergroup relations, which are fundamental in a diverse society. We previously found that adolescents develop in-group versus out-group differences in donating behavior during adolescence (Güroğlu et al. 2014a). Neuroimaging studies in adults report that adult participants show stronger reward activity when they interact with in-group members compared to out-group

members (Hughes et al. 2017). Thus, other-oriented choices are driven by both prosocial motivations and selfish motives, and prosocial behavior becomes more strongly oriented toward in-group members when adolescents grow up. We argued that the developmental changes in the communication between the medial PFC and the ventral striatum may be important for experiencing social values for others and developing a social identity (Jankowski et al. 2014, Telzer et al. 2013).

How can out-group motivations be stimulated in adolescence? A recent study showed that when adult participants are viewing crowdfunding websites (i.e., websites that provide financial support to individuals and groups), they engage the ventral striatum, a region that is particularly sensitive in adolescence. Participants who engaged the ventral striatum more while observing crowdfunding subsequently donated more (Genevsky et al. 2017). Adult participants also show stronger ventral striatum activity when other people are watching their donation decisions than when they are alone (Izuma et al. 2010). These findings show at least two important motivators that may influence adolescents' behavior: being rewarded during group activities and being observed by others. These two activities may affect the goals of adolescents to develop larger social networks and reduce in-group/out-group distinctions. When these motivations promote self-esteem and a positive self-image, they may have a reinforcing effect on prosocial values (Crocetti et al. 2016). Thus, when self-oriented motives align with other-oriented motives, they have the greatest chance to result in meaningful contributions to society.

To provide opportunities for youth to contribute and to ensure healthy psychological development, the most impact can probably be achieved through goals that are aligned rather than conflicting. An important direction for future research is to examine self- and other-oriented processes in different contexts, such as education and social relations (family and peers). Some interesting initial insights emerged from social neuroscience studies may provide a starting point for adolescent-specific interventions. Researchers have recently argued that most opportunities to create change in intervention designs arise when the goals of the intervention (e.g., reducing smoking) align with the goals of the adolescents (e.g., creating impact) (Yeager et al. 2018). It has also been argued that adolescence is characterized by a strong need to contribute, possibly driven by the need to be admired (Yeager et al. 2018) and the need to perform actions that have purpose and meaning (Fulgini 2019). These opportunities could be created in domains such as educational achievement (e.g., contributing to advancing the school curriculum), peer networks (e.g., becoming influencers, organizing larger social networks) and society at large (e.g., promoting social safety, reducing inequalities, changing climate policies). In each of these domains, a better understanding of the processes underlying self-development, perspective taking, and the valuing of the needs of others can help reduce parochialism and increase creative opportunities for social influence and societal impact. During adolescence there are dynamic changes in recruitment of the medial PFC, a region important for both self- and other-related processes. These dynamic changes are key to the intertwined development of self and others, especially in the way that the medial PFC communicates with social brain regions such as the TPJ and with social-affective subcortical regions such as the ventral striatum. Adolescence, a key moment in the maturation of the neural networks that underlie the cognitive, social, and affective skills central to these processes, would seem to be an ideal time to provide social and personal learning opportunities.

SUMMARY POINTS

1. Self- and other-oriented development are intertwined developmental processes that both involve the medial prefrontal cortex.

2. Perspective taking in terms of cognitive mentalizing develops further in adolescence and relies on a network of social brain regions including the medial prefrontal cortex and the temporal parietal junction.
3. Giving and sharing is dependent on contextual factors such as in-group/out-group preferences and reciprocal relationships. Between childhood and adulthood, there is a transition from rule-based sharing to contextual sensitivity.
4. Vicarious gaining relies on similar social-affective brain regions as gaining for self, including the ventral striatum. In adolescence, these processes are intertwined for close family members and in-group peers.
5. The development of self- and other-oriented processes may ultimately predict how young people contribute to society in terms of education and intergroup relations.

FUTURE ISSUES

1. Are there sensitive windows in the development of the medial prefrontal cortex for developing a coherent self-concept and identity?
2. How do adolescents balance between multiple self-relevant goals, such as completing school assignments and engaging in social activities?
3. What is the role of social status in adolescence when investing in demands by society?
4. What is the role of the developing brain for complex future-oriented choices related to education, work, and other contributions to society (e.g., volunteering)?
5. Which new social opportunities are provided by growing up in a digitalized society with connections to others in different geographical locations?
6. How does elevated reward sensitivity in adolescence, for example, in response to social media likes, create both challenges and opportunities to become good citizens?

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This timely review raised the important question of whether neural changes during adolescence provide a window for increased social influence.

One of the first functional neuroimaging studies showing that vicarious gaining for others is dependent on experienced closeness with the target.

Important study showing for the first time that peers influence neural activity when taking risks more in adolescents than in adults.

Elegant functional neuroimaging study showing how building reciprocal relations during multiple trust trials results in stronger medial prefrontal cortex activity in adolescents compared to adults.

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This large behavioral study indicates a sensitive window for peer sensitivity, especially in early adolescence.

This longitudinal structural neuroimaging study demonstrated prolonged developmental changes in social brain structures over the entire adolescence period.

This functional neuroimaging study in adults demonstrated that neural activity in the ventral striatum during vicarious rewards relates to real-life prosocial behavior.

The first functional neuroimaging study demonstrating heightened medial prefrontal cortex activity when adolescents evaluate traits of themselves.

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Highly innovative longitudinal study showing that the same neural sensitivity in the ventral striatum can lead to multiple pathways in development.

Influential review article showing the importance of evaluating adolescents' needs for social status and admiration when developing successful interventions.



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