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Autonomy recruits neural support for interest and learning

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Abstract
According to self-determination theory (SDT), an experience of autonomy energizes both interest and learning. The purpose of the present study was to investigate how an experience of autonomy recruits the neural activity needed to energize and support that interest and performance. Using event-related functional magnetic resonance imaging (fMRI), we exposed 22 undergraduates (11 females, 11 males) to 81 learning trials. We hypothesized that (1) an experience of autonomy would be associated with anterior insular cortex (AIC) activations (reflecting autonomy energization), (2) these AIC activations would recruit both striatum activations (reflecting autonomy satisfaction and hence interest) and dorsolateral prefrontal cortex (DLPFC) activations (reflecting cognitive engagement), (3) striatum activations would predict self-reported interest, and (4) DLPFC activations would predict objectively-scored learning. Multilevel and parametric analyses of the fMRI data supported all predictions. These findings demonstrate the neural substrates through which autonomy energizes interest and learning. We discuss how these neuroscientific findings advance SDT and deepen our understanding of an experience of psychological need satisfaction.

Keywords Anterior insular cortex (AIC) · Autonomy · Dorsolateral prefrontal cortex · Educational neuroscience · fMRI · Self-determination theory · Striatum

Introduction

According to self-determination theory, autonomy is the psychological need to experience self-direction and personal endorsement in the initiation and regulation of one's behavior (Ryan & Deci, 2017). As people engage in learning activities, how much self-direction and personal endorsement they experience (i.e., autonomy) predicts how interesting they find the task to be, how much they learn, and how well they perform. Autonomy's capacity to predict interest, learning, and performance has been demonstrated in correlational (Froiland & Worrell, 2016; Joo et al., 2010; Reeve & Jang, 2006), experimental (Jang, 2008; Jang et al., 2016a; Vansteenkiste et al., 2005), longitudinal (Cheon et al., 2012; Jang et al., 2012), and meta-analytic (Bureau et al., 2022; Cerasoli et al., 2016) studies. In the present study we used the methods of neuroscience to investigate how an experience of autonomy in the early part of a learning activity recruits neural support to energize and enable these gains in interest, learning, and performance.

Autonomy's neural substrates

The traditional neuroscientific understanding of human motivation has always emphasized the ventral striatum as the neural center of reward processing (Schultz, 2015). The striatum is divided into a ventral (lower) and a dorsal (upper) division. The ventral striatum consists mainly of the nucleus accumbens (but also the ventral parts of the caudate nucleus and the putamen), while the dorsal striatum consists of the caudate nucleus and the putamen. The ventral striatum plays a key role in "the hedonic valuation of situations or stimuli". The dorsal striatum is also a component of the brain's reward circuitry, but its functions differ from those of the ventral striatum (Burton et al., 2015; O'Doherty et al., 2004). The dorsal striatum utilizes and integrates the

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valuation information to motivate and regulate decision-making, self-control, or goal-directed behavior.

In the initial investigations to identify autonomy's neural substrates, researchers first specified the ventral striatum as a region of interest (ROI) (Leotti & Delgado, 2011, 2014). These early researchers introduced an experimental manipulation of choice (a well-known antecedent of autonomy; Patall, 2013; Schneider et al., 2018) to find that the ventral striatum showed greater activation when participants pursued a personal gain in the choice than in the no-choice condition, leading to the conclusion that autonomy episodes were rewarding (Leotti & Delgado, 2011, 2014). In addition to their hypothesis-based ROI analyses, Leotti and Delgado (2011, 2014) further conducted exploratory whole-brain analyses. These results showed that the dorsal striatum as well as the ventral striatum was more activated in the choice condition than in the no-choice condition.

Leotti and Delgado's (2011, 2014) exploratory whole-brain analyses also showed that the anterior insular cortex (AIC), together with the ventral and dorsal striatum, was more activated in the choice condition than in the no-choice condition. In a later study, Murayama and his colleagues (2015) found that the AIC, along with the ventral striatum, was more activated in a self-determined-choice condition than in a forced-choice condition. The relation between the AIC and autonomy was further supported by a group of researchers who found that AIC activity was consistently observed when participants experienced satisfactions of their basic psychological needs (e.g., autonomy and competence) both during the imagination of situations (Lee & Reeve, 2013; Lee et al., 2012) and during actual task performance (Lee & Reeve, 2017). In addition, AIC activity correlated positively and strongly (r=.72 with left AIC activity; r=.79 with right AIC activity) with the degree of participants' self-reported psychological need satisfaction (Lee & Reeve, 2013).

The AIC is a part of an afferent system that serves as the neural foundation for feelings, as the AIC integrates bodily reactions to current situations and surrounding stimuli into subjective feelings (Craig, 2002; Damasio & Carvalho, 2013; Harrison et al., 2010), including moment-to-moment changes in feelings of interest-curiosity (Lee & Reeve, 2017) and enjoyment-happiness (Rutledge et al., 2014). In addition, the AIC shows co-activation with the striatum. When participants engaged in intrinsically motivating activities that allowed them to feel interest, they showed AIC-striatum co-activations, compared to when they engaged in non-intrinsically motivating versions of these same tasks (Lee & Reeve, 2017). Collectively, these programs of research suggest the conclusion that the key neural mechanisms that underlie the psychological experience of autonomy are AIC activations, striatum activations, and the AIC-striatum link (Reeve & Lee, 2019).

Based on the theoretical and neuroscientific understanding of the autonomous motivational state, we predicted that when participants first engage in a task and begin to experience a sense of self-direction they will first show AIC activity; further, as that initial sense of self-direction becomes a fuller sense of personal endorsement they will then show ventral and dorsal striatum activity (based on Lee & Reeve, 2017; Reeve & Lee, 2019). However, this hypothesized temporal sequence between a subjective experience of autonomy, AIC activations, and striatum activations is not clear. This is because no study to date has differentiated between when participants first encounter an experimental task and begin to experience high vs. low autonomy versus when participants actually experience autonomy satisfaction while performing that task. We suggest that an experience of autonomy typically begins with an anticipatory state in which the environment offers the person an opportunity to pursue self-direction and/or a personal interest (i.e., early-stage autonomy), and it continues as the person's task engagement becomes characterized by feelings of personal causation, volition, and self-endorsement (i.e., late-stage autonomy).

To investigate this possible early-stage/late-stage distinction within an experience of autonomy, we adopted a neuroscience method of data collection. We had participants lay inside an MRI scanner and react to a series of learning activities (the stimuli) presented to them in two stages while we collected real-time brain activation data. The first stage of stimulus exposure was meant to offer a potential opportunity to experience autonomy (i.e., "How much do you freely want to learn this?") that we expected to be reflected in the participants' extent of AIC activations. The second stage of stimulus exposure was meant to capture how need satisfying the learning experience was (i.e., "How interesting was it?") that we expected to be reflected in participants' extent of ventral and dorsal striatal activations.

An experience of autonomy may also energize cognitive processes (e.g., mental effort) during task performance. We expected this would be the case because autonomy during a learning activity predicts extent of conceptual learning (Jang, 2008; Jang et al., 2016a; Kusurkar et al., 2013; Vansteenkiste et al., 2004, 2005). In the present study, we exposed participants to new material to be learned, and we expected that an initial experience of high vs. low autonomy on a given trial would energize in-trial attention and mental effort, as reflected by dorsolateral prefrontal cortex (DLPFC) activity. Like many brain regions, the (right) DLPFC shows activation during initial attention to a stimulus as well as for a few seconds of sustained attention. DLPFC activity is a reliable marker of extent of mental effort and cognitive

control during a learning activity (Carter et al., 1998; Miller & Cohen, 2001), as it helps prepare (Vassena et al., 2014) and carry out (Engstrom et al., 2013) the mental effort necessary to engage in the learning activity (e.g., a mental arithmetic task). Accordingly, we expected that participants would show greater learning on those trials in which they also showed high (rather than low) DLPFC activations.

Hypotheses

The investigation's overarching two-fold prediction was that *autonomy would predict interest* and that *autonomy would predict learning*. *Hypothesis 1* (H1) was that trial-by-trial autonomy ratings would predict trial-by-trial interest scores. *Hypothesis 2* (H2) was that trial-by-trial autonomy ratings would predict trial-by-trial learning scores (i.e., performance). These two primary predictions appear in Fig. 1. Figure 1 further illustrates the neural processes hypothesized to underlie these two primary predictions. Hypotheses 3–7 describe and organize our brain-based hypotheses. These five hypotheses are not meant to propose mediational effects, because the present study was not powered to investigate them.

Early-stage predictor

Hypothesis 3 was that early-stage autonomy during a forthcoming learning opportunity would predict extent of early-stage AIC brain activations. We based this prediction on the many neuroscience studies confirming the association between autonomy and AIC activations (e.g., Lee et al., 2012; Lee & Reeve, 2013, 2017). In the present study, H3 represents our prediction of the neural underpinning of autonomy as it first emerges during a learning opportunity.

Early-stage to late-stage predictors

Hypotheses 4 and *5* were that early-stage AIC brain activations during stimulus presentation would predict late-stage ventral and dorsal striatum activations (H4) and late-stage DLPFC activations (H5). Conceptually, we based H4 and H5 on the predictions that an experience of autonomy would lead to both interest/intrinsic satisfaction (H4) and to heightened cognitive engagement (H5), as has been found in classroom longitudinal studies using self-report questionnaires (Jang et al., 2012, 2016b). The difference between our predictions and those earlier self-report studies was that we sought to measure the neural activities that energize and

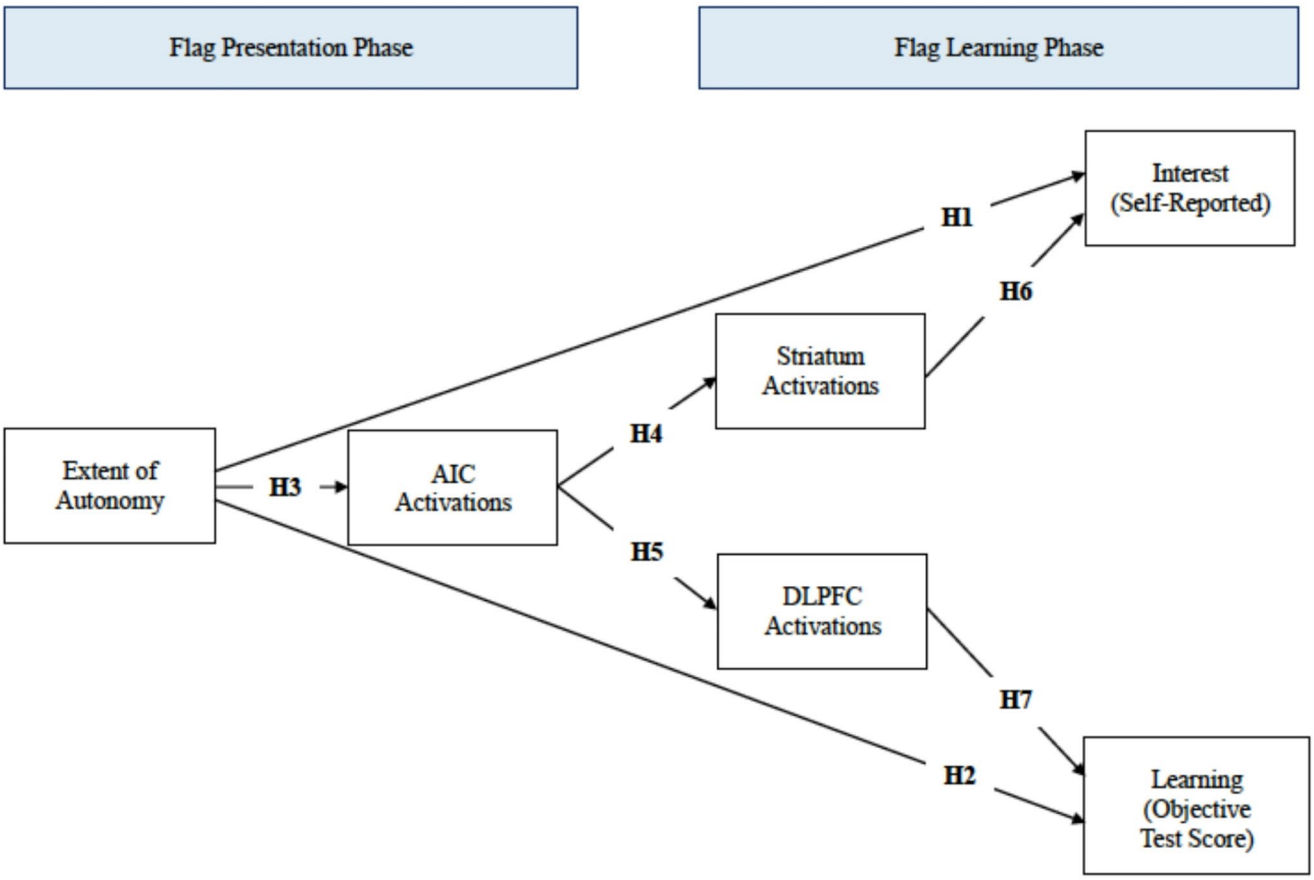

Fig. 1 Hypothesized model. *H* = hypothesis

enable interest/intrinsic satisfactions (i.e., ventral and dorsal striatum activations, H4) and heightened cognitive engagement (i.e., DLPFC activations, H5).

Late-stage predictors

Hypothesis 6 was that extent of late-stage ventral and dorsal striatum brain activations would predict participants' self-reported interest ratings. H6 represents our prediction of the neural underpinning of interest as it emerges during a learning opportunity. *Hypothesis 7* was that extent of late-stage dorsolateral prefrontal cortex (DLPFC) brain activations would predict participants' objective learning score (i.e., performance) on that same trial. H7 represents our prediction of the neural underpinning of cognitive engagement as it emerges during a learning opportunity.

When taken as a whole, H1 and H2 predicted the direct positive effects of subjectively-felt autonomy on subjectively-felt interest (H1) and objectively-scored learning (H2), while H3, H4, H5, H6, and H7 predicted the neural basis underlying these two primary effects.

Method

Transparency and openness

This study was not preregistered. However, the data sets, the Mplus syntax used to analyze these datasets, and the output files are available on the Open Science Framework (OSF) project site: https://osf.io/65pny/?view_only=4cca0c8ff4e74013aaa700d150436f8f. Also available at this OSF project site are the experimental materials (flag stimuli, learning test), the raw fMRI data, and the AFNI processing script.

Participants

Twenty-seven undergraduates (14 females, 13 males) with a mean age of 23.2 years-old (SD=2.6) attending a large private university participated in the study. Each participant had normal or corrected-to-normal vision, was neurologically healthy, and right-handed. The participants provided informed consent and received compensation for their participation. One participant's data were excluded because he responded that he was familiar with most of the flags on the pretest. Four participants' data were also excluded because three participants monotonously responded to autonomy or interest ratings during task performance and the other participant barely recalled the information about the flags on the surprise test, which we judged to reflect insincere task engagement. Therefore, we used the data from 22 participants (11 females, 11 males; mean age of 23.2 [SD=2.9]) for the data analyses. The final sample size was similar to or larger than the sample sizes used in previous fMRI studies of intrinsic motivation (or psychological need satisfaction) using a within-subject design and conducting parametric analyses (Gruber et al., 2014; Lee & Reeve, 2017).

Task

The task involved learning about national flags (e.g., what a symbol or color on the flag means). After pilot testing, 81 national flags were identified (from a larger pool of national flags) that were relatively unfamiliar to our potential participants and that contained new information that could be learned. For instance, Panama's flag displays two stars to represent the nation's two political parties, while Finland's flag displays a large blue cross in which the blue color represents the nation's 1,000 lakes. In addition to removing universally familiar flags, we also removed national flags that were visually complex (e.g., high cognitive demand; Belize, Swaziland). High-resolution images of each flag were taken from internet sites and loaded as images into E-Prime software (Psychological Software Tools, Inc., Pittsburgh, PA). We created this new 81-trial image-based learning activity to accommodate to the fMRI setting, which operates best with briefly presented (2–4 s) image-based stimuli, and to offer participants an authentic learning activity capable of generating varying trial-to-trial levels of autonomy, interest, cognitive engagement, and learning.

Autonomy measure

To measure autonomy in the context of an fMRI study, we used the single item, "How much do you freely want to learn this?" The use of a single item measure is standard practice in neuroscience research, because participants' brain activity needs to be matched in real time with the report of their subjective experience. Brain activity occurs second-to-second, so self-reported experience needs to be assessed very quickly (e.g., within one second) during fMRI scanning—hence the pressing need to use a single item measure. To create this item, we started with Milyavskaya and her colleagues' "want to" phrase used to connote autonomous motivation in studies of self-concordant goal pursuit (Milyavskaya et al., 2015) and then added the adverb "freely" so that "freely want to" could represent "self-endorsement", which is the hallmark of autonomy (Ryan & Deci, 2017, p. 10). "Free" is commonly used in questionnaire measures of autonomy, including "I feel free" from the Activity-Feelings Scale (AFS; Reeve & Sickenius, 1994), "I was free to do things my own way" from the Balanced Measure of Psychological Needs (BMPN; Sheldon & Hilpert, 2012), "I feel a sense of choice and freedom in the things I undertake" from

the Basic Psychological Need Satisfaction and Frustration Scale (Chen et al., 2015), and "I feel a certain freedom of action" from the Autonomy scale (Standage et al., 2006).

To confirm that our newly created, single-item autonomy measure reflected a similar psychological experience as assessed by these widely-used, multifaceted, and previously-validated multiple-item measures of autonomy, we conducted a pilot test (see Supplemental Materials). The pilot test employed the same methodology as used in the main experiment, as described below, except that the series of flag stimuli were presented outside the MRI scanner and participants also completed the AFS and BMPN questionnaires. In the pilot test, scores on our single-item measure correlated significantly with autonomy scores on both the AFS (r=.55, p=.002) and BMPN (r=.58, p=.001), especially after correcting for the measurement error within the AFS (α=0.80), r=.62, p<.001, and the BMPN (α=0.76), r=.67, p<.001.

Learning measure

Before entering the fMRI setting, participants completed a pretest (see the OSF project site). In this pretest, participants viewed a multi-page document featuring individual pictures of the 81 national flags (without country names) and participants were asked to indicate whether or not they were familiar with each flag. Instructions were: "Please place a check mark in the box of any flag with which you are familiar—that is, you are familiar with the flag or you know the name of the country of that flag." The purpose of this pretest was to identify the subset of the 81 flags that each individual participant was not familiar with—so that we could assess the learning of new information. On average, participants checked 19.4 flags as familiar and left 61.6 flags unchecked as unfamiliar. In the analyses (described later), we made a pre-analysis decision to exclude the data associated with all those flags that the participant checked as familiar on the pretest.

After the fMRI scanning, there was a surprise (i.e., unannounced) test of learning that lasted about 15 min. The test was a multi-page document that re-listed all 81 flags with a question listed beside each flag (see the OSF project site). The question asked for the information about that flag to be learned. For instance, for the flag of Lebanon, the question was written as "Cedar tree =?", though the answers for some questions had two parts (e.g., the meaning of blue in the Greek flag was both "the sea" and "the sky"). Participants' answers were scored as incorrect=0 (blank or answer is incorrect based on the information to be learned), partially correct=1 (answer is half correct and half incorrect based on the information to be learned), or correct=2 (answer is correct based on the information to be learned). Using this 0 to 2 rubric, scores on the post recall learning test were scored with perfect interrater reliability, r=1 (i.e., the two raters agreed on all learning scores).

Procedure

This study was approved by the Institutional Review Board of Korea National University of Education. An event-related fMRI experiment consisting of three separate runs was performed. Each run included 27 trials and lasted for 9 min 30 s. Within each of the 81 trials, there were two phases (see Fig. 2): early-stage flag presentation followed by late-stage flag learning.

As shown in Fig. 2, each trial began with the flag presentation phase. One national flag, randomly selected from the array of 81 flags, was presented for two seconds. The country name was then added so that the national flag and its country's name were presented together for an additional two seconds. After participants saw the flag and country name, they were asked to rate how much they freely wanted to learn about that particular national flag on a 1–3 scale (1=not at all; 2=moderately; 3=a great deal) for two seconds. Using their right hand, participants button-pressed their 1, 2, or 3 autonomy rating on each individual trial.

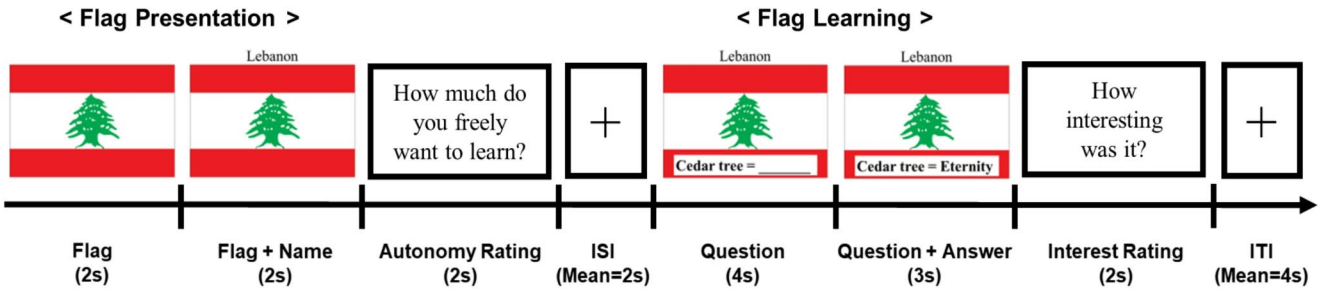

Fig. 2 Trial-by-trial research design. *Note*: In each trial, there were two phases: flag presentation followed by flag learning. In the flag presentation phase, one randomly selected national flag was presented, and the country name was added in the middle of flag presentation. After seeing the national flag, participants were asked to rate how much they freely wanted to learn about the national flag. In the flag learning phase, the material to be learned about the national flag was presented, and the answer was presented afterward. Then, participants rated how interesting flag learning was on that particular trial. "s" = seconds

This score served as our within-subjects (repeated measures) measure of an experience of autonomy. Following the autonomy rating, a fixation cross was presented at the inter-stimulus interval for an average of 2 s (1500-2500ms).

In the flag learning phase, a key characteristic of the national flag was identified for four seconds. The information to be learned about that flag was then presented for three seconds. For instance, in the Fig. 2 illustration, the key characteristics was "Cedar tree =?" and the material to be learned was "Eternity". After participants had this opportunity to learn something new, they were then asked to rate how interesting that particular learning experience was on a 1–3 scale (1 = not at all; 2 = moderately; 3 = a great deal) for two seconds. This "How interesting was it?" rating served as our measure of self-reported interest on that trial. Following this rating, a fixation cross was presented at the inter-trial interval for an average of 4 s (2000–6000 ms), and then the next trial began. Trial order and the variation of the inter-stimulus and inter-trial intervals were determined using OptSeq (http://surfer.nmr.mgh.harvard.edu/optseq/).

During the fMRI scanning, functional images were acquired as participants performed the experimental task. After the experimental task ended, anatomic images were acquired. After they left the MRI scanner, participants were debriefed and received compensation for their participation.

fMRI data acquisition

A 3T Trio MRI scanner (Siemens, Erlangen, Germany) was used for functional and anatomic imaging. Using a T2*-weighted gradient-echo echo planar imaging (EPI) sequence sensitive to blood oxygenation level-dependent (BOLD) contrast, 32-slice functional images were acquired (TR = 2000 ms, TE = 30 ms, flip angle = 90°, field of view = 224 × 224, in-plane resolution = 3.5 × 3.5 mm, slice thickness = 4 mm with no gap). After obtaining functional images, high-resolution T1-weighted anatomic images were acquired by using a MP-RAGE sequence with the following parameters: TR = 1900 ms, TE = 2.52 ms, flip angle = 9°, field of view = 256 × 256, in-plane resolution = 1 × 1 mm, and slice thickness = 1 mm with no gap. The anatomic images were used for anatomical localization to facilitate the precise determination of the structures corresponding to the functional activation foci.

fMRI data analysis

The brain images were analyzed by using AFNI (Analysis of Functional NeuroImages; Cox, 1996; http://afni.nimh.nih.gov). To allow hemodynamics and MRI signals to reach a steady state, the first three images of each run were discarded (as is standard practice in fMRI studies). In preprocessing, the functional images were interpolated to the same time point at the beginning of the TR for temporal alignment. Then, the temporally aligned functional images were registered to the anatomic images of each participant for spatial alignment and registered to the base volume of the functional images for head motion correction. The realigned functional images were spatially blurred with a 5-mm full-width at half-maximum (FWHM) Gaussian kernel. Instead of using a commonly used 8-mm FWHM Gaussian kernel, we had decided to use a narrower one to prevent the cluster-wise threshold for multiple comparison correction from being too conservative. The functional data were normalized as a percent of the mean for conducting statistical analyses after the values of voxels outside the brain were excluded.

In individual analyses, each participant's preprocessed data were analyzed using a general linear model (GLM). In the GLM, the regressors convoluted with hemodynamic response functions (HRF) were computed. In order to conduct the parametric analysis, two regressors of interest were considered. One regressor was for the time points that national flags were presented, which was modulated by each participant's autonomy rating during flag presentation. The other regressor was for the time points that the information to be learned were presented, which were modulated by each participant's interest rating during flag learning and by each participant's surprise test score for each national flag. To control for the effects of head motion artifacts, six regressors for head motion parameters were also included as covariates. Using each participant's standardized high-resolution anatomic images, statistical data were transformed to fit the Montreal Neurological Institute (MNI) template and resampled to $2 \times 2 \times 2$ mm^3 voxels.

As a group analysis, the parametric analysis was performed to identify the neural activity related to participants' 1–3 autonomy rating during flag presentation, the neural activity related to participants' 1–3 interest rating during flag learning, and the neural activity related to participants' 0–2 learning score on each trial.

The Monte-Carlo simulation method (Forman et al., 1995) was used for multiple comparison correction, which determined the cluster-wise threshold (corrected $p < .05$) considering both the voxel-wise threshold ($p < .005$) and cluster size ($n \geq 55$, a minimum volume of 440 mm^3). The brain regions significantly activated in the parametric analysis were reported in MNI coordinates. ROIs were set from the brain regions significantly activated in these analyses, and the BOLD signal changes of all trials in these ROIs were calculated from the individuals' MNI-normalized preprocessed data.

Analytical strategy to test hypotheses

We tested seven hypotheses (see Fig. 1). Hypotheses 1–3 predicted that the autonomy rating at the beginning of each trial would predict self-reported interest (H1), a high learning test score (H2), and early-trial AIC activations (H3). Hypothesis 4 predicted a positive association between participants' early-trial AIC activations and their corresponding late-trial striatum activations (irrespective of autonomy rating). Hypothesis 5 predicted a positive association between participants' early-trial AIC activations and their corresponding late-trial DLPFC activations (irrespective of autonomy rating). Hypothesis 6 predicted a positive association between participants' late-trial striatum activations and their corresponding interest rating on that trial (irrespective of autonomy rating). Hypothesis 7 predicted a positive association between participants' late-trial DLPFC activations and their corresponding objective learning score on that trial (irrespective of autonomy rating).

To evaluate H1, H2, H4, and H5, given the nested structure of these data (trial-by-trial scores were nested within individuals), we conducted multilevel analyses with Mplus version 8.3. We conducted multilevel correlation analyses to examine the associations among participants' trial-by-trial autonomy ratings and their trial-by-trial interest ratings (H1) and trial-by-trial learning test scores (H2). We further conducted a multilevel path analysis to examine the associations among participants' early-trial AIC and late-trial striatum activations (H4) and late-trial DLPFC activations (H5). These multilevel analyses focused on the within-subjects trial-by-trial relationships while controlling for between-participant effects.

To evaluate H3, H6, and H7, using the fMRI data, we conducted a parametric analysis. H3 examined the neural activity during flag presentation (i.e., early-trial phase) as participants made their 1–3 button-press autonomy rating (the modulating parameter). H6 examined the neural activity during flag learning (i.e., late-trial phase) as participants made their 1–3 button-press interest rating (the modulating parameter). H7 examined the neural activity during flag learning (i.e., late-trial phase) as raters' scored participants' 0–2 learning score for each national flag (the modulating parameter; see fMRI Data Analysis section above).

Results

Pre-scanning results

On the pretest participants rated 19.4 (SD=13.6, *range*=8 to 66) out of 81 (24.0%) national flags as familiar. Data associated with these familiar flags were removed from the data analyses. In the analyses, we tested our hypotheses with respect to the remaining 61.6 (76.0%) of the 81 possible trials (*range*=15 to 73).

Behavioral results

Participants' mean ratings of autonomy and interest were 2.20 (SE=0.10) and 2.18 (SE=0.07) on a 1–3 scale respectively. Participants' mean posttest learning score was 0.31 (SE=0.05) on a 0–2 scale. To test H1 and H2, we conducted multilevel correlation analyses.

H1: autonomy predicts interest

The multilevel correlational analyses showed that, after controlling for the between-participant effects, participants' trial-by-trial autonomy ratings predicted their corresponding trial-by-trial interest ratings (b=0.14, SE=0.04, p<.001). This confirms H1 by showing that participants' interest ratings were significantly greater on the trials in which they reported high autonomy.

H2: autonomy predicts learning

The multilevel correlational analyses further showed that, after controlling for the between-participant effects, participants' trial-by-trial autonomy ratings predicted their corresponding flag-by-flag learning scores (b=0.10, SE=0.04, p<.05). This confirms H2 by showing that participants' learning was significantly greater on those trials in which they reported high autonomy.

fMRI results

To test H3, H6, and H7, we conducted a parametric analysis to identify activated brain regions. H3 used participants' autonomy rating during flag presentation to predict brain activations. H6 used participants' interest rating during flag learning to predict brain activations. H7 used participants' posttest learning score to predict brain activations.

H3: autonomy predicts AIC activations

As shown in the upper part of Table 1, the right anterior insular cortex (AIC; Fig. 3), the right DLPFC, the left supplementary motor area, the right inferior parietal lobe, the right fusiform gyrus, and the left cerebellum were more activated during the presentation of the national flags in which participants made high autonomy ratings (corrected p<.05). No brain region showed lesser neural activity when participants made high autonomy ratings. This confirms H3 by showing

Table 1 Results of the parametric analysis for H3, H6, and H7

Brain Region	BA	Volume	Side	MNI Coordinates			Maximum intensity value
				x	y	z	
Autonomy rating parameter (during flag presentation)							
Positive							
Anterior insular cortex	13	560	R	38	4	4	4.63
Dorsolateral prefrontal cortex	9	1632	R	48	10	28	5.87
	46	944	R	46	28	12	4.34
Supplementary motor area	6	1616	L	-4	4	52	5.74
Inferior parietal lobe	40	936	R	34	-62	44	4.30
Fusiform gyrus	37	2456	R	34	-62	-18	5.21
Cerebellum		1200	L	-26	-80	-20	4.11
Interest rating parameter (during flag learning)							
Positive							
Striatum (caudate nucleus)		792	R	14	4	16	4.37
Middle frontal gyrus	10	800	L	-28	56	8	4.37
Inferior frontal gyrus	45	664	L	-32	34	6	4.86
Middle temporal gyrus	21	776	L	-38	-12	-18	4.66
	21	600	R	42	-46	-12	4.03
Fusiform gyrus	37	1144	L	-54	-50	-4	5.84
Learning score parameter (during flag learning)							
Positive							
Dorsolateral prefrontal cortex	9	656	R	40	10	26	5.83
Inferior frontal gyrus	45	7360	L	-52	26	4	6.82
Angular gyrus	39	15,288	L	-28	-58	36	7.16
Supramarginal gyrus	40	2616	L	-30	-60	30	5.92
Fusiform gyrus	37	832	R	44	-46	-16	5.10
	37	552	L	-28	-56	-14	4.48
Occipital lobe	18	1608	R	26	-86	0	4.84
	18	1144	R	20	-76	-20	4.90

The cluster-wise threshold (correct $p<.05$) for multiple comparison correction is determined by voxel-wise threshold ($p<.005$) and the minimum volume (55 contiguous voxels; 440 mm^3). BA = Broadmann area to note the spatial location in the brain of the activated area. Volume = size of the voxel area of the activated brain area. Side = right or left hemisphere. MNI Coordinates: x = left side of the brain to the right side; y = posterior to anterior location; z = bottom or inferior area of the brain to the top or superior area. Maximum intensity value = statistical value showing the greatest difference among activated voxels in the brain region

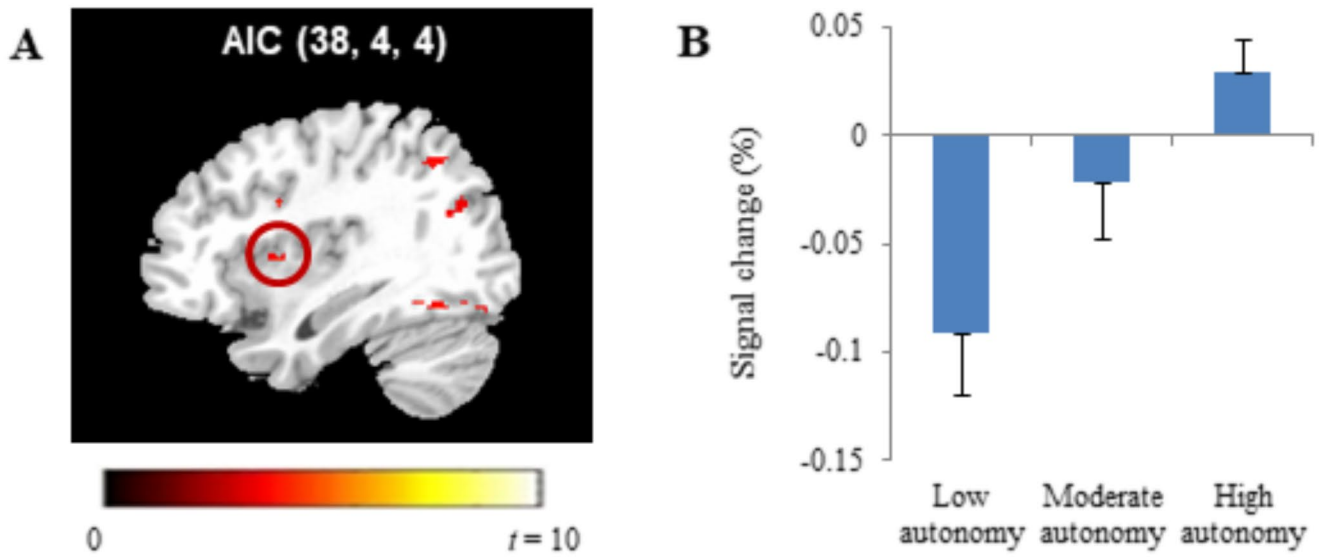

Fig. 3 Autonomy ratings predict AIC activations. The right AIC was more activated during flag presentation as participants' perceived autonomy ratings were higher (A, test of H3). BOLD signal changes in the right AIC are presented in more detail depending on the degree of participants' perceived autonomy (B)

that participants' AIC activations were significantly greater on the trials in which they made high autonomy ratings.

H6: interest predicts dorsal, but not ventral, striatum activations

As shown in the middle part of Table 1, the right dorsal striatum (caudate nucleus; Fig. 4A), the left middle and inferior frontal gyrus, the bilateral middle temporal gyrus, and the left fusiform gyrus were more activated during the learning phase of the national flags in which participants made high interest ratings (corrected $p<.05$). The ventral striatum did not show greater neural activity, and no brain region showed lesser neural activity when participants made high interest ratings. This partially confirms H6 by showing that participants' dorsal (but not ventral) striatum activations were significantly greater on the trials in which they made high interest ratings.

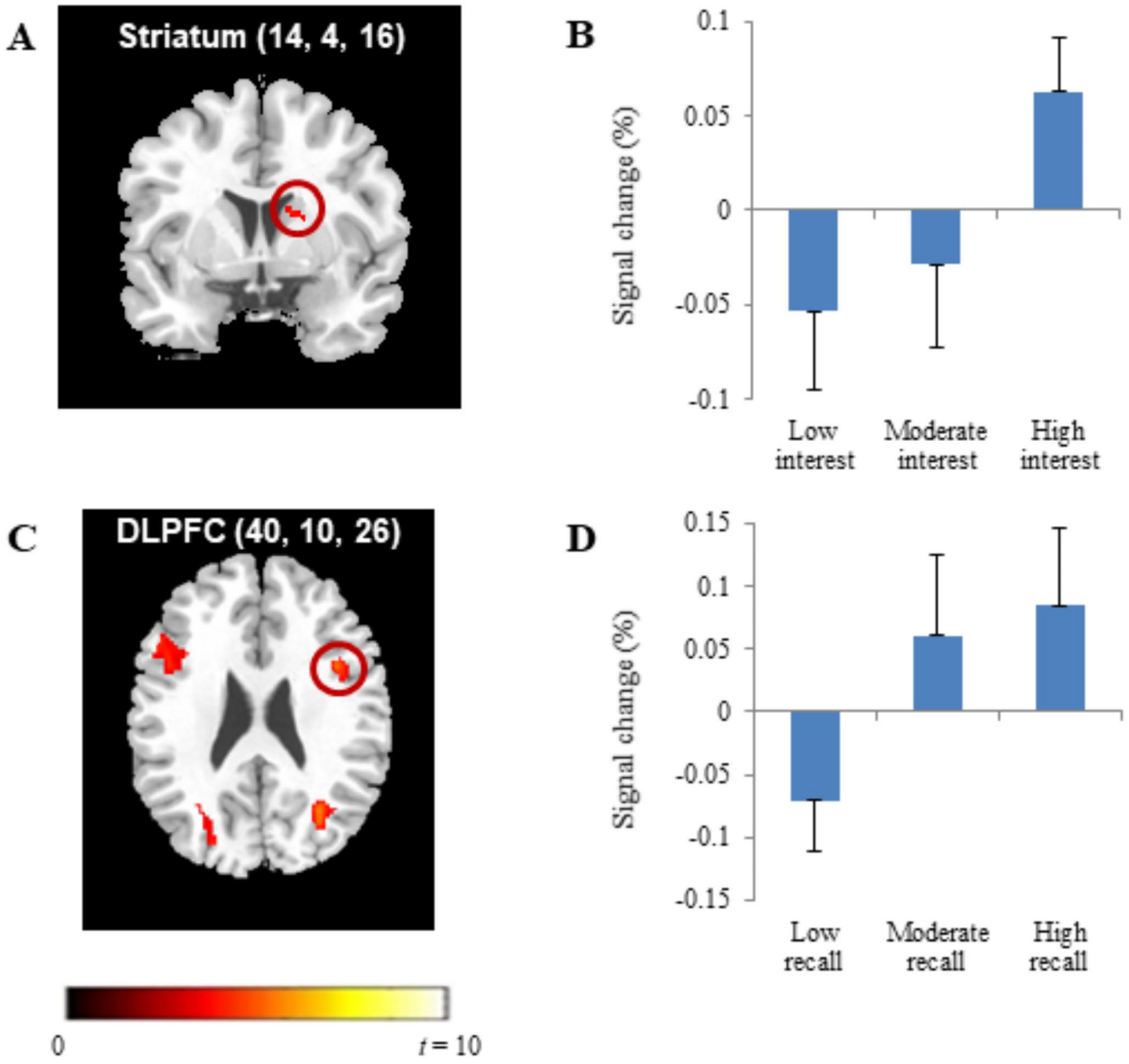

Fig. 4 Interest ratings predict striatum activations; Learning Scores Predict DLPFC Activations. The right striatum was more activated during flag learning as participants' perceived interest ratings were higher (A, test of H6). The right DLPFC was more activated during flag learning as participants' learning scores were higher (C, test of H7). BOLD signal changes in the right striatum are presented in more detail depending on the degree of participants' perceived interest (B), while BOLD signal changes in the right DLPFC are presented depending on the degree of participants' learning scores (D)

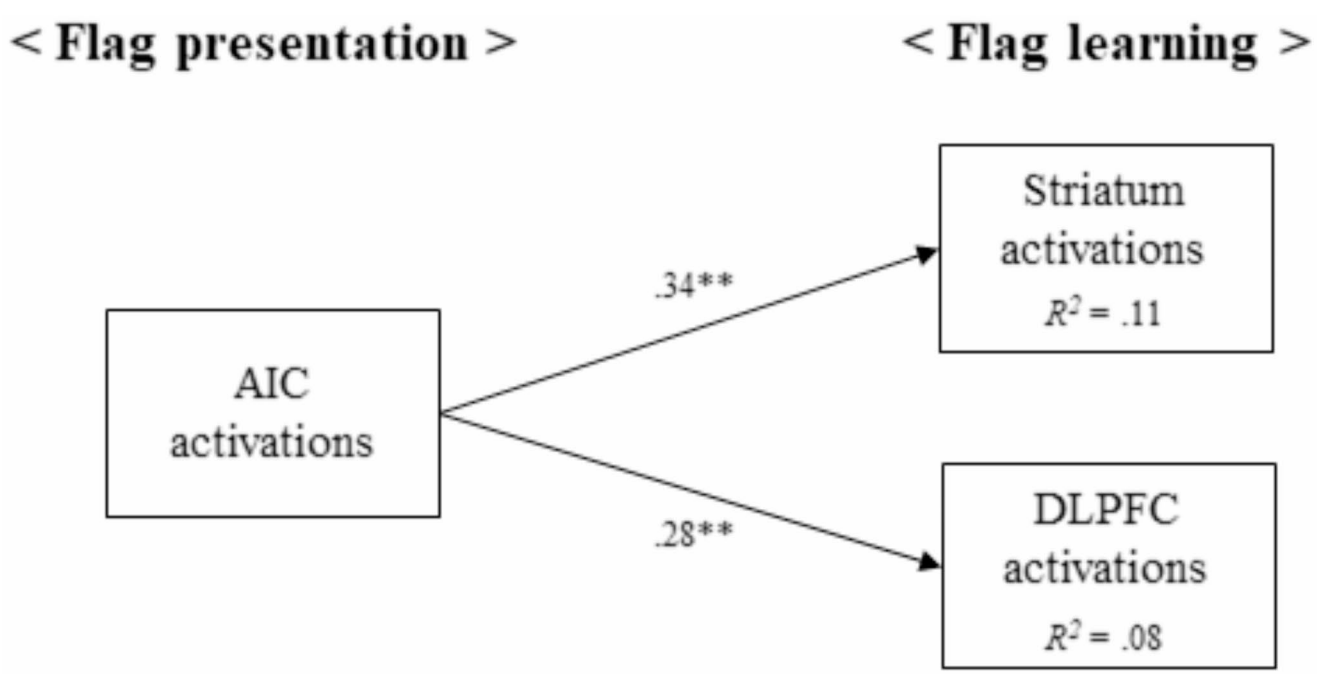

Fig. 5 Standardized parameter estimates for the Trial-by-trial neural path model to Test H4 and H5. ** $p<.01$

H7: learning predicts DLPFC activations

As shown in the bottom part of Table 1, the right DLPFC (Fig. 4C), the left inferior frontal gyrus, the left angular gyrus, the left supramarginal gyrus, the bilateral fusiform gyrus, and the right occipital lobe were more activated during the learning phase of the national flags in which participants achieved high learning scores (corrected $p<.05$). No brain region showed lesser neural activity when participants achieved high learning scores. This confirms H7 by showing that participants' DLPFC activations were significantly greater on the trials in which they showed higher learning scores.

Multilevel neural path analysis To test H4 and H5, we conducted a multilevel path analysis which examined the associations of participants' early-trial BOLD signal changes in the AIC (see Fig. 3) with the late-trial BOLD signal changes in the dorsal striatum (see Fig. 4A; H4) and with the late-trial BOLD signal changes in the DLPFC (see Fig. 4C; H5).

H4: AIC activations predict dorsal striatum activations

As shown in Fig. 5, there was a positive trial-by-trial association between participants' AIC activations during flag presentation and their corresponding dorsal striatum activations during flag learning, controlling for the between-subject effects ($b=0.34$, $SE=0.06$, $p<.001$). This confirms H4 by showing that participants' late-trial dorsal striatum activations were greater on those trials which their early-trial AIC activations were greater.

H5: AIC activations predict DLPFC activations

As also shown in Fig. 5, there was a positive trial-by-trial association between participants' AIC activations during flag presentation and their corresponding DLPFC activations during flag learning, controlling for the between-subject effects ($b=0.28$, $SE=0.04$, $p<.001$). This confirms H5 by showing that participants' late-trial DLPFC activations were greater on those trials which their early-trial AIC activations were greater.

Discussion

We adopted the methods of neuroscience to better understand how an experience of autonomy unfolds over time to recruit the neural support needed to energize interest and learning. When participants first encountered the learning material (stimulus presentation phase) and perceived it as something they freely wanted to do, we observed corresponding greater AIC activations (see Fig. 3; H3). When these same participants encountered the learning material and did not perceive it as something they freely wanted to learn, we did not observe these same AIC activations (see Fig. 3B). This is consistent with previous findings, such as experimental manipulations of high versus low personal choice predicting corresponding high versus low AIC

activations (Leotti & Delgado, 2011, 2014; Murayama et al., 2015).

The AIC is known to form subjective feelings about external situations by utilizing bodily-based, feeling-related schema (Craig, 2009; Critchley et al., 2004). AIC information is most critical when processing uncertainty in the context of decision making (when people lack sufficient objective information on which to base their feelings; Singer et al., 2009). That is, the AIC enables people to become consciously aware of "gut-felt", experiential-based feelings. We suggest that AIC activity is also recruited to formulate subjective feelings of psychologically-based needs (e.g., autonomy), as has been suggested in earlier neuroscientific investigations (Lee & Reeve, 2017; Leotti & Delgado, 2011, 2014; Murayama et al., 2015). Overall, our findings made it clear that AIC activations accompanied an experience of autonomy.

When participants found the new learning material to be interesting, we observed greater striatum activations (see Fig. 4A; H6). This is also consistent with previous findings, such as striatum activations being recruited when people experience competence satisfaction while performing a task (Lee & Reeve, 2017; Murayama et al., 2010). Because intrinsic motivation is conceptualized as the motivation that arises out of autonomy and competence need satisfaction (Ryan & Deci, 2017), it is not surprising that striatum activations, which occurred during episodes of competence satisfaction, also occurred during episodes of autonomy satisfaction. The striatum is known to play a crucial role in reward processing (Haber & Knutson, 2010), including not only incentive-based satisfactions (Berridge, 2004) but also self-based satisfactions (Lee, 2023; Reeve & Lee, 2019). We therefore conclude that striatum activity underlies not only extrinsic motivation but also intrinsic motivation (e.g., autonomy and competence satisfactions).

However, we showed that only dorsal, not ventral, striatum activations accompany an experience of autonomy satisfaction. This is partially consistent with previous findings because Murayama and colleagues (2015) reported ventral (but not dorsal) striatal activations and Lee and Reeve (2017) reported ventral and dorsal striatal activations. One possibility is that ventral striatum activity related to the hedonic valuation of stimuli could be less prominent because there was no objective rewarding information (e.g., success vs. failure feedback) in the task of this study. Another possibility is that dorsal striatum activity related to motivated goal-directed behavior could be more prominent because the task of this study (i.e., flag learning) was more cognitively demanding compared to the stopwatch task of Murayama and colleagues (2015).

AIC and striatum co-activations have been recognized as a key neural mechanism of psychological need satisfaction (Lee & Reeve, 2017; Leotti & Delgado, 2011, 2014; Murayama et al., 2015). In the present study, we found, as expected, that AIC activations occurred early during the initial stimulus presentation phase as participants autonomously wanted to engage in the learning activity, while dorsal striatum activations occurred only later as participants experienced intrinsic satisfaction during task engagement and learning. Our new and important finding was that autonomy-related early-stage AIC activity positively predicted interest-related late-stage striatum activity. This finding is similar to another that used a gambling task to show that AIC activations occurred in conjunction with positive initial feelings (i.e., "How happy do you feel at the present moment?"), while striatum activations occurred only later as a post-reward experience (Rutledge et al., 2014). While no neuroscience study has explicitly demonstrated this sequential relation among the neural substrates related to psychological need satisfaction, Lee and Reeve (2017) suggested functional interactions of AIC and striatum as a key neural mechanism of competence-based intrinsic motivation. However, that experiment was unable to answer the following two questions: "Does AIC activity occur earlier than striatum activity?" and "Does AIC activity influence striatum activity?" Based on the present findings, we suggest that early-stage AIC activations do tend to flow into and affect late-stage striatum activations related to intrinsic psychological need satisfaction during task performance.

How these neuroscience findings inform an SDT-based understanding of psychological need satisfaction

During a task or social interaction, people's experience of psychological need satisfaction emerges and unfolds over time. Research on this unfolding process is rare. Because of this, little is known about how an initial sense of autonomy first arises, how this initial sense of autonomy sometimes does and other times does not develop into a fuller experience of need satisfaction, and how this unfolding autonomy experience energizes and enables indicators of positive functioning, such as those examined in the present study (i.e., interest, engagement, and learning). fMRI methodology and data can uniquely help us understand this dynamic unfolding process by revealing the second-by-second changes that occur in autonomy-associated neural activations.

We suggest that AIC activations are central to an initial experience of autonomy. This relation was shown in the present study (Fig. 3), and it has been shown in previous studies as well (Lee & Reeve, 2013, 2017). But to continue into an experience of "satisfaction", we suggest that striatal activity may be necessary. In the present study, participants showed dorsal striatal activity during the flag

learning phase. However, participants did not show ventral striatal activity—neither initially during the flag presentation phase nor later during the flag learning phase. This is slightly inconsistent with many neuroscience studies of motivational satisfaction showing ventral striatum activations. These ventral striatum activations are associated with pleasure, personal gain, and reward (Berridge, 2004; Lee, 2023; Schultz, 2015), and this line of research includes ventral striatal activity observed during an experience of competence (Murayama et al., 2010; Lee & Reeve, 2017) and relatedness (Inagaki & Eisenberger, 2013; Morelli et al., 2014) satisfaction.

We therefore further suggest the new idea that "need satisfaction" during autonomy satisfaction is not so much success-related pleasure and reward (as in the case of competence and relatedness satisfaction) but, instead, revolves around a subjective experience of personal causation, personal endorsement, and acting volitionally. That is, the experience of autonomy satisfaction unfolds over time based on pre-action and in-action volitional decision-making (i.e., autonomous self-direction), which could be different from the experience of need satisfaction based on in-action or post-action satisfaction from success feedback and personal gain.

Autonomy and curiosity

Given this interpretation, our findings help distinguish between the two closely related motivational experiences of autonomy and curiosity. While autonomy is the psychological need to experience self-direction and personal endorsement in the initiation and regulation of one's behavior (Deci & Ryan, 1985), we conceptualize curiosity as follows: "Encountering environmental novelty, having an opportunity to discover new information, feeling suspense over what might come next, anticipating satisfaction from attaining new information, actually assimilating that new information, and solving a mystery" (Lee & Reeve, 2017, p. 950). Thus, we suggest that curiosity involves first anticipating ("an opportunity to discover new information") and then attaining (i.e., "solving a mystery") motivational satisfaction from a successful incongruity resolution (Loewenstein, 1994).

Neuroscience studies of curiosity have shown that, when experiencing curiosity, people tend to show only ventral and dorsal striatum activations (Gruber et al., 2014) or AIC activations as well (Lee & Reeve, 2017). Lau and colleagues (2020) additionally found that ventral striatum activations are critical for people to experience the initial curiosity before they have an opportunity to assimilate the new information and to resolve curiosity. In this sense, curiosity unfolds over time based on the anticipation of satisfying/rewarding end states. We can therefore suggest that future research pursue the hypothesis that ventral striatum activations are more central to an initial experience of curiosity while AIC activations are more central to an initial experience of autonomy.

We can suggest further research strategies to investigate the distinction between autonomy and curiosity. Research could first assess self-reports and brain scans associated with autonomy-evoking and curiosity-evoking stimuli and then identify a unique autonomy effect by partialling out curiosity self-reports and brain scans and identify a unique curiosity effect by partialling out autonomy self-reports and brain scans. To conduct more causal analyses, future research will likely need to leave the fMRI setting to instead adopt neuroscience settings such as magnetoencephalography (MEG), which can track ongoing brain activations millisecond-by-millisecond in real time and transcranial magnetic stimulation (TMS), which is a noninvasive way to activate or de-activate specific brain structures (to investigate causal effects).

Autonomy and learning

Our findings also inform the relation between autonomy and indicators of positive functioning such as cognitive engagement and learning. We showed that greater DLPFC activations accompanied high learning scores (see Fig. 4C; H7). Interestingly, when AIC activations occurred during the stimulus presentation phase, it became significantly more likely that participants would then later experience DLPFC activations during the learning phase (see Fig. 5). DLPFC activity can serve as a neural marker of extent of cognitive engagement (mental effort) in the learning activity (Carter et al., 1998; Engstrom et al., 2013; Miller & Cohen, 2001). This is supported by the fact that the brain regions related to word reading such as the left inferior frontal gyrus and the left fusiform gyrus (Bokde et al., 2001; McCandliss et al., 2003) also showed greater activations when participants achieved high learning scores. Classroom-based research has shown that student experiences of perceived autonomy do predict their subsequent cognitive engagement, as shown in both experimental (Vansteenkiste et al., 2005) and longitudinal (Jang et al., 2016b) studies. Our interpretation of the present findings is that DLPFC activations supported and reflected participants' cognitive engagement and mental effort that proved to be useful in learning.

One unexpected finding was that we also observed DLPFC activations during the initial flag presentation phase (see upper part of Table 1). This suggests that participants recruited greater mental effort not only while exposed to material they freely wanted to learn but also while mobilizing pre-learning attention and mental effort.

Limitations and alternative interpretations

This study has three possible limitations. First, we did not experimentally manipulate participants' experiences of high vs. low autonomy. Instead, we exposed participants to a variety of stimuli and asked them to report the rise and fall of their trial-by-trial experiences of autonomy. Because we did not experimentally manipulate high vs. low autonomy, we recognize that our findings are open to a "third variable" alternative interpretation, such as potentially co-occurring experiences of curiosity or perceived competence. That said, within the context of our within-subjects research design, we created a two-stage experience in which participants first reported an initial sense of autonomy as we made a first brain scan, second engaged in the learning activity as we made a second brain scan, and finally reported their level of interest during that trial. Our within-trial findings were consistent enough with this temporal ordering of events to causal relations that future research can pursue using experimental research designs made possible by the aforementioned MEG and TMS neuroscience methodologies.

Second, it might be argued that what we measured at the beginning of each trial was not only "high vs. low autonomy" but also "strong vs. weak motivation". It is easy to rule out strong motivations that correlate negatively with autonomy (e.g., contingent reward and pressure-inducing motivations, such as introjection, ego-involvement, and perfectionism), but it is harder to rule out strong motivations that correlate positively with autonomy, such as curiosity and value. That said, past research established high AIC activity as an excellent marker of an experience of perceived autonomy (r=.79, p<.001; see Lee & Reeve, 2013, Fig. 6, page 543). Just as importantly, this same research showed low AIC activity when participants experience general motivations (i.e., extrinsic motivation, positive valence, behavioral energization; see Lee & Reeve, 2013, Fig. 2, p. 541). This means that patterns of AIC activity can be used as one means to confirm and disconfirm the presence of different types of motivations.

Third, we assessed autonomy with a single-item measure. This might be considered a limitation to the present study because SDT theorists generally see autonomy as a multifaceted state encompassing personal ownership, self-direction, volition, and a sense of perceived choice (Chen et al., 2015). In contrast, the use of a brief, single-item measure to assess psychological states represents best practices in fMRI studies. This is because, in the fMRI setting, brain activation data are collected simultaneously when the participant presses a button to report a low, moderate, or high level of the psychological state. Because the brain scans occur in brief time, this means that the self-report experience also needs to occur in brief time. Even though our autonomy measure included only a single item, its scores did correspond closely with participants' AIC brain activity. We therefore suggest that the high AIC activity observed during self-reports of high autonomy and the low AIC activity observed during self-reports of low autonomy (see Fig. 3) provide supportive evidence (along with the pilot test data) for the validity of our single-item autonomy measure.

Conclusion

Our methodological focus on brain activity helps document the underlying biology through which autonomy enables interest and learning. Our findings largely supported our predictions. In doing so, they provide neuroscience-based evidence to support SDT in four new ways:

(1) A task-embedded experience of high autonomy is associated with high AIC activity, while an experience of low autonomy is associated with low AIC activity (Fig. 3).
(2) As people experience a relatively high level of autonomy, early-stage AIC activity occurs first that is then followed by late-stage dorsal striatal activity and DLPFC activity.
(3) This late-stage striatal activity is associated with task interest, while this late-stage DLPFC activity is associated with task learning.
(4) The "satisfaction" in autonomy need satisfaction (i.e., self-endorsement of one's action) is qualitatively different from the satisfaction from success-based motivational satisfactions (e.g., pleasure/reward; competence and relatedness need satisfaction).

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Declarations

Conflict of interest None of the authors on this paper has any conflict of interest to report.

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