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A neuroscientific perspective on basic psychological needs

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Abstract

Objective: Self-determination theory's (SDT) most basic propositions are, first, that all people possess an inherent set of psychological needs and, second, that autonomy, competence, and relatedness are the three critical psychological satisfactions needed to maintain and promote personal growth and well-being. In this article, we identify the neural basis of the psychological needs and, in doing so, seek to advance the integration of SDT and neuroscience.

Method: We examine the neural underpinnings of SDT-based motivational states and traits for autonomy, competence, and relatedness. To study motivational states, participants are exposed to situational conditions known to affect their psychological needs, and neuroscience methods (e.g., fMRI) are used to examine changes in their brain activity. To study motivational traits, participants complete self-report trait measures that are then correlated with their brain activity observed during need-satisfying activities.

Results: For both motivational states and traits and across all three needs, intrinsic satisfaction is associated with striatum-based reward processing, anterior insula–based subjective feelings, and the integration of these subjective feelings with reward-based processing.

Conclusions: Psychological need satisfaction is associated with striatum activity, anterior insula activity, and the functional coactivation between these two brain areas. Given these findings, it is now clear that several opportunities exist to integrate SDT motivational constructs with neuroscientific study, so we suggest eight new questions for future research.

KEYWORDS
anterior insular cortex (AIC), motivational neuroscience, psychological need satisfaction, self-determination theory, striatum

1 | INTRODUCTION

Self-determination theory (SDT) is a theory of human motivation that explains how socioenvironmental conditions sometimes support but other times thwart people's adaptive functioning, healthy development, and well-being (Ryan & Deci, 2017). SDT starts with the assumptions that all people possess a natural tendency toward activity, growth, and healthy development, and that the motivational energy underlying this natural growth tendency is a set of basic psychological needs. That said, the theory also recognizes that people's daily experiences and life trajectories vary widely, as some people generally take a strong interest in their surroundings, seek out optimal challenges, relate to others prosocially, and therefore flourish, whereas others are generally indolent, defensive, relate to others antisocially, and therefore flounder. This means that people's natural tendency toward growth and development is conditional (rather than automatic), such that healthy development is dependent on requisite support from socioenvironmental conditions.

A psychological need is a subjective experience that is essential and necessary to experience, sustain, and promote

TABLE 1 Purpose of each mini-theory and the central role psychological needs play within each mini-theory

SDT mini-theory	Purpose of the mini-theory	Role of psychological needs
Basic needs theory	Highlights the motivational properties of the three psychological needs and how their satisfaction relates to effective functioning and well-being.	Need satisfaction is associated with vitality, life satisfaction, and well-being.
Cognitive evaluation theory	Explains how events in the social environment (e.g., rewards) sometimes support but other times undermine intrinsic motivation and the quality of learning and performance.	Socioenvironmental conditions that support need satisfaction facilitate intrinsic motivation and performance; those that thwart need satisfaction produce amotivation and interfere with performance.
Organismic integration theory	Explains how extrinsically motivated behaviors become autonomously motivated. Specifies the antecedents, consequences, and unique characteristics of each type of extrinsic motivation.	Extent of need satisfaction fuels internalization and integration of personally valued, societally recommended behaviors and regulations.
Causality orientation theory	Highlights individual differences in causality orientations—autonomous, controlled, and impersonal—as developmental outcomes and as personality-based predictors of adaptive functioning.	People with high levels of the autonomy orientation use need satisfaction as an important guide to their behavior, whereas people with high levels of the other two orientations do not.
Goal contents theory	Highlights the goals people pursue. Explains why some goals (intrinsic) lead to positive functioning and well-being, whereas other goals (extrinsic) do not.	Intrinsic goals afford opportunities for psychological need satisfaction and hence utilize an energy source that facilitates goal progress.
Relationship motivation theory	Explains that close, high-quality, mutually satisfying relationships are characterized by the giving and receiving of both autonomy and relatedness need satisfaction.	Need satisfaction mediates between relationship characteristics (e.g., extent of autonomy support) and indicators of relationship satisfaction.

personal growth, healthy development, and psychological well-being (Ryan & Deci, 2000, 2017; Sheldon, Ryan, & Reis, 1996). The three psychological satisfactions that provide these "psychological nutriments" for flourishing are autonomy, competence, and relatedness.

Autonomy is the psychological need to experience self-direction and personal endorsement in the initiation and regulation of one's behavior (Ryan & Deci, 2017). The hallmarks of autonomy need satisfaction are volitional action and wholehearted self-endorsement (i.e., personal ownership) of that action. *Competence* is the psychological need to be effective in one's interactions with the environment, and it reflects the desire to extend one's capacities and skills and, in doing so, to seek out optimal challenges, take them on, and exert effort and strategic thinking until personal growth is experienced (Ryan & Deci, 2017). The hallmarks of competence need satisfaction are experiences of effectance, mastery, and making progress. *Relatedness* is the psychological need to establish close emotional bonds and attachments with other people, and it reflects the desire to be emotionally connected to and interpersonally involved in warm relationships (Baumeister & Leary, 1995; Ryan, 1993). The hallmarks of relatedness need satisfaction are feeling socially connected and being actively engaged in both the giving and receiving of care and benevolence to the significant people in one's life.

The benefits of autonomy, competence, and relatedness need satisfaction are many, including enhanced engagement in one's surroundings (Jang, Kim, & Reeve, 2016), personal growth (Niemiec et al., 2006), internalization (Jang, 2008), personality integration (Sheldon & Kasser, 1995), health (Ryan, Patrick, Deci, & Williams, 2008), and well-being—both biological (Reeve & Tseng, 2011) and psychological (Sheldon et al., 1996). Similarly, the personal relevance of the psychological need construct is robust, as all people benefit from need satisfaction, regardless of their age, gender, language, nationality, culture, socioeconomic status, ability level, or historical time period, as psychological needs are universal endowments embedded within everyone's nervous system (Chen et al., 2015; Chirkov & Ryan, 2001; Chirkov, Ryan, & Sheldon, 2011).

Additionally, the psychological need construct plays a central role across all six mini-theories within the larger SDT explanatory framework, as shown in Table 1. In basic needs theory, for instance, psychological need satisfaction provides the essential experiences that generate vitality and psychological well-being. In cognitive evaluation theory, autonomy and competence need satisfactions are the basis of intrinsic motivation, whereas autonomy frustration leads to external regulation and competence frustration leads to amotivation. In organismic integration theory, need satisfaction fuels the internalization and integration of societally recommended regulations and behaviors. In causality orientations theory, experiences of need satisfaction are central guides to the initiation and regulation of some people's daily behaviors and decision making (i.e., those with an autonomy causality orientation). In goal contents theory, goal pursuits that lead to experiences of need satisfaction fuel more goal progress and well-being than do goal pursuits that do not lead to experiences of need satisfaction. In relationships motivation theory, the giving and receiving of autonomy and relatedness satisfactions characterize what it means to have an emotionally close interpersonal relationship.

SDT conceptualizes psychological needs as essential *requirements* for positive functioning and well-being. That is, the more autonomy, competence, and relatedness satisfaction one experiences, the better will be his or her functioning and well-being. Satisfaction, however, is only one possible need state. A psychological need can also be deprived, anticipated (potentially forthcoming but not yet satisfied), or frustrated (Cheon et al., 2018). These various need states are mostly determined by environmental conditions, as environmental indifference to the individual's psychological needs leads to need deprivation, environmental affordances lead to need anticipation, and environmental thwarts lead to need frustration. All of these need states fall under the umbrella of a "context satisfies or thwarts needs" framework and therefore orient attention to environmental rather than to personality, factors (Prentice, Halusic, & Sheldon, 2014, p. 76).

The more personality-based approach is to conceptualize psychological needs as *motives* (Sheldon, 2011; Sheldon & Gunz, 2009). Here, needs can be desires, and some people can desire the psychological need more than others. Or, some people can be unsatisfied with how much need satisfaction their environmental surroundings provide and therefore effortfully seek out more need-satisfying conditions and experiences (Legault, Ray, Hudgins, Pelosi, & Shannon, 2017). Needs as motives are usually understood through a lens of individual differences in need strength, need desire, or need importance, as is the case in motive disposition theory (MDT; Hofer & Busch, 2011; Schuler, Sheldon, & Frohlich, 2010), but also within the SDT framework itself (Legault et al., 2017). The basic idea is that people have different developmental histories (e.g., authoritative vs. authoritarian parents, Legault et al., 2017; Eastern vs. Western societies, Chen et al., 2015), and these different developmental experiences create individual differences as to how much they desire, value, or deem as important an experience of autonomy, competence, or relatedness. To date, SDT-based neuroscience research has studied only need satisfaction (needs-as-requirements) and not yet investigated individual differences in need strength (needs-as-motives) or other possible need states (deprivation, frustration).

2 | NEUROSCIENCE PERSPECTIVE

Practically all SDT-based investigations explain human motivation and personality development at the psychological level. Neuroscientific methods and data offer the opportunity to add a new perspective, new ways of measuring motivation, and new knowledge about many SDT motivational constructs, even those that are currently recognized as rather well understood at the psychological level. As to new perspectives, most motivational constructs are understood in only an incomplete way. Much is known, but much remains unknown. A neuroscientific perspective can add a fresh point of view on well-known phenomena, such as the undermining effect (i.e., the pursuit of tangible extrinsic rewards during an inherently interesting activity will decrease the person's future intrinsic motivation for that activity; Murayama, Matsumoto, Izuma, & Matsumoto, 2010) and personal agency (i.e., volitional, self-generated action; Lee & Reeve, 2013). Part of this fresh perspective comes from a matter of timescale, as neuroscientists investigate motivational processes in milliseconds, which is not the sort of data participants can report on questionnaires. It also comes from new ways of measuring motivation, as neuroscientific data (e.g., brain scans) are both objective and real time. Neuroscientists also employ a different unit of analysis, as personality psychologists generally explain behavior using psychological constructs, whereas neuroscientists generally explain the neural bases of these psychological constructs.

We believe that these two perspectives can eventually form a wonderful partnership, and that is what we have tried to do in our program of research—to explain the neural bases of psychological need satisfaction. In this spirit, we undertook our neuroscience-based program of research to answer new questions about the nature and function of intrinsic motivation and the psychological needs, and we adopted a neuroscientific perspective because we felt that these questions could not be adequately answered outside a neuroscientific perspective. For instance, some of our initial questions were as follows: Where in the brain do people process intrinsic motivation and the psychological needs? Is the experience of psychological need satisfaction processed cortically (consciously) or subcortically (nonconsciously)? Are need satisfaction and need frustration two separate and independently functioning motivational experiences, or do they represent two sides of the same coin but with contrasting valences?

Most of the neuroscientific investigations of SDT-based psychological processes focus on motivational states rather than on motivational traits. Thus, much of the existing neuroscience-based research within the SDT framework focuses relatively more on situationally or environmentally induced changes in motivational states and relatively less on enduring and trans-situational personality traits. This is probably because neuroscience methodology mostly uses functional neuroimaging methodologies, such as functional magnetic resonance imaging (fMRI) and electroencephalogram (EEG), and a within-subjects, repeated-measures research design. This has led neuroscientists to investigate situationally induced (stimulus-induced), moment-to-moment changes in motivational states more frequently than between- or interindividual differences in motivational traits, though some exceptions do exist (e.g., individual differences in causality orientations; Legault & Inzlicht, 2013). Attention to motivational states can eventually lead to greater study of motivational traits because the effort to identify the neural correlates of motivational states can serve as an initial step to understand the neural characteristics of motivational traits. For instance, if the brain regions related to specific motivational states can be recognized, then the neural individual differences associated with varying levels of that motivational state can be examined by targeting those previously identified brain regions as regions of interest (i.e., establishing an a priori hypothesis).

2.1 | SDT-based neuroscience studies of motivational states

SDT-based neuroscience began by trying to identify the neural mechanisms of intrinsic motivation. This starting point is important to the current topic because intrinsic motivation is recognized as the motivation that arises from the satisfaction of the psychological needs for autonomy and competence (Deci & Ryan, 1985b). The general neuroscientific research strategy has been to import experimental tasks that have been previously validated as capable of affecting a change in the experiences of intrinsic motivation, autonomy need satisfaction, or competence need satisfaction (e.g., provision of choice vs. task assignment, exposure to easy anagrams vs. optimally challenging anagrams) and adapt them into a form that is suitable for the scanner, which is a highly restricted environment. As participants lie in the scanner and engage themselves in these tasks, neuroscientists then extract the neural signals they observe during participants' experiences of intrinsic motivation and psychological need satisfaction.

2.1.1 | Intrinsic motivation based on competence satisfaction

People can experience intrinsic motivation as they pursue competence need satisfaction (Deci & Ryan, 1985b). In many neuroscience experiments, participants perform a series of interesting tasks and receive performance feedback that is designed to effect a change in their perceived competence (Elliott, Frith, & Dolan, 1997; Lee & Kim, 2014; Lee & Reeve, 2017; Murayama et al., 2010). That is, as participants effectively performed the interesting tasks and received positive (i.e., success, improvement) feedback, they experienced competence satisfaction and subsequently intrinsic motivation. These studies have consistently found that the brain's reward center (i.e., striatum) is recruited in the processes of intrinsic motivation, just as these same brain regions (i.e., striatum) are crucial for the processes of extrinsic motivation.

For example, Murayama and colleagues (2010) conducted a neuroscience study in which both intrinsic and extrinsic motivation conditions existed. In this study, the experience of intrinsic motivation based on competence satisfaction was manipulated as participants performed an interesting stop-watch task and received positive feedback contingent upon their performance, and the experience of extrinsic motivation was manipulated as participants performed the same task and received monetary rewards contingent upon their performance. Results showed that the neural activations of the striatum (i.e., caudate nucleus) were related to motivation regardless of its sources (i.e., extrinsic vs. intrinsic).

We also conducted a neuroscience study examining and confirming the neural correlates of intrinsic motivation based on competence satisfaction (Lee & Reeve, 2017). In this study, participants sometimes worked on and solved optimally challenging anagrams, whereas at other times they worked on easy anagrams (i.e., a within-subjects, repeated-measures research design). In this way, we provided participants with opportunities to pursue an optimal challenge, to anticipate a feeling of enjoyment from being challenged, to benefit from guidance and scaffolding that allows them to extend their capacities, and to experience a sense of satisfaction from a job well done (i.e., feeling effectance, making progress, developing greater capacity). (In a pilot test, participants rated the perceived difficulty level of each anagram so that we could use these ratings to control for the possible task difficulty confound in the main analyses.) Three key results emerged. First, the striatum was recruited more during the competence-satisfying optimal challenges than during the competence-neglecting, under-challenging anagrams. Second, not only was the striatum more activated during competence-satisfying, optimally challenging anagrams, but so was the anterior insular cortex (AIC or anterior insula). This result appears in Figure 1. It shows that participants showed significantly greater AIC activation (as represented by signal change percent) when they solved optimally challenging and competence-satisfying anagrams than when they solved too-easy and competence-neglecting anagrams. Figure 1 also shows that this greater AIC activation effect occurred bilaterally—that is, both in the right anterior insula and in the left anterior insula. Interestingly, the striatum and AIC were consistently more activated during the competence-satisfying optimal challenges than during the competence-neglecting, under-challenging anagrams, even controlling for

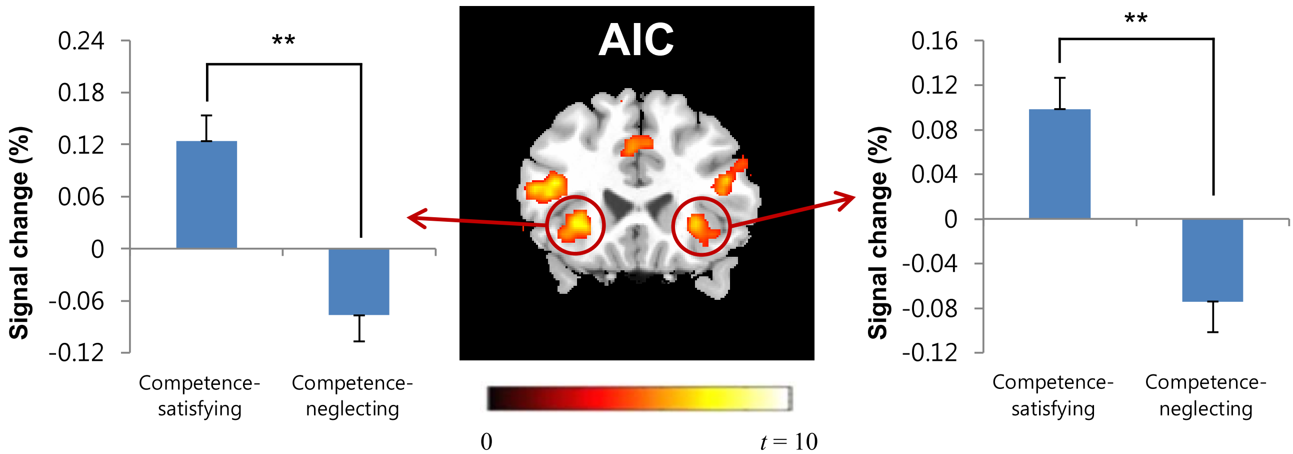

FIGURE 1 Bilateral anterior insular cortex (AIC) was more activated during optimally challenging and progress-enabling versions of a task than were comparable versions of the same task that were under-challenging and non-progress-enabling [Colour figure can be viewed at wileyonlinelibrary.com]

the effects of task difficulty. Third, a particularly interesting result was that psychophysiological interaction analyses showed that striatum activations co-occurred with AIC activations during the performance of competence-enabling tasks. This result shows the functioning interconnectivity between the striatum and AIC, which suggests the neural integration of reward-related information with subjective feelings during competence need satisfaction. This functional interconnectivity appears in Figure 2, which suggests that both striatum and AIC activations are associated with experimental manipulations known to produce the rise and fall in competence need satisfaction.

The anticipation of an experience of competence satisfaction has also been studied using neuroscience methods. Using an EEG methodology, participants who were exposed to conditions of optimal challenge (vs. a lack of challenge) showed cortical activation (a stimulus-preceding negativity [SPN] response) when they were anticipating positive performance feedback (Meng, Pei, Zheng, & Ma, 2016). Such an experience of suspense over what will happen next, having an opportunity to discover new information, and anticipating satisfaction from attaining new or competence-affirming information has been associated with experiences of curiosity and intrinsic motivation (Abuhamdeh, Csikszentmihalyi, & Jalal, 2015; Lee & Reeve, 2017).

2.1.2 | Intrinsic motivation based on autonomy satisfaction

Just as is the case with competence satisfaction, the rise in autonomy satisfaction also allows people to experience intrinsic motivation (Deci & Ryan, 1985b). In many neuroscience experiments, autonomy satisfaction–based experiences of intrinsic motivation have been manipulated by the provision of personal choice (Leotti & Delgado, 2011, 2014; Murayama et al., 2015). These studies find that intrinsic motivation recruits not only the brain regions related to reward processing (e.g., striatum, midbrain) but also the brain regions related to self-processing (e.g., anterior insula). For example, Leotti and Delgado (2011) examined the neural

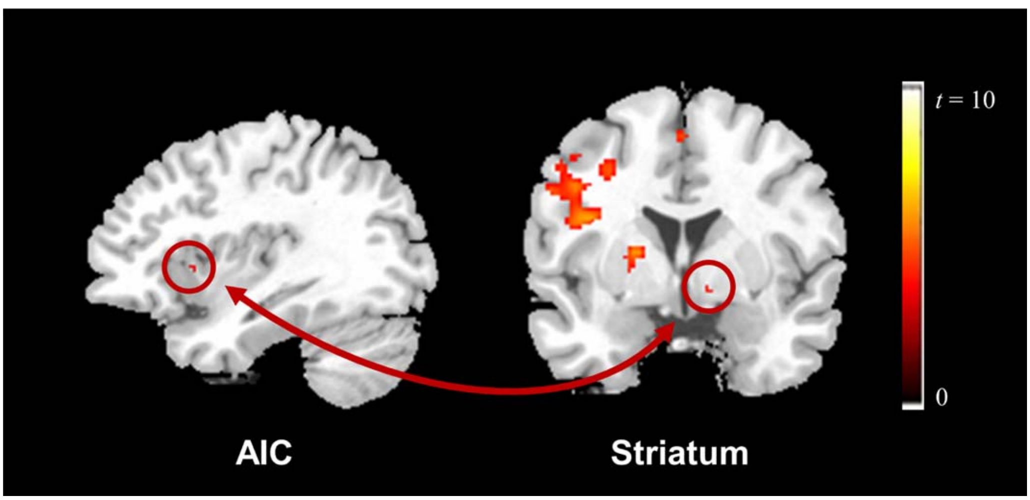

FIGURE 2 Functional interconnectivity between the anterior insular cortex (AIC) and striatum [Colour figure can be viewed at wileyonlinelibrary.com]

differences when participants knew that they were to be allocated personal choices versus when they knew they would not be allocated personal choices. Based on an a priori hypothesis, they set the striatum, the brain's reward center, as a region of interest and compared the degrees of striatal activations in the choice versus no-choice conditions. As hypothesized, the striatum was more activated in the choice condition. In the whole-brain exploratory analyses, however, these researchers found that, in addition to the striatum, the AIC, anterior cingulate cortex (ACC), and amygdala were more activated when participants had personal choice than when they did not have personal choice.

These neural findings were replicated by other neuroscience studies using similar types of experimental manipulations (Leotti & Delgado, 2014; Murayama et al., 2015). For example, Murayama and colleagues (2015) examined the neural activations when participants experienced self-determined choices compared to the neural activations when they experienced forced choices. That is, participants performed a task as they autonomously chose one among a range of similar but different options, and they also performed the same task after being forced to choose one predetermined option. Results consistently showed that the midbrain, which is one of the key brain regions related to reward processing, AIC, and ACC were more recruited when participants experienced self-determined choices than when they experienced forced choices. Results also showed that the negatively valenced brain reactions, observed in the ventromedial prefrontal cortex (VMPFC), emerged after receiving failure feedback in the forced-choice condition, whereas these same negatively valenced reactions did not emerge after receiving failure feedback in the self-determined-choice condition. Similarly, people who receive failure ("change-oriented") feedback delivered in an autonomy-supportive way experience positive, rather than negative, affect (Carpentier & Mageau, 2013), which suggests that autonomy satisfaction is associated with brain resilience (i.e., minimal VMPFC activations) and hence with performance enhancement rather than with performance impairment.

We examined the neural correlates of an experience of autonomy during a learning activity and its neural influences on motivation and cognition during task performance (Reeve & Lee, 2018). In this experiment, we did not manipulate autonomy satisfaction by the provision of personal choice, but instead asked participants first to see dozens of different national flags, second to rate their degree of autonomy toward learning new information about each individual flag, and third to actually invest the effort involved in learning that new information about each individual flag. In this way, participants engaged themselves in a learning activity in which some trials were associated with initially higher levels of autonomy, whereas other trials were associated with initially lower levels of autonomy. On those trials in which participants reported high (vs. low) perceived autonomy, we observed significant AIC activations. We also observed greater striatum activations when participants reported higher interest (i.e., intrinsic satisfaction) while they actually learned about the specific national flag. In addition, we observed greater dorsolateral prefrontal cortex (DLPFC) activations when participants recalled more information about each flag on an unannounced recall test (DLPFC activity is a reliable marker of extent of mental effort during a learning activity; Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; Miller & Cohen, 2001). Interestingly, autonomy-based AIC activations before task performance positively influenced striatum and DLPFC activations during task performance. What these findings suggest is that the AIC–striatum link is a key neural mechanism of intrinsic motivation and the AIC–DLPFC link is a key neural mechanism of cognitive engagement (and hence learning).

2.1.3 | Intrinsic motivation based on relatedness satisfaction

The need for relatedness is also considered to be a fundamental psychological facilitator of intrinsic motivation (Ryan & Deci, 2000); however, the current confidence for this statement is lower than it is for the needs for competence and autonomy. Though there are few studies directly examining the neural correlates of intrinsic motivation based on relatedness satisfaction, we can find indirect evidence from the neural findings about different but similar psychological states. Some neuroscientists have conducted neuroscience studies within the context of close relationships. For example, Bartels and Zeki (2000) compared the neural activations when participants who loved passionately viewed pictures of their partners versus when they viewed pictures of their friends. Results showed that participants displayed greater activity of the striatum, AIC, and ACC when viewing pictures of lovers than when viewing pictures of friends. Bartels and Zeki (2004) conducted another neuroscience study about maternal love and consistently found that the striatum, AIC, and ACC were more activated when mothers viewed pictures of their own children than when they viewed pictures of other children. These results suggest that the neural system of the striatum, AIC, and ACC is involved in the feeling of close relationships.

There are some neuroscience studies that could be related to relatedness frustration, though there are few neuroscience studies about either competence need frustration or autonomy need frustration. For example, Eisenberger, Lieberman, and Williams (2003) conducted a neuroscience study about social rejection. In this study, the feeling of social rejection was manipulated as participants played a game of cyberball but were for a time socially excluded. During episodes of social exclusion, participants showed activations in the ACC, AIC, and ventral prefrontal cortex. These findings suggest that the ACC and AIC play key roles not only when people experience satisfaction from social interactions but also when they experience frustration from social interactions. This neural pattern is understandable because the AIC is a well-known brain region for the processes of emotion, feeling, and motivation of both positive valence and negative valence (Damasio et al., 2000) and because it is frequently observed that the neural signals from the AIC are rapidly relayed to the ACC (Allman et al., 2010).

We can also get an intuitive idea from neuroscience studies that have focused on particular clinical patients. According to neurology studies about autism, dysfunctions (e.g., hypoactivity) in the AIC are related to autism (Uddin & Menon, 2009). Considering that people with autism tend to show impaired social interactions, the AIC seems to be crucial for the generation or execution of the need for social interactions. Neurology studies also found that dysfunctions in the AIC can cause impaired judgment in other people's trustworthiness and, as a result, generate problems in engaging in mutual cooperation (Belfi, Koscik, & Tranel, 2015). This means that the function of the AIC is associated with the sense of whether one's social interactions are satisfying, as well as whether one's social interactions are frustrating.

2.1.4 | Conclusions and cautions

Collectively, neuroscientific findings about intrinsic motivation based on the satisfaction of the psychological needs for competence, autonomy, and relatedness suggest the following neural characteristics of intrinsic motivation. First, the experience of intrinsic motivation recruits brain regions related to reward processing (e.g., striatum, ventromedial prefrontal cortex). Considering that these brain regions are generally activated in the processes of extrinsic motivation (Cardinal, Parkinson, Hall, & Everitt, 2002; O'Doherty, 2004), we can suggest that the brain regions related to reward processing play important roles in human motivation regardless of its sources (i.e., extrinsic vs. intrinsic). Second, the AIC seems to be the unique neural basis of intrinsic motivation. Numerous studies have consistently found that AIC activity is closely related to the experience of intrinsic motivation, which itself is based on the satisfaction of psychological needs. The AIC is known to be associated with processing "subjective feelings from the body" (Craig, 2009; Damasio, 1996). It represents internal bodily needs (e.g., hunger, pain, fatigue, drug craving), monitors their satisfaction/frustration (e.g., satiation, deprivation), and integrates the bodily information into subjective feelings (Goldstein et al., 2009; Naqvi & Bechara, 2009). Here, we suggest that the AIC does for psychological needs what it does for physical needs.

These conclusions about the motivational contributions of the striatum and anterior insula represent "forward inferences" extracted from neuroimaging data. The forward inference is that because an experimental manipulation known to effect a change in a specific motivational state caused the observed brain activity, the psychological state is logically associated with that brain area. That is, when participants engaged themselves in optimal challenges, they experienced competence satisfaction and showed anterior insular activations; hence, the forward inference is that changes in competence satisfaction are associated with changes in AIC activity. The caution, however, arises from the problem of "reverse inference" (Poldrack, 2011).

With reverse inference, an activated brain area is first observed (e.g., a post hoc finding, a meta-analytic review of the literature) that then leads researchers to infer the presence of the psychological state (e.g., when anterior insula activations occur, they signal that psychological need satisfaction also occurred). The limitation of any reverse inference is that the activated brain area is typically associated not just with that one particular psychological state but, instead, with a wide range of other psychological states. Anterior insula activity, for instance, is associated not only with psychological need satisfaction but also with empathy, envy, disgust, craving, pain, and a wide range of subjective "gut-felt" feelings (Craig, 2009). Reverse inference is not such a problem with ventral striatal activity because ventral striatal activations are closely linked to reward motivation but not to non-reward psychological states (Ariely & Berns, 2010). Thus, there are not many alternative interpretations to the reverse inference that when ventral striatal activations occur, they signal that reward-based motivation has occurred. To rule out the alternative interpretations to the more ambiguous AIC–psychological need satisfaction association, future research studies will be necessary, such as those involving the a priori experimental stimulation (or disruption) of AIC activity to see whether the experimental manipulations stimulate or disrupt psychological need satisfaction, using research methods such as transcranial magnetic stimulation of a specific targeted brain area (Duque, Olivier, & Rushworth, 2013; Parkin, Ekhtiari, & Walsh, 2015) or ontogenetics, which uses beams of light to deactivate (temporarily turn off) a specific brain area (Jennings, Rizzi, Stamatakis, Ung, & Stuber, 2013). Until such causality-seeking studies can be carried out, the proposition that anterior insula cortex activations are the neural basis of intrinsic motivation and the psychological needs should be considered more of a working hypothesis than a conclusion statement per se.

2.2 | SDT-based neuroscience studies of motivational traits

SDT-based neuroscience investigations of motivational traits have so far been rather limited. A typical neuroscience study involving motivational traits might investigate people's self-reported motivational traits and examine their cognitive functioning (e.g., self-regulation), using objectively neuroscientific methods to measure those cognitive functions in action. There have been relatively few studies that have directly examined the neural characteristics of motivational traits themselves.

2.2.1 | Effects of SDT-related motivational traits on human functioning

Some SDT researchers have been interested in the notion that people can have trait-level individual differences in self-determined motivation in their general life (Weinstein, Przybylski, & Ryan, 2012). That is, even as people experience the same learning or social situations, their perceived self-determination and intrinsic motivation can vary. There are neuroscience studies examining the neural influences of these SDT-related motivational traits on human cognitive functions. For example, Legault and Inzlicht (2013) found that individuals with higher general autonomous motivation (as assessed by scores on the General Causality Orientations Scale; Deci & Ryan, 1985a) showed greater error-related negativity (ERN) governed by the ACC during the performance of the go/no-go task in their Study 1. Considering that the ERN is related to the error detection mechanism during task performance, the authors suggested that people who generally perceive situations more autonomously tend toward better task performance because they display better self-regulation (specifically, a better monitoring process). In their Study 2, the authors replicated these findings, but they did so by using social psychological manipulations of participants' autonomous motivation (to afford causality inferences), as individuals who were manipulated to experience high (vs. low) levels of autonomous motivation showed better task performance through greater ERN.

Di Domenico and colleagues (2013, 2016) also examined the relations of people's general psychological need satisfaction and their self-regulation during task performance. In these studies, participants were asked to decide which of two occupations was the more preferred, and degrees of decisional conflict were experimentally manipulated. While participants performed this task, their neural activities were recorded by functional near infrared spectroscopy (fNIRS; Di Domenico, Fournier, Ayaz, & Ruocco, 2013) or event-related potentials (ERPs; Di Domenico, Le, Liu, Ayaz, & Fournier, 2016). Results showed that self-related information processing (e.g., ACC or medial prefrontal cortex activity) was crucial for resolving self-related decision conflicts, and individuals who generally reported higher psychological need satisfaction in life demonstrated greater ACC or medial prefrontal cortex activity when self-related decision conflicts existed. Based on these results, the authors suggested that if people show high levels of general need satisfaction, they also tend to show high levels of task performance through the involvement of "self-coherent functioning."

2.2.2 | Trait-level differences in striatum activity

There have been neuroscientific studies examining the modulating effects of motivational traits on neural activities related to motivational processes. In these studies, neuroscientists have generally examined the relations between the traits of people and their neural consequences (Vul, Harris, Winkielman, & Pashler, 2009). That is, personality neuroscientists have sought to identify the neural mechanisms correlated with people's perceived (i.e., self-reported) motivational traits. For example, there have been studies examining the modulating effects of the behavioral activation system (BAS) or behavioral inhibition system (BIS) on striatum activity related to reward processing (Beaver et al., 2006; Hahn et al., 2009; Simon et al., 2010). Because the BAS refers to approach motivation that leaves people sensitive to rewarding stimuli and situations and because the BIS refers to avoidance motivation that leaves people sensitive to punishing stimuli and situations (Carver & White, 1994), researchers hypothesized that individual differences in the BAS and BIS are correlated with degrees of neural reward processing. As expected, participants with high BAS scores showed greater striatum activity during the receipt of rewards, whereas participants with high BIS scores showed lesser striatum activity in the same situations (Simon et al., 2010). In a meta-analysis of such studies, Plichta and Scheres (2014) confirmed a positive relation between personality-based impulsivity and striatum activity during reward processing.

Another example is the collection of neuroscience studies examining the relations between achievement goal orientation and striatum activity during feedback processing (Lee & Kim, 2014; Swanson & Tricomi, 2014). Achievement goal researchers have postulated that learners can have different tendencies in the achievement contexts: mastery goal orientation (i.e., emphasizing mastery itself) versus performance goal orientation (i.e., emphasizing doing better than others or showing high ability; Ames, 1992; Dweck & Leggett, 1988). In line with this postulate, learners with mastery goal orientation tend to view the experience of difficulty as part of the general processes of learning, whereas learners with performance goal orientation tend to view the experience of difficulty as an indicator of their lack of ability. Lee and Kim (2014) found that the striatum was activated when participants received positive feedback, whereas the striatum was deactivated when participants received negative feedback. They also found that performance-oriented (compared to mastery-oriented) participants showed more deactivations in

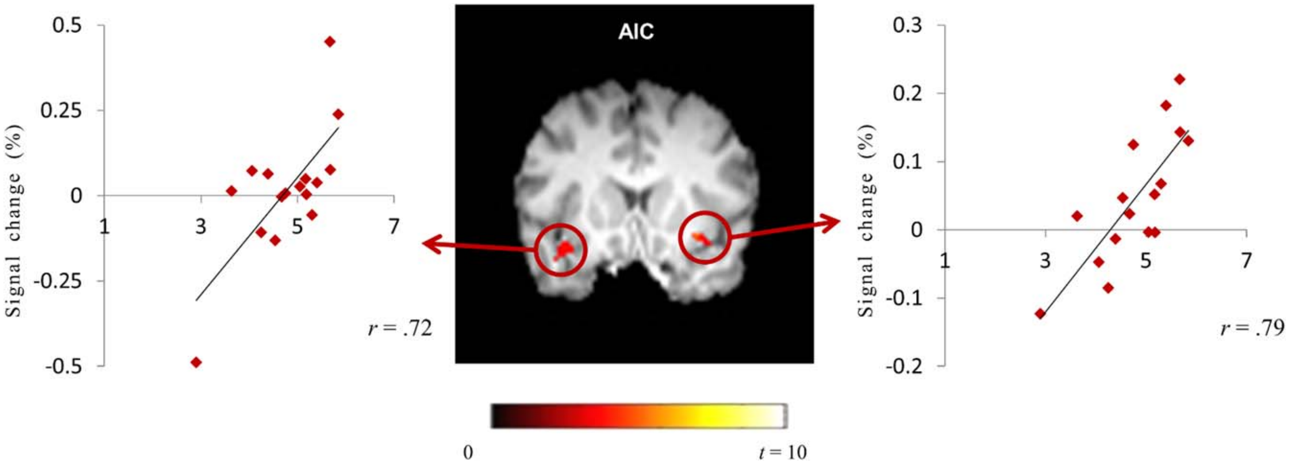

FIGURE 3 Bilateral anterior insular cortex (AIC) associations with self-reported psychological need satisfaction scores [Colour figure can be viewed at wileyonlinelibrary.com]

striatum activity when receiving negative feedback, which confirmed the fact that performance-oriented learners are motivationally vulnerable in the face of obstacles.

2.2.3 | Trait-level differences in AIC activity

Lee and colleagues sought not only to identify the unique neural correlates of intrinsic motivation based on the satisfaction of competence and autonomy (motivational states) but also to examine the modulating effects of participants' self-reported psychological need satisfaction in general (motivational traits). In these studies, participants were asked to imagine the same situation that was presented as an intrinsically motivating task in some cases but as an extrinsically motivating task in other cases, and their neural activations during task performance were examined. The AIC was more activated when participants imagined intrinsically motivating situations (e.g., working with freedom) than when they imagined extrinsically motivating situations (e.g., working for incentives; Lee & Reeve, 2013; Lee, Reeve, Xue, & Xiong, 2012). In addition, results further revealed a large positive correlation between the extent of participants' psychological need satisfaction in general and the extent of AIC activity they showed while imagining intrinsically motivating situations (Lee & Reeve, 2013). This result appears in Figure 3, which suggests that trait-level psychological need satisfaction scores predicted the extent to which participants showed bilateral AIC activations during intrinsically motivating situations.

In addition to the abovementioned functional imaging studies, there are also volumetric (i.e., gray matter volume) neuroscience studies examining the relations between motivational traits and AIC activity. Lewis, Kanai, Rees, and Bates (2014) examined the relations between people's psychological well-being in general and their gray matter volumes in the AIC. In this study, psychological well-being in general referred to individual differences in life satisfaction. The authors found that the more participants reported higher levels of general psychological well-being, the greater gray matter volumes that existed in the physical structure of their AIC brain region. These neural findings suggest that greater AIC volume enables greater life satisfaction, or that greater life satisfaction perhaps catalyzes greater AIC volume.

3 | FUTURE INTEGRATION OF SDT AND NEUROSCIENCE

The psychological need construct is a core unifying principle within the SDT explanatory framework (as per Table 1), and it offers one pathway forward to integrate the SDT macrotheory with the enormous and rapidly developing fields of affective, cognitive, and motivational neuroscience. These future opportunities to integrate SDT and neuroscience will likely occur in the examination of both motivational states and motivational traits.

From our neuroscientifically based program of research, we suggest that activity in both the striatum and anterior insula is closely associated with psychological need satisfaction (Figure 2), and also that AIC activity is particularly and rather uniquely associated with both the antecedents (Figure 1) and subjective experiences (Figure 3) of psychological need satisfaction. To the extent that AIC activity is uniquely and centrally important to the psychological need construct, we suggest that these findings open up several important avenues of future research. To help advance the integration of SDT and neuroscience, we identify here a number of gaps and pressing questions in the literature that we believe currently exist and are worth pursuing.

1. To integrate basic needs theory and neuroscience, one wonders whether autonomy, competence, and relatedness need satisfactions show a single pattern of neural activity

(one single region of interest), or whether autonomy, competence, and relatedness need satisfactions each show a different pattern of neural activity (three different regions of interest). Answering this question will likely require more precise measurement capabilities than are currently available using fMRI.

2. Psychological needs can be deprived, anticipated, satisfied, frustrated, or desired. This raises the question as to whether need states are processed in different areas or whether a single brain area processes the full array of need states.
3. To integrate causality orientations theory and neuroscience, it is important to note that no study has yet investigated the possible association between the autonomy causality orientation and AIC activity. Such a personality-based study can capitalize on functional imaging methods but also on neuroscientific methods that are more amenable to individual differences investigations, such as between-person differences in (a) resting state fMRI and EEG, (b) activation thresholds or sensitivities, (c) gray matter shape or volume, and (d) greater gray matter density and connectivity analyses.
4. To integrate goal contents theory and neuroscience, intrinsic goals are those that are closely associated with psychological need satisfaction, whereas extrinsic goals are those that are not associated with psychological need satisfaction (Kasser & Ryan, 1996). This raises the question as to whether or not participants who pursue need-satisfying intrinsic goals show greater AIC (and perhaps greater striatum) activity.
5. To integrate organismic integration theory and neuroscience, psychological need satisfaction is hypothesized to be a necessary condition for the internalization of extrinsic motivations. This raises the question as to whether participants who internalize an environmental request show greater AIC activity than do participants who fail to internalize the request, which is another way of asking whether an experience of need satisfaction adds motivational fuel to the internalization process.
6. According to SDT's "dual-process model" (Bartholomew, Ntoumanis, Ryan, & Thøgersen-Ntoumani, 2011), need frustration is a separate psychological process than is need satisfaction. Are need satisfaction and need frustration two separate motivational processes, or are they one single experience in which need frustration is simply the opposite valence of need satisfaction? If the neural activities of need satisfaction and frustration do not overlap, then that would suggest two distinct processes. Another possibility is that need satisfaction may be more associated with the left AIC, and need frustration may be more associated with the right AIC (a possibility suggested from the work of Panksepp, 1998).
7. Psychological need satisfaction generates a wide range of important benefits, from deeper cognitive engagement to greater achievement and well-being. What is the role of the functional interconnectivities between the AIC and other brain areas (e.g., DLPFC, striatum, ACC) that might explain the facilitating contribution of psychological needs to outcomes such as cognitive engagement, well-being, and mindfulness?
8. Does a larger brain area or does a particular pattern, shape, or density of gray matter in a brain area afford the person a greater capacity to experience that SDT-related motivational state? That is, does greater insula volume afford the individual a greater capacity to experience need satisfaction or intrinsic motivation in one's life? Or, do experiences of need satisfaction and intrinsic motivation have developmental implications for greater insula volume or for a particular pattern, shape, or density of gray matter within the insula?

4 | CONCLUSION

SDT's most basic propositions are that all people possess inherent psychological needs for autonomy, competence, and relatedness and, further, that the satisfaction of these needs maintains and promotes personal growth and psychological well-being. Research on the neural basis of psychological need satisfaction shows that need satisfaction is associated with striatum activity, anterior insula activity, and the functional co-activation between these two brain areas. As the neural underpinnings of this basic motivational process become better understood, several opportunities to integrate neuroscience with SDT motivational states and traits are now emerging to help advance our understanding of human motivation and personality.

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CONFLICT OF INTERESTS

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