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Güroğlu, B.

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ARTICLE

The power of friendship: The developmental significance of friendships from a neuroscience perspective

Berna Güroğlu 

Leiden University, Leiden, The Netherlands

Correspondence

Berna Güroğlu, Department of Developmental and Educational Psychology, Leiden University, Pieter de la Court Building, Wassenaarseweg 52, 2333 AK Leiden, The Netherlands.
Email: bguroglu@fsw.leidenuniv.nl

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Abstract

Forming and maintaining friendships is one of the most important developmental tasks in adolescence. Supportive and high-quality friendships have been related to positive developmental outcomes and mental health, both concurrently and in the long term. Friendships also protect against negative effects of adverse experiences, such as peer victimization and internalizing behaviors. Despite this ample evidence relating friendships to well-being, we know relatively little about the underlying mechanisms involved. In this article, I review brain imaging research on friendships and highlight its contribution to our understanding of how interactions with friends relate to well-being. Studies suggest that friendships involve reward and motivational processes (involving the ventral striatum and the ventromedial prefrontal cortex), and self- and other-related mentalizing processes (involving the medial prefrontal cortex and the temporoparietal regions). I conclude with suggestions for research on how neural patterns relate to individual differences in psychosocial outcomes and mental health.

KEY WORDS

brain development, friendships, rewards

“To me, my friends are my everything,” says a 16-year-old when asked about her friendships. This is a sentiment many people might recognize, particularly from their teenage years: Most 10- to 18-year-olds name a friend as one of the top three most important people in their lives (Kiesner et al., 2004). Friendships contribute to positive psychosocial adjustment in multiple domains, such as greater well-being, lower symptoms of depression, less delinquent and risky behaviors, and higher academic achievement; they also protect against the negative effects of victimization and internalizing behaviors (Bagwell & Bukowski, 2018; Vitaro et al., 2009). Supportive adolescent friendships also predict healthy

psychosocial functioning later in life (Van Harmelen et al., 2017) and their benefits even extend to lower death rates and longer life (e.g., Holt-Lunstad et al., 2010).

Developmental psychologists have emphasized the increasing developmental significance of friendships across childhood and adolescence, which cannot be understood without examining friendship characteristics such as friendship stability or quality (Hartup, 1996). Whereas friends in early childhood mainly provide companionship and fun, adolescent friendships also start fulfilling other needs for trust, intimacy, attachment, and emotional support (Berndt, 2004; Hartup & Stevens, 1997). This developmental change in friendship

Abbreviations: fMRI, functional Magnetic Resonance Imaging; IPL, inferior parietal lobule; mPFC, medial prefrontal cortex; NAcc, nucleus accumbens; PFC, prefrontal cortex; pTPJ, posterior temporoparietal junction; SES, socioeconomic status; SPL, superior parietal lobule; TPJ, temporoparietal junction; vmPFC, ventromedial prefrontal cortex; VS, ventral striatum.

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quality is also reflected in prosocial behavior toward friends. With age, adolescents show increasingly more giving, sharing, and trusting behaviors toward their friends and thereby also differentiate more between friends and other disliked, neutral, or unfamiliar peers (Güroğlu et al., 2014).

Despite a large body of evidence on the contributions of friendships to social and emotional development and mental health, we know relatively little about the underlying mechanisms involved. In the last two decades, researchers have conducted more neuroimaging studies investigating the neural basis of social interactions with familiar and unfamiliar peers (for reviews, see Güroğlu, 2020; Güroğlu & Veenstra, 2021). Functional Magnetic Resonance Imaging (fMRI) is a safe and non-invasive brain imaging technique that can easily be used in developmental studies to investigate brain function. Imaging paradigms allow for concurrent assessments of information processing without relying on retrospective self- or other reports or observations. This cognitive neuroscience approach provides unique information by, for example, allowing researchers to examine whether the same neural response underlies different behavioral outcomes or when a behavioral response is absent (e.g., examining how the mere presence of peers modulates neural activation patterns).

In this article, I review research examining friendships from a developmental cognitive neuroscience perspective and demonstrate that evidence supports the specific involvement of reward and mentalizing processes in friendships. Throughout the article, I highlight the contributions of these neuroscientific findings in understanding how friendships relate to developmental outcomes and mental health, and I discuss directions for research.

FRIENDSHIPS AND REWARDS

Rewards refer to stimuli of positive reinforcement; they are an appetitive stimulus that acts as a reinforcer and when associated with a certain behavior, are likely to increase the probability of that behavior occurring. Rewards can be basic, such as eating a favorite food, or social and more complex, such as spending time with a good friend. Are friendships special because they are rewarding? This was the question behind a neuroimaging study investigating the neural correlates of social interactions with friends (Güroğlu et al., 2008). Addressing how friendships differ from other peer relationships requires comparing brain activity during interactions with different types of peers. My colleagues and I recruited a *complete* peer group (a student orchestra), consisting of a relatively homogeneous sample of university students, mostly from a Western European background, to participate in the study. Prior to the scanning session, the students provided information on their relationships

with each orchestra member, which enabled modulation of the social interaction simulation task used in the scanner. During the task, students were presented with a personalized set of stimuli consisting of their friends, as well as disliked and neutral peers. On each trial, they were invited to imagine that they saw one of these peers in a real-life setting, and were asked to indicate whether they would like to approach the individual to start an interaction, move away to avoid an interaction, or do neither (i.e., remain neutral). Several brain regions—the ventral striatum (VS), including the nucleus accumbens (NAcc), the amygdala, the hippocampus, and the ventromedial prefrontal cortex (vmPFC)—were involved more significantly in interactions with friends than in interactions with other peers (see Figure 1).

The involvement of the vmPFC and the VS during interactions with friends is striking. By now, researchers agree on the central role of the VS in the reward circuitry of the brain (e.g., Delgado, 2007). Together, the vmPFC and the VS have been hypothesized to form a *valuation system* in the brain (cf. Bartra et al., 2013), where they guide decision making by responding to rewards, including money, social rewards (e.g., social interactions, social status, social behavior; see Pfeiffer et al., 2014), and vicarious rewards (i.e., rewards for close others, such as best friends, mothers, and fathers, but not for disliked or unfamiliar others; see Braams et al., 2014; Brandner et al., 2021). The VS and the vmPFC in young adults also show more activation when they watch emotional stimuli and believe their friend is also watching these stimuli (i.e., during sharing of emotions) than when they watch the same stimuli alone (Wagner et al., 2015).

The importance of the reward system for friendships is further supported by two studies that examined the neural basis of prosocial and selfish decision making in the peer context in adolescence (Schreuders et al., 2019) and young adulthood (Schreuders, Klapwijk, et al., 2018). These experimental studies combined simple allocation game paradigms to assess prosocial behavior with fMRI to determine their underlying neural correlates. The study participants were predominantly of Western European backgrounds and came from mid- to high-socioeconomic status (SES) families. Participants were asked to share valuable coins with another player who was either a friend, a disliked peer, a neutral peer, or an unfamiliar peer. Friends, disliked peers, and neutral peers were identified using sociometric nominations by classmates prior to the scanning session. On each trial of the fMRI task, participants could choose one of two coin distributions, with one leading to a more optimal outcome for the other player (i.e., prosocial choice). On average, both adults and adolescents chose prosocial distributions for their friends more frequently than for other peers, and they made prosocial decisions less frequently (i.e., suggesting selfishness) for disliked peers.

In both age groups, prosocial decisions for friends were related to more frequent activity in the putamen,

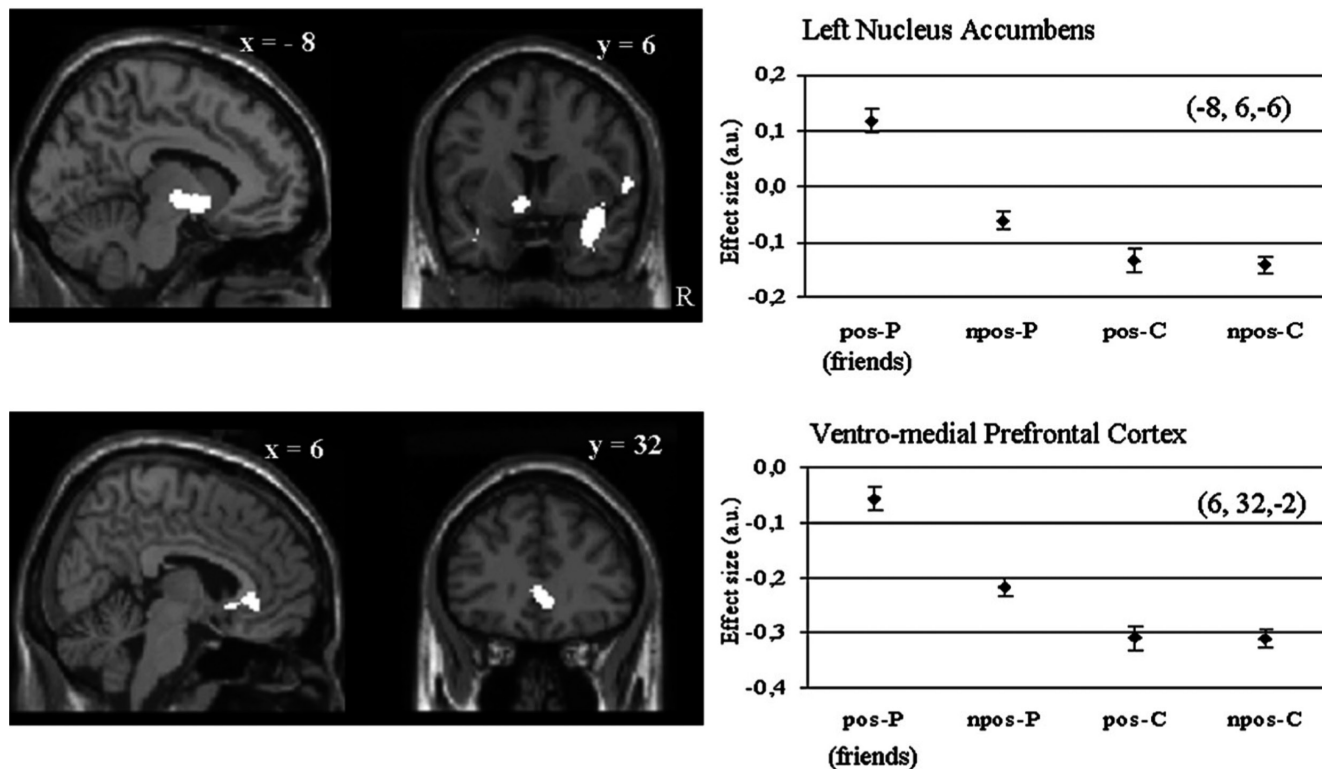


FIGURE 1 Brain regions of activation during social interactions with friends. Social interactions with friends relate to higher activation in the nucleus accumbens and the ventromedial prefrontal cortex. *Note:* npos-C, nonpositive celebrity; npos-P, nonpositive peer; pos-C, positive celebrity; pos-P, positive peers (i.e., friends). Reprinted with permission from Güroğlu et al. (2008)

a part of the VS. This heightened activity during prosocial choices in the context of friendship (i.e., a positive relationship) might have implications for the continuation of prosocial behavior, and hence for the continuation of positive interactions. In young adults, selfish decisions for disliked others were also related to higher putamen activation. Based on the involvement of the same brain region in prosocial decisions for friends and selfish decisions for disliked peers, the same neural basis might contribute to forming or maintaining relationships over time, where friendships are sustained by prosocial behaviors, whereas relationships based on dislike are sustained by selfish behaviors. Developmental comparisons and longitudinal studies are needed to investigate the neural processes that underlie how social interactions evolve into relationships over time.

One longitudinal study (again, of adolescents from Western European and mid- to high-SES families) investigated age-related changes in neural responses while winning rewards for best friends across 4 years (Schreuders et al., 2021). Specifically, the study examined developmental patterns of vicarious reward processing in the NAcc in relation to friendship stability across the 4-year period. Individuals with stable and unstable friendships differed in the developmental trajectories of NAcc activity over time. Striatum activity while winning for best friends changed quadratically in

adolescents with stable best friendships, with a peak in midadolescence, whereas changes in striatum responses did not change by age in adolescents with unstable best friendships when winning for their best friend. In other words, a relationship characteristic (i.e., stability) modulated the developmental pattern of neural responses related to outcomes that concerned the person in the relationship. Given the unique neural responses to winning for best friends in the stable friendship group, the results suggest that adolescence is a sensitive time to develop close relationships.

In another study, VS responses to winning for the best friend correlated positively with positive friendship quality (e.g., trust, support, intimacy) for 8- to 25-year-old females (Braams et al., 2014). In the study mentioned earlier, putamen activity during prosocial choices for friends related negatively to negative friendship quality (e.g., fighting, arguing) in midadolescence, suggesting that adolescents with high levels of negative friendship quality had lower VS activity when they acted prosocially toward their friends (Schreuders et al., 2019). In another study mentioned earlier, for participants with unstable friendships, VS response to winning for friends related positively to friendship closeness (Schreuders et al., 2021). Together, these findings support the idea that reward and motivational responses to positive outcomes for best friends relate to friendship characteristics, such as stability and quality.

FRIENDSHIPS AND MENTALIZING

Friendships differ from other relationships not only in terms of their rewarding or motivational value but also in terms of behavior toward friends when compared to others. With age, young children develop a strong preference for ingroup members (Fehr et al., 2008), with 5- to 6-year-olds already sharing significantly more with their friends than with strangers (Yu et al., 2016, a study of Chinese children that is in line with prior findings from Western, middle-class samples). This differentiation of friends from other peers in terms of prosocial behavior (e.g., in giving and sharing) also increases with age across adolescence (Güroğlu et al., 2014). Sharing with friends is independent of strategic concerns such as expectations of reciprocity (Lenz & Paulus, 2021) and is related to perspective-taking skills (Van de Groep et al., 2019). Moreover, age-related increases in self-reported perspective-taking skills across adolescence mediate age-related increases in prosocial behavior toward friends (Güroğlu et al., 2014). As such, evidence suggests a role for mentalizing processes, which broadly refer to understanding others' minds, perspectives, and intentionality, in social behavior toward friends.

The relevance of mentalizing skills for prosocial behavior toward friends is also supported by two neuroimaging studies on social decision making with friends (Schreuders, Klapwijk, et al., 2018; Schreuders et al., 2019). When making prosocial decisions for friends compared to disliked or unfamiliar others, the posterior parietal brain regions around the temporoparietal junction (TPJ) had stronger activation in both young adults and adolescents; earlier studies suggest these regions are involved in mentalizing processes, such as understanding intentionality and perspective taking (see Figure 2). One explanation for these findings is that prosocial behaviors for liked others are supported more readily by integrating others' perspectives into decision making. Individuals who think about others more frequently may also be more likely to behave prosocially in interactions, which may relate to developing and maintaining positive relationships like friendships. Considering that the

posterior-parietal brain regions develop in a protracted way across adolescence (Tamnes et al., 2017), development in the regions that support thinking about others might also explain changes in friendships across adolescence, when social concepts such as trust and support become increasingly more important.

A recent study on brain structure using the same sample as described previously (Braams et al., 2014; Schreuders et al., 2021) also supports the role of mentalizing processes in friendships (Becht et al., 2021). In the study, of 8- to 25-year-olds, researchers examined the link between friendship quality and structure of the *social brain network* (i.e., the brain regions involved in social cognition). Stronger cortical thinning in the medial prefrontal cortex (mPFC) was related to increasing levels of friendship quality over time. The mPFC is involved in self-referential processes, in comparing oneself to others, and in the development of self-concept and the integration of perspectives related to self and others (Crone & Fuligni, 2020). As such, accelerated cortical thinning of the mPFC might reflect regional specialization or fine tuning of the neural circuits related to processing mental states of the self in relation to others. In experimental studies, mPFC involvement in the peer context (i.e., when being observed by a peer) was higher in early adolescents than in older adolescents (Somerville et al., 2013; Van Hoorn et al., 2016). This heightened mPFC activity was also related to self-reports of feeling embarrassed, which indicates self-consciousness (Somerville et al., 2013). Tentatively, young adolescents might process social information regarding their interaction partner more in relation to themselves, which might contribute to the formation of the relational aspects of self-concept (Crone & Fuligni, 2020).

Together, these findings that link TPJ and mPFC activity to friendships can be interpreted to suggest that friendships relate to how individuals process the social world around them. In one study, of 25- to 32-year-olds from mostly Western European backgrounds, similarity in neural processing of social interactions in the temporoparietal brain regions predicted social distance within a social network of friends (Parkinson et al., 2018). In

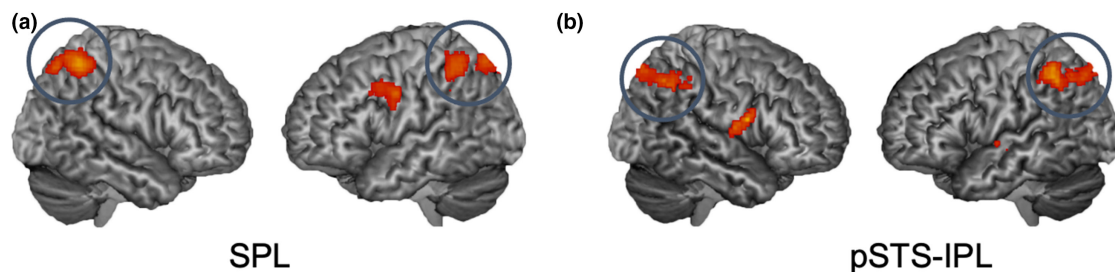


FIGURE 2 Prosocial behavior towards friends relate to higher activation in the temporo-parietal brain regions. (a) Brain regions involved in the contrast of prosocial choices for friends > for unfamiliar peers in an adolescent sample (Schreuders et al., 2019). (b) Brain regions involved in the contrast of prosocial choices for friends > disliked peers in a young adult sample. *Note:* IPL: inferior parietal lobule (encircled in (b)); pTPJ: posterior temporoparietal junction; SPL: superior parietal lobule (encircled in (a)). Reprinted with permission from Schreuders et al. (2018) and Schreuders et al. (2019).

another study, of 7- to 8-year-olds, most of whom were from Western European backgrounds, closeness in a classroom friendship network related positively to similarity of the structure of the social brain network, including the TPJ, the mPFC, and the precuneus (D'Onofrio et al., 2021). Considering the correlational nature of these findings, we cannot make causal inferences. But we can speculate that mentalizing processes and similarity therein might support forming and continuing friendships by an enhanced social focus on the other person. Friendship experiences over time might also promote prosocial and other-regarding behaviors, which might be reflected in brain structure and function. Researchers need to examine these bidirectional links between changes in friendship characteristics and the neural processes that support the development of positive relationships across adolescence.

CONCLUDING REMARKS AND LOOKING AHEAD

Taken together, the neuroimaging studies I have reviewed highlight the involvement of brain regions that support neural processes related to reward and mentalizing in interactions with friends. Specifically, friendships involve reward and motivational processes supported by activation of the VS and the vmPFC, as well as self- and other-related mentalizing processes supported by activation of the TPJ and the mPFC (see Figure 3). Although current research does not allow for strong conclusions, these findings point to several avenues for study.

First, the involvement of reward-related brain regions in interactions with friends is intriguing from a developmental perspective. In contrast to the protracted developmental trajectory of the cortical brain regions, subcortical regions such as the VS develop more with the onset of puberty (Nelson et al., 2005). For example, the response of the NAcc to monetary rewards increases with age across adolescence and peaks around ages 15 to

16 (Schreuders, Braams, et al., 2018). Along these lines, in one study, increased risk-taking behavior in the presence of friends (compared to when alone) was related to increased striatum activity in adolescence (Chein et al., 2011). Therefore, we can hypothesize that early adolescent sensitivity to the social context of friendships might be explained by heightened neural sensitivity to social rewards. Most research on the neural processes in relation to friendships has been conducted with young adults. More studies with developmental samples are needed to test whether the developmental trajectories of brain regions involved in reward and motivation relate to the developmental significance of friendships in early and midadolescence.

Second, we can distinguish between findings from studies that have examined neural patterns related to behavior (i.e., decision-making) in the context of relationships (cf. Chein et al., 2011; Schreuders, Klapwijk, et al., 2018; Schreuders et al., 2019; Van Hoorn et al., 2016) and findings from studies that have examined neural processing without behavioral output (cf. Parkinson et al., 2018; Schreuders et al., 2021; Somerville et al., 2013). Because behavior is often strongly coupled with relationships (e.g., more prosocial choices for friends and selfish choices for disliked peers), it is challenging to disentangle the neural basis of behavior (independent of context) from processes that are modulated strongly by context. However, studies that use fMRI tasks and that do not assess behavior (e.g., assessing reward processing or the effects of peer presence) benefit from behavioral assessments that can be related to imaging results, such as friendship characteristics (Schreuders et al., 2021), assessments of emotional states (Somerville et al., 2013), and social networks (Parkinson et al., 2018). Ultimately, longitudinal investigations are crucial to examine the causal relations among neural processes, social behavior, and the development of friendships.

Finally, the ultimate question is whether brain research can provide information on how friendships contribute to positive well-being and mental health. Altered

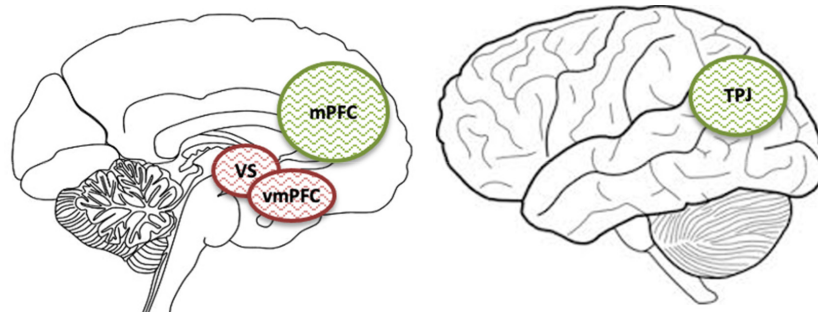


FIGURE 3 Brain regions implicated in interactions with friends. Brain regions implicated in reward and motivational processes (in red) and self- and other-related mentalizing processes (in green) underlie interactions with friends. These processes related to reward and mentalizing may be mechanisms through which friendships contribute to positive psychosocial adjustment and protect individuals against negative developmental outcomes. *Note:* mPFC: medial prefrontal cortex; TPJ: temporoparietal junction; vmPFC, ventromedial prefrontal cortex; VS, ventral striatum

functioning of both the striatum and the vmPFC has been linked to loneliness, mood disorders (e.g., depression), and other adversities like cumulative stress (e.g., Davey et al., 2008; Hanson et al., 2016). As such, the VS may play a crucial role in the link between early life adversity and the later development of depression (Goff & Tottenham, 2015). Although the link between activation of the VS and the vmPFC and social interactions with friends is correlational, it might suggest that friendships have an inherently positive impact on individuals through activation of reward circuitry. This speculation is based on analogies with tonic activation (i.e., sustained neural responses) in the VS and the vmPFC in friendship contexts. By increasing tonic activity in these brain regions, friendships might protect against depressed mood or, in turn, a lack of interactions with friends may decrease tonic activity, resulting in an increased vulnerability for depression (cf. Güroğlu et al., 2008).

Processes underlying reward and motivation are one way friendships might influence well-being. In a study, activation of the TPJ, along with activation of other social brain regions such as the mPFC and the precuneus, supported the mental health of romantic partners (Dodell-Feder et al., 2016), suggesting that processes underlying social cognition might also explain the link between positive relationships and well-being. Moreover, friendships might contribute to well-being in other ways. In one study, adolescents who spent more time with their peers had fewer neural responses 2 years later to adverse social experiences, such as social exclusion (Masten et al., 2012). Positive interactions with friends may contribute to mental health by reducing activation of a neural “alarm” system involved in social exclusion. Individuals who are less sensitive to negative social experiences, such as social exclusion, may also be more likely to have friends and spend more time with them. Finally, mechanisms may involve connectivity patterns across different brain regions. Functional connectivity between brain regions of cognitive control (in the prefrontal cortex [PFC]) and motivation (in subcortical areas) develops and strengthens with age, which may underscore the developmental significance of motivation for behavior regulation (Somerville & Casey, 2010). Connectivity between subcortical brain regions of reward and valuation (supported by positive interactions with friends) and the PFC involved in the control of negative emotions might underlie the protective role of friendships and should be further investigated.

In conclusion, the studies I have reviewed illustrate that neuroimaging techniques offer valuable insights into the neural processes involved in friendships. I focused exclusively on fMRI studies that examined relations between neural processes and friendships. The developmental changes I discussed (i.e., brain development and social development) are affected by puberty-related hormonal changes, which are also associated with mood and anxiety disorders (Davey et al., 2008; Nelson et al.,

2005). In recent models, social and neural mechanisms have been suggested to mediate the link between puberty and the development of internalizing problems (Pfeifer & Allen, 2021). Moreover, considering the higher prevalence of mood and anxiety disorders in girls, as well as gender differences in friendship characteristics (e.g., girls report higher levels of friendship closeness and quality; Schreuders et al., 2021), gender might moderate how pubertal processes relate to brain and social development. Therefore, to understand thoroughly the developmental significance of friendships and their contributions to well-being, researchers must also examine puberty and gender effects.

Finally, research reported here is based predominantly on samples from Western Europe and the United States, so results might be biased. Despite similarities across friendships from different cultures, cultural differences also exist. Researchers need to acknowledge friendships as a multifaceted and complex phenomenon and investigate cross-cultural differences in the neural underpinnings of friendships (Keller, 2004).

Recently, researchers have had greater interest in investigating individual differences within neuroscience research (Becht & Mills, 2020). Investigating the mechanisms of how friendships contribute to resilience and mental health requires longitudinal research that combines neuroimaging assessments with behavioral measures of not only physical and mental health outcomes but also individual characteristics. Researchers studying friendship from a neuroscience perspective should integrate individual differences (e.g., investigating links with friendship quality or social competence), long-term peer experiences (e.g., friendship stability, status in the peer group such as chronic peer rejection), and health outcomes (e.g., well-being, internalizing or externalizing problems). Such an integrative approach will aid in understanding the transactional links among friendship contexts, neural systems, and trajectories of developmental outcomes.

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ORCID

Berna Güroğlu  <https://orcid.org/0000-0002-5418-8737>

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