

Neurobiological susceptibility to peer influence in adolescence

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Abstract and Keywords

Peers have a profound impact on shaping adolescents' attitudes and norms about the consequences of engaging in health risk behaviors. However, not all adolescents are equally susceptible to peer influence. Thus, a question that remains unanswered is whether there are potential biomarkers that index an individual's level of susceptibility to peer environments. The present review considers emerging evidence on the construct of peer influence susceptibility and proposes neurobiological biomarkers that might render some adolescents more susceptible to peer influence than others. Using a differential susceptibility framework, this chapter discusses how individual variation in peer influence susceptibility interacts with different types of peer environments (e.g., risk-promoting versus risk-averse) to predict shifts in adolescent behavior. This perspective suggests that a heightened susceptibility to peer influence may not only increase maladaptive, antisocial behavior in negative peer environments, but may also promote adaptive, prosocial behavior in positive peer environments.

Keywords: adolescence, risk taking, neurobiological susceptibility, peer influence, biomarkers, functional magnetic resonance imaging (fMRI), differential susceptibility

Introduction

Across rodents, non-human primates, and humans, adolescence is marked by a universal "social restructuring" characterized by increasingly complex social development (e.g., perspective taking) and inhibitory control and a reorientation from parental to peer contexts (Blakemore and Mills, 2014; Nelson, Leibenluft, McClure, and Pine, 2005). Compared with children, adolescents spend more time with peers, form more sophisticated and hierarchical social relationships, are more sensitive to peer acceptance, and become increasingly self-conscious (Blakemore and Mills, 2014; Brown, 2004; Steinberg and Morris, 2001). This social reorientation and heightened sensitivity to peer contexts may render adolescents particularly susceptible to social influence. Indeed, compared to children and adults, adolescents engage in more risk taking in the presence of peers (e.g., Gard-

ner and Steinberg, 2005), tend to conform to the attitudes of their peers about risky (Knoll, Magis-Weinberg, Speekenbrink, and Blakemore, 2015) and prosocial (Foulkes, Leung, Fuhrmann, Knoll, and Blakemore, 2018) behaviors, show heightened embarrassment when being observed by their peers (Somerville et al., 2013), and show compromised emotion regulation in the presence of socially appetitive cues (Perino, Miernicki, and Telzer, 2016; Somerville, Hare, and Casey, 2011). Heightened social influence susceptibility may reflect maturational changes in how the brain responds to social information. Indeed, functional reorganization and maturation of the developing brain continues well into young adulthood (Sowell et al., 2003, 2004). Such neural plasticity, in conjunction with dynamic social environments, may render adolescents particularly sensitive to social influences in their environment and play a critical role in shaping both positive and negative developmental trajectories.

The current chapter presents emerging findings from developmental science, social psychology, and cognitive neuroscience that begin to address the construct of susceptibility to peer influence, particularly in moderating adolescents' conformity to their peers' risky behaviors. First, we provide a brief overview of the increasingly salient role of peers in socializing risk-related attitudes and behaviors during adolescence. Using the differential susceptibility theory as a framework, we consider how an individual's social influence susceptibility emerges and interacts with various peer environments in ways that provoke shifts in adolescent behavior. We then explore candidate biomarkers of social influence susceptibility that may index an individual's level of susceptibility to social contexts, with a particular focus on neurobiological biomarkers. Finally, we conclude with future directions examining how a heightened susceptibility to peer influence can facilitate both adaptive and maladaptive behavior, depending on the type of peer environment.

Peer influences on adolescent risk taking

A widely held belief shared by many parents, educators, and policymakers is that peers steer youth toward engaging in negative, health-compromising behaviors that they otherwise would not have participated in alone. Indeed, decades of research have shown that peers' engagement in risk-taking behaviors is a consistent and robust predictor of adolescents' own risk-taking behaviors (Prinstein and Dodge, 2008). In fact, peer interactions in infancy and toddlerhood start to facilitate the early ontogeny of group reputation concerns (Engelmann, Herrmann, and Tomasello, 2018; Engelmann, Over, Herrmann, and Tomasello, 2013) and norm-based behavior, such as learning and reinforcing contextual and societal norms (Schmidt, Butler, Heinz, and Tomasello, 2016; Schmidt, Rakoczy, and Tomasello, 2012; reviewed in Tomasello, 2014), both of which contribute to individuals' susceptibility to social influence. However, often overlooked is that conformity to peer influences can be a positive social skill throughout human ontogeny, and perhaps especially in adolescence, because it enables individuals to develop stronger affiliations with others and gain entry into diverse social groups (Tomasello, 2014, 2016; Tomasello, Kruger, and Ratner, 1993). Compared to those with a lower susceptibility to peer influence, individuals with a greater susceptibility to peer influence may be more likely to leverage this de-

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veloping social skill, thus benefiting from the many important and meaningful social connections inherent in conforming to others. Despite the social advantages conferred by peer conformity, researchers have primarily examined how an increased susceptibility to peer influence can exacerbate associations between peer influence and disproportionate rates of risk taking during adolescence (Allen et al., 2006; Prinstein et al., 2011; Widman et al., 2016). Studying individual differences in susceptibility to peer influence represents a promising opportunity to disentangle the person- versus environment-specific factors that contribute to both the positive and negative effects of peer conformity during adolescence.

Peer environments afford a unique opportunity for adolescents to develop and update their own risk-related attitudes and behaviors over time. Several theories from social and developmental psychology have suggested that conformity is motivated by a desire to align oneself with positive role models and consequently develop a more favorable sense of self-identity (Baldwin, 1895; Berger, 2008; Cooley, 1902; Gibbons, Gerrard, Blanton, and Russell, 1998; Mead, 1934). Being especially attuned to social evaluation as peer relationships become increasingly salient may lead some adolescents to conform to the norms and behaviors of their peer group in an effort to enhance social belonging (i.e., “fitting in”) or establish a more favorable self-identity. Adolescents often prioritize enhancing their reputational status to a greater extent than children and adults—even beyond their pursuit of friendships, romantic interests, or personal achievements (e.g., academic) (LaFontana and Cillessen, 2010). Adolescents who have, or value attaining, high social status are particularly susceptible to peer influence, which has long-term consequences on health outcomes (Cillessen and Mayeux, 2004). For example, peers’ deviant behaviors predict adolescents’ future deviant behaviors, especially among adolescents who are highly susceptible to high-status peers (Choukas-Bradley, Giletta, Widman, Cohen, and Prinstein, 2014; Prinstein, Brechwald, and Cohen, 2011).

Adolescents’ engagement in health risk behaviors is not only shaped by the type of peers that an individual selectively affiliates with (peer selection), but also by the actual or perceived norms of the peer group (peer socialization). Shifts in risk-related attitudes or behaviors can occur in response to social influence from one peer, small peer groups, or broader social networks, which also vary in magnitude based on the strength and quality of those social ties (reviewed in Telzer, Rogers, and Van Hoorn, 2017). The most common method of understanding risk-taking trajectories is investigating the degree to which perceived and actual peer norms socialize adolescents’ engagement in health risk behaviors over time (reviewed in Albert et al., 2013; Brechwald and Prinstein, 2011; Simons-Morton and Farhat, 2010), as (mis)perceptions of peer norms about risk taking have been shown to redirect adolescents’ antecedent attitudes and behaviors toward riskier *and* healthier outcomes. Peers can socialize adolescents’ risky decision making in both implicit and explicit ways. Implicit forms of peer influence include positive reinforcement of deviant behavior during peer interactions (i.e., deviancy training) (Dishion, Spracklen, Andrews, and Patterson, 1996), being physically present (e.g., Gardner and Steinberg, 2005), or modeling specific attitudes or behaviors that are then internalized by adolescents as valued in the peer context (e.g., Cascio et al., 2015; Knoll, Leung, Foulkes, and Blakemore, 2017;

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Knoll et al., 2015; Welborn et al., 2015). In some cases, adolescents over- or under-estimate peers' attitudes and behaviors around health risk behaviors and use these erroneous peer norms to guide their own decisions, a phenomenon known as the false consensus effect (Helms et al., 2014; Prinstein and Wang, 2005). Importantly, peer norms need only be perceived to influence behavior, as perceptions of peers' risk behaviors can be an even stronger predictor of adolescents' own risk behavior compared to actual peer behavior (Fromme and Ruela, 1994; Iannotti and Bush, 1992; Slagt, Dubas, Deković, Haselager, and van Aken, 2015). Peers can also influence adolescent behavior explicitly, by providing feedback (e.g., likes) (e.g., van Hoorn, van Dijk, Güroğlu, and Crone, 2016; van Hoorn, van Dijk, Meuwese, Rieffe, and Crone, 2014) or verbally reinforcing group norms (e.g., Chein, Albert, O'Brien, Uckert, and Steinberg, 2011). Although both forms of peer influence are associated with changes in adolescents' health-related risk taking (e.g., Cascio et al., 2015; Chein, Albert, O'Brien, Uckert, and Steinberg, 2011; Dishion, Spracklen, Andrews, and Patterson, 1996; Falk et al., 2014), previous work suggests that explicit peer influence may be more effective at altering adolescent risk behavior than implicit forms of peer influence (Engelmann, Moore, Monica Capra, and Berns, 2012; Munoz Centifanti, Modecki, Maclellan, and Gowling, 2014; Somerville et al., 2018). However, implicit or indirect peer pressures likely occur more frequently in real life (Simons-Morton and Farhat, 2010).

Increasingly, researchers are showing that peer effects on adolescents' risky decisions are more nuanced than previously reported. Peers can redirect adolescent risk behavior toward fundamentally different health outcomes based on the extent of peer involvement (e.g., mere presence versus peer monitoring), type of decision context (e.g., "hot" or "cold" decisions), and whether risk outcomes additionally impact others (Do, Guassi Moreira, and Telzer, 2016; Powers et al., 2018; Somerville et al., 2018). Furthermore, the association between peers' and adolescents' risk-taking behaviors can be moderated by several psychosocial factors at the individual level (reviewed in Brechwald and Prinstein, 2011). For example, individual differences in self-regulation (e.g., Gardner, Dishion, and Connell, 2008), social reputation (e.g., Prinstein, Meade, and Cohen, 2003), and family conflict (e.g., Prinstein, Boergers, and Spirito, 2001) can exacerbate or buffer the degree to which peer pressures alter health-related attitudes or behaviors. Taken together, these findings suggest that although peers strongly influence adolescent risk taking, several environmental and psychosocial conditions can amplify or attenuate these relations.

Although peer influence is characteristically associated with monotonic increases in adolescent risk taking, there is emerging support for the role of peers in promoting risk-averse preferences, which can buffer against the normative uptick in health risk behaviors during adolescence. For instance, adolescents actually engage in less risky behavior when their peers explicitly endorse risk-averse preferences (Cascio et al., 2015; Engelmann et al., 2012), an effect that is stronger among early and late adolescents relative to adults (Engelmann et al., 2012). The social status of the influencing peers can further moderate adolescents' conformity to peers' health risk behaviors. Whereas adolescents exhibit higher rates of conformity when risk-related attitudes and behaviors are endorsed by high status (e.g., popular) peers, adolescents are more likely to diverge from—and act

against—these norms if endorsed by less desirable (e.g., low status) peers (i.e., anticonformity) (Brechwald and Prinstein, 2011; Cohen and Prinstein, 2006; Teunissen et al., 2012; Widman et al., 2016). In fact, high status peers may be more effective at discouraging rather than encouraging health-compromising risk taking during adolescence (Teunissen et al., 2012), underscoring the equally powerful effect of peers for influencing positive health outcomes during adolescence. Indeed, peers can promote prosocial, other-focused behaviors, such as sharing, cooperating, helping, intentions to volunteer, as well as learning and exploration (Barry and Wentzel, 2006; Choukas-Bradley, Giletta, Cohen, and Prinstein, 2015; Foulkes et al., 2018; Silva, Shulman, Chein, and Steinberg, 2016; van Hoorn, van Dijk, Güroğlu, and Crone, 2016; Wentzel, Filisetti, and Looney, 2007). If peers can also redirect adolescents toward positive behavior change (Telzer, van Hoorn, Rogers, and Do, 2018; van Hoorn, Fuligni, Crone, and Galván, 2016), then interventions that capitalize on adolescents' peer influence susceptibility in positive environments may be particularly promising for improving youth adjustment.

Although adolescents are, on average, more susceptible to peer influences compared to children and adults, not all adolescents may be equally influenced by their peers (Allen et al., 2006; Brittain, 1963; Prinstein et al., 2011; Steinberg and Monahan, 2007; Widman et al., 2016). Studies rarely have examined individual variability in, or susceptibility to, peer influence. However, extant research using both self-reported and performance-based approaches to study susceptibility have demonstrated that this is a normally distributed construct (Prinstein et al., 2011; Widman et al., 2016), suggesting approximately equal proportions of those extremely high or low in susceptibility as compared to other age mates. Individual differences in gender, pubertal development, social anxiety, and sensitivity to peer status have been shown to render some adolescents more at risk to negative peer pressures than others (Prinstein et al., 2011; Widman et al., 2016). Furthermore, adolescents who show a higher sensitivity to peer influences tend to experience distinct psychosocial outcomes compared to those who are relatively resistant to peer pressures (Allen et al., 2006; Prinstein et al., 2011). For example, one study reported longitudinal associations between best friends' and adolescents' own deviant behavior only among adolescents who demonstrated high levels of peer influence susceptibility to high-status classmates on a laboratory-based task (Prinstein et al., 2011). Notably, adolescents with a low susceptibility to high-status peers or a general (i.e., high or low) susceptibility to low-status peers did not show peer-related changes in deviant behavior over time (Prinstein et al., 2011), suggesting that those with a high susceptibility to (high-status) peers may be particularly more vulnerable to negative peer socialization effects over time. Moreover, growing evidence suggests that adolescents are also highly susceptible to prosocial peer influences (Foulkes et al., 2018; van Hoorn, Fuligni, et al., 2016; van Hoorn, van Dijk, et al., 2016; van Hoorn et al., 2014), yet little is known about the long-term consequences of having a high sensitivity to peer influence in more positive social contexts. Taken together, these data underscore the need to examine between-person variation in the level of susceptibility to peer influence in future research, particularly in response to different types of peers and social contexts.

Differential susceptibility to peer influence: A biological sensitivity perspective

Research on adolescent development has increasingly shifted its focus toward understanding person-by-environment interactions. This approach diverges from a long history of studies suggesting that environmental effects apply equally to all youth, which fail to consider that an adolescent's personal characteristics may determine if, and how much, the environment influences developmental outcomes. Several biological sensitivity models have been proposed to describe how person- and environment-level characteristics interact to predict developmental outcomes. The differential susceptibility theory (Belsky et al., 2007; Belsky and Pluess, 2009; Schriber and Guyer, 2016) and biological sensitivity to context theory (Boyce and Ellis, 2005; Ellis et al., 2011) propose that some individuals are more at risk than others if a personal vulnerability and negative environmental stressor interact beyond a certain threshold. Those who have an increased susceptibility to the environment are considered to be at a developmental disadvantage, as they are disproportionately impacted by environmental adversity compared to those who may not be as susceptible to their social environment. Although highly susceptible individuals are adversely affected by negative environmental contexts, susceptible youth are also more likely to benefit disproportionately from positive environmental contexts. In other words, heightened susceptibility to the environment can influence adolescent adjustment in a for-better *and* for-worse manner, resulting in more adaptive outcomes in positive contexts (for better) and more maladaptive outcomes in negative contexts (for worse). In contrast, the adjustment of low susceptible individuals is less affected by changes in the environment, regardless of how enriching or impoverished the context may be.

The differential susceptibility model is particularly relevant for investigating the various ways in which peers influence shifts in adolescent behavior, and the role of individual susceptibility in moderating these associations. In particular, adolescents' biological systems will shape the way they perceive and attend to their environments, resulting in youth reacting to their environments to match its demands. Thus, adolescents may be more or less sensitive to peer contexts as indexed by biomarkers of peer influence susceptibility. For example, adolescents who are more sensitive (e.g., greater neurobiological sensitivity to peer-related cues) *and* are in a negative peer environment (e.g., around deviant peers) may be pushed to engage in risk taking, whereas in a positive peer environment (e.g., around prosocial peers) may be pushed to engage in prosocial behaviors. In contrast, adolescents who are less sensitive (e.g., blunted neurobiological sensitivity to peer contexts) will be less affected by the type of environment they are in and overall less susceptible to peer influence (Figure 1). A closer examination of potential biomarkers of susceptibility to social influence may provide new insight into the mechanisms that push some adolescents towards or away from increased risk behaviors in peer contexts.

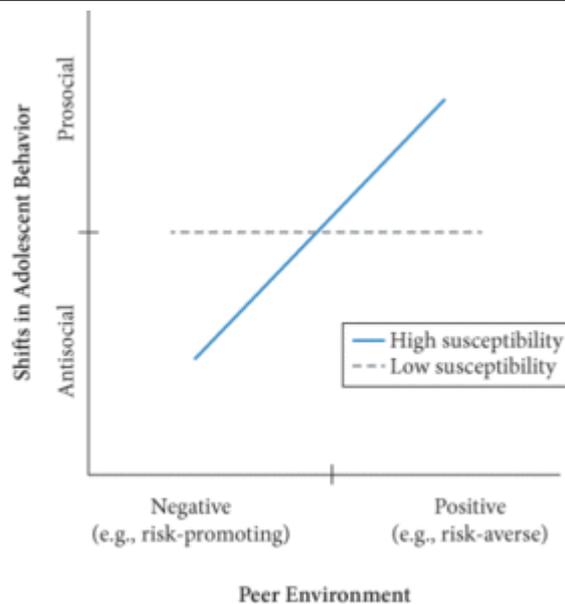


Figure 1. Understanding neurobiological susceptibility to peer influence from a differential susceptibility framework. According to the differential susceptibility theory, adolescents with a higher susceptibility to social contexts (solid blue line) may be differentially impacted by their environment in a for better *and* for worse manner; not only do they show a higher vulnerability to engage in greater antisocial behavior in negative peer environments, but they also show a higher sensitivity to engage in greater prosocial behavior in positive peer environments. In contrast, adolescents with a lower susceptibility to social contexts (dashed gray line) may show average peer-related shifts in behavior that may not be disproportionately more enhanced or vulnerable in positive or negative peer environments, respectively.

Neural biomarkers of adolescent susceptibility to peer influence

Prior work suggests that an individual's level of susceptibility to their environment can be indexed by three types of biomarkers: 1) phenotypic markers, or observable traits (e.g., temperament); 2) genetic markers (e.g., presence of dopamine receptor D4 polymorphism); and 3) endophenotypic markers, or traits that fall somewhere between phenotypic and genetic markers (e.g., neurobiology). While extensive literature from developmental psychology has examined various phenotypic and genetic markers of differential susceptibility to peer influence (e.g., reviewed in Belsky and Pluess, 2009), less attention has been paid to understanding how endophenotypic markers—beyond physiological responses—interact with peer environments to affect adolescent behavior. In particular, little is known about which neurobiological markers relate to and explain differences in susceptibility (see Schriber and Guyer, 2016; for exceptions see Whittle et al., 2011; Yap et al.,

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2008). Given extensive reorganization in brain structure and function during adolescence, coupled with a social restructuring of the brain that confers social contexts highly salient (Nelson, Jarcho, and Guyer, 2016), considering how neural networks serve as moderators of social experience can greatly inform theories of adolescent development (Schriber and Guyer, 2016). While one or several susceptibility biomarkers may cumulatively enhance an individual's sensitivity to their social environments over time, these behavioral and neurobiological predispositions can manifest in critically different ways based on the type of environments that individuals are exposed to. Thus, while person- and environment-specific factors independently affect susceptibility to social influence in adolescence, examining interactions between these characteristics is critical for identifying those who may be most susceptible not only to maladaptive outcomes, but also adaptive outcomes (as in differential susceptibility theory).

Normative ontogenetic changes in the adolescent brain confer heightened neurobiological responses to peer contexts that are distinct from other developmental periods. Insight from developmental cognitive neuroscience has identified that brain regions involved in social, cognitive, and affective processing are involved in encoding social information from peer contexts that later inform adolescent behavior (reviewed in Telzer, van Hoorn, et al., 2018). Using functional magnetic resonance imaging (fMRI), this research has started to delineate the neural correlates of different aspects of peer socialization (e.g., peer presence or explicit feedback), social belonging (e.g., peer exclusion or acceptance), and affective processing of peer-related stimuli (e.g., happy versus angry peer faces) (Chein et al., 2011; Guyer et al., 2009; Pfeifer et al., 2011), with the goal of identifying the basic mechanisms that explain the role of peers in adolescent decision making and behavior. Of course, a major caveat of fMRI research is that a single brain region can be coopted for multiple psychological functions, limiting the specificity of future conclusions about the neural mechanisms of peer influence. For example, while the ventral striatum (VS) is classically implicated in reward processing during adolescence (reviewed in Telzer, 2016), it has also been associated with emotion regulation (Pfeifer et al., 2011) and learning (Davidow et al., 2016). In other words, while a psychological process might show consistent and robust relations with a specific brain region, it is improbable that there is a one-to-one mapping of a single psychological function on to a single brain region (Poldrack, 2011).

In spite of these methodological limitations, an intriguing possibility is that differential activation in social, cognitive, and affective brain systems reflects youths' susceptibility to peers at a neurobiological level. Affective regions, such as the VS, ventromedial prefrontal cortex (vmPFC), orbitofrontal cortex (OFC), and the amygdala, are implicated in processing social rewards and punishments, as well as detecting socially and motivationally salient information (Guyer, McClure-Tone, Shiffrin, Pine, and Nelson, 2009; Pfeifer et al., 2011; Telzer, 2016; Telzer et al., 2018). In addition, the social brain network, which includes the temporoparietal junction (TPJ), posterior superior temporal sulcus (pSTS), and dorsal and medial prefrontal cortex (dmPFC, mPFC), is involved in higher order social cognition, such as self-other processing or mentalizing about others' thoughts and feelings to inform one's own behavior (Blakemore, 2008; Blakemore and Mills, 2014; Crone

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and Dahl, 2012; Telzer, 2016; Telzer et al., 2018). Finally, cognitive control regions, such as the medial and ventral/dorsal lateral prefrontal cortex (mPFC, vlPFC, dlPFC) and anterior cingulate cortex (ACC), play an important role in regulating reactivity within, and connectivity between, regions that encode social information from the environment (Falk et al., 2014; Haber and Knutson, 2010; Masten et al., 2009; Telzer et al., 2018).

Across diverse social contexts (e.g., being observed by peers, making risky decisions, watching static and dynamic faces), adolescents exhibit greater activation than children and/or adults in affective and social cognitive regions, as well as altered (as evidenced by both greater and lower) activation in regulatory regions (Do and Galván, 2016; Galvan et al., 2006; McCormick, Perino, and Telzer, 2018), an effect that is modulated by peer contexts (e.g., when a peer is present) (Ambrosia et al., 2018; Chein et al., 2011; Falk et al., 2014; Peake, Dishion, Stormshak, Moore, and Pfeifer, 2013; Pfeifer et al., 2013; Telzer, Miernicki, et al., 2018). While a wide range of peer influences are linked to changes in adolescent risk taking at the behavioral and neural level (Albert, Chein, and Steinberg, 2013; Telzer et al., 2017; van Hoorn et al., 2016), the role of neurobiological susceptibility markers in moderating these relations has received considerably less attention. An approach gaining traction in recent work explores how potential markers of neurobiological susceptibility can predict changes in adolescent risk-taking behavior.

Of particular interest to this investigation is the dopaminergic mesolimbic circuitry, which is thought to sensitize the adolescent brain to overweigh the sense of reward associated with engaging in risk behaviors in the presence of peers (e.g., Chein et al., 2011). Compared to adults, adolescents who evince greater VS and OFC activation when taking risks in the presence of peers report lower resistance to peer influence and show greater increases in risk-taking behavior following peer influence (Chein et al., 2011). In addition, adolescents who change their attitudes to align more with their peers show increased activation in the vmPFC, suggesting that conforming to their peers may be intrinsically valued, thereby increasing the efficacy of social influence pressures over time (Welborn et al., 2015). Finally, conforming to peers' behaviors is instrumental for gaining social acceptance and establishing stronger peer connections, an effect that may be exacerbated in youth who are rejected by their peers. Indeed, adolescents experiencing peer adversity (e.g., chronic peer victimization (Telzer, Miernicki, et al., 2018); chronic peer conflict (Telzer, Fuligni, Lieberman, Miernicki, and Galván, 2015) show enhanced activation in the VS, insula, and amygdala during risk taking, potentially reflecting the anticipation of social rewards (e.g., peer approval) by engaging in risky behavior.

Prior studies from behavioral genetics have suggested that negative peer pressures influence real-world risk-taking behaviors (e.g., substance use), an effect only found among individuals with an enhanced genetic sensitivity to environmental experiences as indexed by different polymorphisms of the dopamine D4 receptor (DRD4) gene (Griffin, Harrington Cleveland, Schlomer, Vandenberg, and Feinberg, 2015; Larsen et al., 2010). Specifically, the 7-repeat DRD4 allele is consistently identified as a putative vulnerability factor for physical and mental health outcomes because it appears to decrease dopamine receptor efficiency through its effect on dopaminergic mesolimbic systems (Asghari et al.,

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1995; Hutchison, Lachance, Niaura, Bryan, and Smolen, 2002). Blunted dopamine activity in these neural circuits is often associated with an increased sensitivity to social input from negative peer environments, thereby reinforcing the rewarding nature of engaging in motivated and appetitive behaviors. Indeed, prior work suggests that the 7-repeat DRD4 allele not only impacts reactivity to risk-related cues (Hutchison et al., 2002), but also moderates the role of peer influence processes on health risk behavior (Griffin et al., 2015; Larsen et al., 2010; Mrug and Windle, 2014). Although speculative, one interpretation is that individuals with a genetic susceptibility to peers' deviant behaviors may experience a greater sense of reward from emulating peers' behavior, perhaps out of a purported desire to gain peer acceptance or increase social connection (Griffin et al., 2015; Larsen et al., 2010). Collectively, these findings implicate high dopamine reactivity to risky decisions as a potential biomarker that modulates the perceived reward value associated with capitulating to peer influences, which may subsequently shape both the inability to resist negative peer pressures, as well as a general propensity to engage in risk taking.

In addition to dopamine-associated biomarkers, neural circuits involved in higher-order social cognitive processing (e.g., mentalizing) moderate the effect of peer influence on adolescent decision making. For instance, adolescents who change their own attitudes more towards those of their parents or peers show increased activation in the dmPFC and TPJ, suggesting that when shifting their attitudes, adolescents incorporate the thoughts and intentions of their parents and peers to inform their decision making (Cascio et al., 2015; Welborn et al., 2015). Further supporting the link between social sensitivity and adolescent risk taking, adolescents who show greater activation in social brain regions (e.g., mPFC, precuneus, PCC) when viewing their own peers relative to parents report greater risk-taking behavior and affiliation with risky peers (Saxbe, Del Piero, Immordino-Yang, Kaplan, and Margolin, 2015). Other studies have similarly shown that high reactivity within social brain regions (dmPFC, TPJ, PCC) following peer exclusion prompts increased risk taking in peer contexts (Falk et al., 2014; Peake et al., 2013; Telzer, Miernicki, et al., 2018), perhaps in an attempt to promote social affiliation. For example, after being excluded by a peer, adolescents who are more susceptible to peer influence, as indexed by self-reported resistance to peer influence (RPI), show greater activation in the TPJ when making risky decisions, with TPJ activation predicting heightened risky behavior (Peake et al., 2013). These findings suggest that neural differences observed in peer-evaluative contexts may implicitly upweight the value of peers' risky attitudes and behaviors, thus pushing youth to adjust their behavior to fit in with expected peer group norms (i.e., riskier decisions).

Finally, impaired recruitment of brain regions supporting self-regulation and impulse control may also serve as a biomarker of social influence susceptibility. Highly salient, affectively-arousing peer contexts are hypothesized to compromise self-regulation abilities during adolescence, conferring an increased risk for maladaptive decision making in the presence of peers. For example, increases in dangerous driving behavior (i.e., risk taking that results in car crashes) following explicit peer feedback is only found among adolescents who not only report higher behavioral approach tendencies (e.g., oriented toward

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social rewards), but also exhibit reduced activation in the mPFC, a region implicated in the regulation of emotional states (Segalowitz et al., 2012). Similarly, adolescents reporting higher self-perceived susceptibility to peer influence exhibit greater functional connectivity between brain regions involved in action observation (frontoparietal and temporo-occipital regions) and executive control and decision making (prefrontal cortex) when passively processing others' movements that are socially salient (Grosbras et al., 2007). These findings suggest that, even when passively encoding salient stimuli from the environment, early adolescents with a higher susceptibility to peer influence may already recruit less regulatory resources when they are reasoning about their own behavioral responses, which could result in maladaptive decision making compared to those with a lower susceptibility to peer influence. Relatedly, longitudinal increases in VS activation to emotional expressions are associated with a stronger ability to resist peer influence from childhood to early adolescence (Pfeifer et al., 2011). Although counterintuitive at first glance, the VS has been implicated in emotion regulation (Masten et al., 2009; Wager, Davidson, Hughes, Lindquist, and Ochsner, 2008), suggesting that the VS is serving a regulatory process that may be compromised in adolescents with higher susceptibility to peer influence.

Taken together, these findings suggest that neurobiological processes that encode affective, social-cognitive, and regulatory cues from the environment contribute to peer influence susceptibility. Thus, peer contexts may elicit a reduced regulation of reward-related processing during risky decision making and an intensification of social-affective reactivity. In order to better understand how these neural networks interact and work in tandem to influence adolescent behavior, it is key to examine functional connectivity. Adolescent behavior is determined by dynamically interacting functional brain systems. Increasingly, researchers are implementing connectivity techniques including functional and effective connectivity, which measure the temporal correlation between neurophysiological events (Sporns and Honey, 2007) and the influence one neural network exerts over another (Friston, 2009), respectively. Although still a nascent area of inquiry, studies have emerged showing differences in connectivity patterns are associated with differences in adolescent decision making. For example, adolescents showed heightened mPFC-striatum connectivity when being observed by a peer compared to children and adults, which may represent the integration of social signals with motivational systems that ultimately result in increased risk taking in the presence of peers (Somerville et al., 2013). Indeed, we have shown that longitudinal increases in mPFC-striatum connectivity underlies longitudinal increases in risk taking during adolescence (Qu, Galvan, Fuligni, Lieberman, and Telzer, 2015). Moreover, during rest, VS-mPFC connectivity shows linear increases from childhood to adolescence and correlates with pubertal hormones (Fareri et al., 2015), as well as reward sensitivity (van Duijvenvoorde, Peters, Braams, and Crone, 2016), cognitive control, and substance use (Lee and Telzer, 2016), which may reflect a developmental shift in the way social and motivational systems interact during adolescence. By examining the coupling of these dynamically interacting neural systems across different social contexts and across development, we will gain a deeper understanding of how neural systems work in tandem to inform adolescent behavior.

Neurobiological susceptibility to peer influence: For better *and* for worse?

Most studies to date have examined how peer influence susceptibility relates to negative, deviant behaviors, with far less known about adolescents' susceptibility to positive peer influences. Prior research suggests that greater activation in still-maturing regulatory brain systems can facilitate adolescents' susceptibility to positive peer influences. For instance, adolescents who exhibit greater activation in the response inhibition network (e.g., IFG) are more likely to drive safely in the presence of a peer promoting cautious driving practices, an effect not observed in response to negative peer influences (Cascio et al., 2015). Thus, neural circuits involved in response inhibition may facilitate an increased capacity to resist maladaptive forms of peer pressures during risky decision making. These results highlight the potentially adaptive benefits of peer influence susceptibility, such that ongoing changes in cognitive regulation can be leveraged to redirect adolescents' with an increased susceptibility to peer contexts toward more positive relative to negative decisions.

Previous work from behavioral genetics have also identified genetic biomarkers that serve to buffer negative peer environments. Similar to the role of DRD4 polymorphisms in altering sensitivity to negative environmental influences (Belsky and Pluess, 2009), researchers have shown that the 7-repeat DRD4 allele can also increase susceptibility to positive peer experiences, which ultimately buffers against adolescent delinquency over time (e.g., Kretschmer, Dijkstra, Ormel, Verhulst, and Veenstra, 2013; reviewed in Belsky and Pluess, 2009; Ellis, Boyce, Belsky, Bakermans-Kranenburg, and Van Ijzendoorn, 2011). These results highlight genetic factors as another way to identify individuals who might be most responsive to different social influences, which can be leveraged to foster more positive peer effects on adolescent risk taking.

Moving beyond risk-taking and negative behaviors, researchers have also begun to examine how social contexts interact to promote positive behaviors in adolescents. For example, the presence of peers impacts adolescents' prosocial behaviors (i.e., contributing coins to a group), via enhanced activity in several social brain regions including the mPFC, TPJ, precuneus, and STS (van Hoorn et al., 2016). Such peer effects in social brain regions are largest for younger (12–13-year-old) than older (15–16-year-old) adolescents, suggesting that younger adolescents may be more sensitive to positive social influence from peers. Indeed, behavioral work examining risk perceptions has shown that 12–14-year-olds are more sensitive to social influence from peers than are adults, whereas older adolescents (age 15–18 years) show similar sensitivity to influence as adults (Knoll et al., 2015). These findings suggest that heightened social brain activation may underlie this increased sensitivity to social influence in young adolescents, and expands the scope of social influence work to positive, prosocial behaviors. Together, these studies underscore the increasing salience of peers in adolescence, insofar that they become especially at-

tuned to their peers' evaluations, and highlight both the positive and negative effects of peer conformity.

To our knowledge, no study to date has explicitly tested a neurobiological susceptibility framework for social influence, which posits that neurobiological biomarkers can influence susceptibility in a for-better and for-worse fashion depending on the environmental context. Some initial evidence suggests there may be largely overlapping neural biomarkers for positive and negative social influence susceptibility. Indeed, heightened neural activation in socio-affective brain regions respond to both positive and negative cues. For instance, heightened VS activation, while traditionally discussed as a vulnerability for risk taking, can also be protective against risk taking depending on the social context. When adolescents show heightened VS activation in risk-taking tasks (Galvan, Hare, Voss, Glover, and Casey, 2007; Qu et al., 2015; Telzer, Fuligni, Lieberman, and Galván, 2013), particularly in the presence of peers (Chein et al., 2011), they show increases in real-life risk taking, suggesting that individual differences in VS activation may be a neurobiological susceptibility marker, and in a risky context will promote risky behavior. However, adolescents who show heightened VS activation in positive, prosocial contexts show decreases in risk taking (Telzer et al., 2013), suggesting that the same susceptibility biomarker can promote positive adjustment depending on the social context. Despite the promise of a neurobiological susceptibility to peer influence model, by which biomarkers of susceptibility interact with the social environment, much work is needed to further support this model.

Conclusions and future directions

Given a significant rise in mortality rates from preventable health risk behaviors during adolescence, researchers have directed considerable attention toward identifying innovative approaches to the study of social influence susceptibility. Here, we argue that taking a neurobiological susceptibility to peer influence framework will help us understand potential biomarkers that serve as both vulnerabilities and opportunities for adolescent risk taking, depending on the peer context. Although researchers have only begun to unpack the inherently complex construct of peer influence susceptibility, exciting advances from developmental psychology and cognitive neuroscience suggest that not all adolescents are equally influenced by their peers. Using a diverse set of methods ranging from questionnaires to in-vivo experiments during fMRI, this burgeoning literature seeks to delineate how adolescents' level of behavioral and neurobiological susceptibility to peers can shape whether, how, and how much their own attitudes and behaviors fluctuate across different peer environments. Exploring individual variability in, or susceptibility to, peer influence represents a promising approach for identifying adolescents who may be most at risk or resilient to negative peer pressures, which has important implications for tailoring interventions that prevent risk-taking behavior directly. Yet, despite encouraging evidence from behavioral, genetic, and brain studies, the construct of susceptibility to peer

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influence has largely remained elusive and understudied, particularly in more positive social contexts.

Importantly, further research is needed to address several methodological and conceptual issues that still remain. Methodologically, there is considerable variability not only in the use of self-reported versus performance-based measures of susceptibility to peer influence, but also in the statistical analyses that have been proposed to test susceptibility effects (i.e., moderation analyses). In addition, the effect of individual susceptibility to peers on adolescent conformity to peer pressures is likely going to vary based on whether the behavior is positive (e.g., prosocial) or negative (e.g., antisocial), if it is a behavior that adolescents are already experienced with (e.g., cigarette use, but not cocaine use), and the perceived severity and consequences of engaging in that behavior (e.g., drug use versus cutting class). The nature of peer interactions as well as the latency between exposure to peers' behavior and adolescents' own decisions may also be relevant for determining the extent to which peer influence susceptibility pushes some adolescents toward (or away from) their peers' behaviors more than others. Based on these overall considerations, future empirical work is necessary for developing a more comprehensive account of defining, measuring, and testing the effect of peer influence susceptibility during adolescence.

Guided by a rich literature from developmental science, cognitive neuroscience, and social psychology, this review explores the use of neurobiological biomarkers to index an individual's susceptibility to their social environment. Collectively, this research underscores the need to consider a wider range of peer contexts when studying how adolescent susceptibility and peer contexts independently and mutually influence risk-related attitudes and behaviors. Neurobiological indices of susceptibility to peer influence may be particularly useful for identifying adolescents who are extremely oriented toward peers, which can be leveraged to target peer socialization efforts that encourage healthier attitudes and behaviors during adolescence.

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