

A Neuroeconomic Framework for Creative Cognition

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Abstract

Neuroeconomics is the study of the neurobiological bases of subjective preferences and choices. We present a novel framework that synthesizes findings from the literatures on neuroeconomics and creativity to provide a neurobiological description of creative cognition. We propose that value-based decision-making processes and activity in the locus ceruleus-norepinephrine (LC-NE) neuromodulatory system underlie creative cognition, as well as the large-scale brain network dynamics shown to be associated with creativity. This reconceptualization leads to several falsifiable hypotheses that can further understanding of creativity, decision making, and brain network dynamics.

Keywords

creativity, neuroeconomics, value-based decision making, locus ceruleus-norepinephrine (LC-NE) system, network dynamics

According to the standard definition, products that are both novel and useful within a given context are considered creative (Diedrich, Benedek, Jauk, & Neubauer, 2015; Runco & Jaeger, 2012; see also Sternberg, 1999). However, despite notable recent advances in the neuroscience of creativity (for reviews, see Jung & Vartanian, 2018; Vartanian, Bristol, & Kaufman, 2013) and a wealth of correlational data from brain-imaging studies (for meta-analyses, see Boccia, Piccardi, Palermo, Nori, & Palmiero, 2015; Gonen-Yaacovi et al., 2013; Wu et al., 2015), a critical unanswered question is how the brain produces ideas that satisfy these two criteria. This shortcoming may be due in part to the lack of mechanistic accounts of brain processes that underlie creative cognition.

We work from the assumption that a complete account of creativity will require an understanding not only of its cognitive architecture, but also of the neural systems that underlie it. Toward that end, we propose a novel and neurologically plausible framework for creative cognition. Taking a neuroeconomic approach to creativity, we suggest that value-based decision-making processes underlie creative cognition. Next, we describe how the locus ceruleus-norepinephrine (LC-NE) neuromodulatory system could support creative cognition by adaptively optimizing long-term subjective value associated with preferences and choices. Third,

we suggest that the dynamic interactions within and between brain networks during creative cognition are driven by activity in the LC-NE system and the interconnected brain regions that compute and evaluate subjective value. By bringing together a diverse range of findings from different fields, our framework provides a new conceptualization of creative cognition as driven by value-based decision making. It also points the way to future research by providing novel and testable hypotheses that are relevant to the fields of creativity, decision making, and brain network dynamics.

Value-Based Decision-Making Processes Underlie Creative Cognition

Neuroeconomics of creative cognition

Neuroeconomics is a young but thriving interdisciplinary field concerning the neurobiological processes underlying subjective preferences and choices (Camerer, 2013; Konovalov & Krajbich, 2016; Rangel, Camerer, &

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Montague, 2008). Specifically, it focuses on the computations the brain carries out to make value-based decisions, as well as the biophysical implementation of those computations (Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006; Tajima, Drugowitsch, & Pouget, 2016; Wang, 2002). Value-based choices are pervasive in everyday life, ranging from the mundane to the consequential. Essentially, any choice that requires someone to express his or her subjective preferences and to choose from among two or more alternatives is a value-based choice (e.g., “Do I want an apple or an orange?” “Do I prefer the universe or the multiverse model?”). These choices often lack an intrinsically correct answer and depend instead on subjective preferences. They are called *valued-based* or *economic* choices because most neurobiological models of decision making have integrated economic constructs such as value maximization into their frameworks. These models assume that decision makers make choices by assigning values to the available options and then selecting the option with the highest value (Kable & Glimcher, 2009; Padoa-Schioppa, 2011; Rangel et al., 2008).

The basic premise of the present framework is that creative cognition is similarly supported by value-based decision-making processes. Creative cognition could be just another form of value-based decision making because it is underwritten by the same neural systems that drive value computations in the context of making choices about other commodities (e.g., material goods). That is, process-wise, creative cognition resembles decision making in everyday settings because it too involves generating multiple ideas and then selecting the idea with the highest subjective value (see Vartanian, 2011). We use the term *subjective value* in its traditional economic sense (i.e., the total amount of satisfaction that a good or service brings about) rather than as it is sometimes used within the creativity literature (i.e., to imply the usefulness of an idea; see Harrington, 2018). The notion of subjective value is central to choice theories in many disciplines, including ecology, economics, and psychology, serving as an integrated decision variable by which options are compared (Padoa-Schioppa, 2011; Pearson, Watson, & Platt, 2014; Rangel et al., 2008).

In this view, the value of a creative idea or product refers to the overall satisfaction derived from that idea or product and is critical for driving choice behavior. Creative ideas will be assigned higher values and will be more likely to be selected if they maximize overall satisfaction, which is assessed by how highly they score on attributes such as (but perhaps not limited to) novelty and usefulness within a given context. In this sense, the underlying process is similar to what might occur in other decision contexts. For example, in the context

of dietary choice, a food will be assigned high value if it scores high on attributes such as healthiness and taste (e.g., Hare, Camerer, & Rangel, 2009). Consistent with the ideas of philosopher Paul Souriau (as cited in D. T. Campbell, 1960), who noted that “of all of the ideas which present themselves to our mind, we note only those which have some *value* and can be utilized in reasoning” (p. 386, italics added), the basic premise of our model is that a domain-general machinery that computes value is central to making choices in many contexts, including those that require creative thinking.

Value in any context is simply determined by the following formula: $\text{value} = \sum \text{weight} \times \text{attribute} + \text{error}$ (Berkman, Hutcherson, Livingston, Kahn, & Inzlicht, 2017). Depending on the researcher's theory or the decision context, different combinations of attributes and associated weights can be entered into the equation. In addition, our framework does not equate creativity with value. Rather, value is a way to conceptualize and think about how people judge, or evaluate, creative ideas, products, or solutions. We are proposing that, as is the case with any other decision studied by economists, value is an assessment of a good or product—in this case, an idea, product, or solution. The way in which the attributes and weights used to compute value are combined could be additive or multiplicative, and, critically, our framework is agnostic as to which specific attributes (e.g., novelty, usefulness, surprise) should be used to evaluate creative value.

Within the psychological literature, the idea that creativity involves thought processes that resemble value-based decision making is not without precedent. One well-known example is the family of blind-variation selective-retention models, in which creativity involves generation and selection, the latter of which explicitly incorporates evaluative processes (Basadur, Graen, & Green, 1982; D. T. Campbell, 1960; Simonton, 1999; see also Vartanian, 2011). Specifically, after an initial step that involves the generation of candidate ideas, the second step involves the engagement of an evaluative process to select for further consideration the best idea (or ideas), on the basis of certain criteria. The term *blind* simply indicates that the decision maker has insufficient prior knowledge about an idea's usefulness (Simonton, 2016). Another example is Sternberg and Lubart's investment theory of creativity (Lubart & Sternberg, 1995; Sternberg, 2006, 2012), according to which creative people excel at pursuing and further developing ideas that have growth potential, but happen to be unknown or out of favor within the field in question. In this sense, they “buy low and sell high in the realm of ideas” (Sternberg, 2012, p. 5). The emergence of creative ideas therefore involves evaluative processes that help creative people select unpopular ideas for further nurturing.

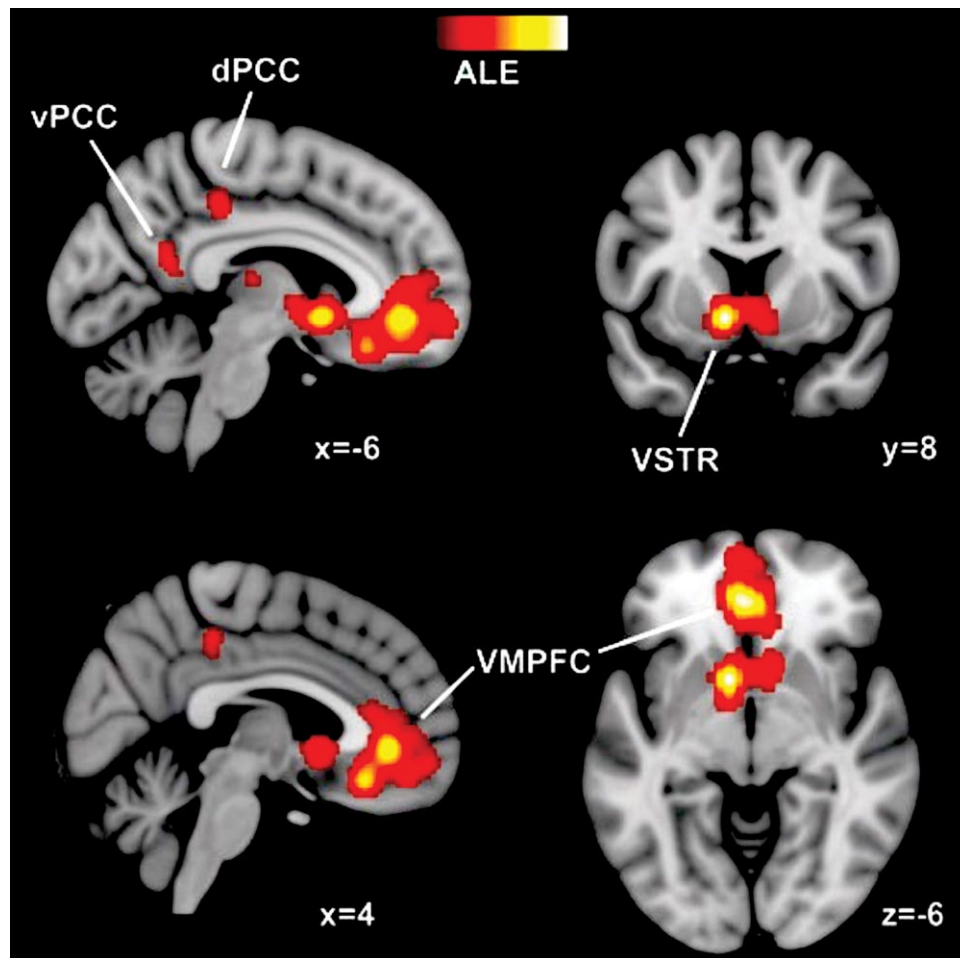


Fig. 1. Representation of value in the human brain. These images show brain regions that a meta-analysis of neuroimaging studies (Clithero & Rangel, 2014) identified as representing value. Brighter colors correspond to areas where the activation likelihood estimation (ALE) indicated greater signal strength. dPCC = dorsal posterior cingulate cortex; vPCC = ventral posterior cingulate cortex; VSTR = ventral striatum; VMPFC = ventromedial prefrontal cortex (overlaps with the orbitofrontal cortex). Note that not all brain areas involved in value-based decision making are shown in this figure. Reproduced with permission from Clithero and Rangel (2014, p. 1293, Fig. 1).

However, although both blind-variation selective-retention models and the investment theory of creativity acknowledge a relationship between value maximization and creative cognition, they do not provide neurobiological and mechanistic descriptions of how value maximization contributes to creativity. In what follows, we review evidence suggesting a relationship between value-based decision making and creativity, and argue that the former helps to realize the latter.

One of the most robust findings from neuroeconomic research is that across species and studies, a specific set of brain regions, including the ventromedial prefrontal cortex (vmPFC), the orbitofrontal cortex (OFC), the posterior cingulate cortex (PCC), and the striatum, is involved in value-based decision making (Padoa-Schioppa & Cai, 2011; Padoa-Schioppa & Conen, 2017;

Rangel et al., 2008; Rich & Wallis, 2016; Fig. 1). For example, functional MRI (fMRI) studies have shown that blood-oxygen-level-dependent (BOLD) signals in the vmPFC correlate with behavioral preferences for beverages (McClure, Li, et al., 2004) and the subjective value of delayed monetary rewards (Kable & Glimcher, 2007; McClure, Laibson, Loewenstein, & Cohen, 2004). Crucially, converging evidence from fMRI (Bartra, McGuire, & Kable, 2013; Clithero & Rangel, 2014; Grueschow, Polania, Hare, & Ruff, 2015), lesion (Buckley et al., 2009; Camille, Griffiths, Vo, Fellows, & Kable, 2011; Hogeveen, Hauner, Chau, Krueger, & Grafman, 2017), and electrophysiological (Padoa-Schioppa, 2011; Padoa-Schioppa & Assad, 2006; Rich & Wallis, 2016) studies suggests that a set of brain regions comprising the OFC, vmPFC, medial prefrontal cortex (mPFC), and PCC not

only represents value, but also evaluates choice alternatives during value-based decision making.

This body of evidence has led to the *common-currency hypothesis*, which suggests that a small set of specific brain areas encodes the subjective values associated with many different types of rewards on a common neural scale, regardless of the variation in the stimulus types giving rise to the evaluations (Levy & Glimcher, 2012). Perhaps not surprisingly, the same set of regions also underlies aesthetic experiences (Pearce et al., 2016), given that preferences for attractive faces (Kim, Adolphs, O'Doherty, & Shimojo, 2007; O'Doherty et al., 2003), harmonious color combinations (Ikeda, Matsuyoshi, Sawamoto, Fukuyama, & Osaka, 2015), geometric shapes (Jacobsen, Schubotz, Höfel, & Cramon, 2006), and paintings or musical excerpts (Ishizu & Zeki, 2011) also reflect the subjective value assigned to stimuli of varying reward properties (see also Brown, Gao, Tisdelle, Eickhoff, & Liotti, 2011; Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011; Salimpoor & Zatorre, 2013; Vartanian & Skov, 2014). Moreover, functional connectivity between the nucleus accumbens and vmPFC predicts how much participants are willing to spend on musical excerpts (Salimpoor et al., 2013), suggesting that evaluative processes can also influence economic choices. These findings suggest that the brain networks supporting subjective valuation are also implicated in aesthetic judgments. We argue here that this involvement extends to creative cognition.

On the basis of findings from neuroeconomics and studies of preference formation, we advance a new conceptualization of creativity. Specifically, previous work suggests that two key processes support creative cognition: generation and evaluation of ideas (Basadur et al., 1982; D. T. Campbell, 1960; Simonton, 1999, 2013, 2018). Generation involves coming up with many possible solutions or ideas in response to a problem or prompt, whereas evaluation refers to testing those solutions or ideas and selecting the best option (or options). Here we posit that these processes also compare the subjective values of the options, which are determined by integrating various criteria such as novelty and usefulness (Runco & Jaeger, 2012; Sternberg, 1999). Thus, we propose that value-based decision-making processes (e.g., assigning, representing, and comparing values) underlie creative cognition.

Value-based decision-making models assume that choices are made by assigning an overall value to each option, and that this overall value is computed as the weighted sum, product, or both of the option's values on different attributes (e.g., Harris, Clithero, & Hutcherson, 2018; Hutcherson, Bushong, & Rangel, 2015; Hutcherson, Montaser-Kouhsari, Woodward, & Rangel, 2015; Suzuki, Cross, & O'Doherty, 2017). For example,

neurocomputational evidence suggests that when making food decisions, people dynamically construct the overall value of a food from the weighted sum of its value on two attributes: perceived healthiness and taste (Hare et al., 2009; Sullivan, Hutcherson, Harris, & Rangel, 2015). Whether an individual chooses to consume a healthy or unhealthy food (e.g., chips vs. broccoli) depends not only on the perceived healthiness and taste of the food, but also on the weight assigned to each attribute, which can be modulated by contextual factors (Hare, Malmaud, & Rangel, 2011; Tusche & Hutcherson, 2018). The specific decision context determines which attributes will be considered, as well as the weight assigned to each attribute (e.g., the value of helping might depend on the weighted sum of how much one cares about oneself and others; see Hutcherson, Bushong, & Rangel, 2015).

We suggest that within the context of creativity, the value of an idea will also be dynamically constructed from the weighted sum, product, or both of attributes—in this case, attributes such as novelty and usefulness. Because the weight assigned to each attribute changes in different contexts, novelty and usefulness might not contribute to overall subjective value to the same extent across all contexts. In a study consistent with these ideas, Diedrich et al. (2015) found that judgments of usefulness come into play only after an idea has been deemed novel, which suggests that the weight assigned to each attribute might change at different stages of evaluation. Although the field has focused primarily on the attributes of novelty and usefulness, our framework is not limited to these attributes. Indeed, we hope to provide a general framework for investigating how other attributes and contextual factors (e.g., surprise; see Simonton, 2012, 2018) could also contribute to the computation of value.

Conceptualizing creative cognition as value-based decision making leads to several novel neurobiological predictions. First, we predict that computations in neuroeconomic-valuation regions of the brain (e.g., mPFC, OFC, PCC) are associated with evaluative processes during creative cognition. Indeed, this prediction has already found support in fMRI studies that explicitly compared generative and evaluative processes during creative cognition. For example, Ellamil, Dobson, Beeman, and Christoff (2012) instructed participants in an fMRI scanner to first design book covers and then evaluate their designs and ideas. Compared with their generation of drawings, their evaluation was associated with greater activation in a set of regions including the medial frontal gyrus and PCC—both of which are involved in value-based decision making. Similarly, Mayseless, Aharon-Peretz, and Shamay-Tsoory (2014) demonstrated that evaluating the originality of ideas

was associated with activation in a set of regions including the PCC. Further, an electroencephalogram (EEG) study found that evaluating ideas improved originality on a divergent-thinking task. In addition, idea evaluation was associated with increased frontal alpha synchronization—an activity that might reflect memory retrieval and integration processes (Hao et al., 2016). Neuroeconomic EEG studies have also shown that valuation processes reflect the integration of information from sensory and memory-related regions (Harris, Adolphs, Camerer, & Rangel, 2011). Together, these results support our first prediction and underscore the role played by value-based decision-making processes during the evaluation of ideas. They also indicate that EEG data can be used to examine the temporal dynamics of valuation processes during creative cognition.

Second, because increased fMRI BOLD activity in valuation regions has been associated with increased subjective value (e.g., Kable & Glimcher, 2007), we also predict that neural responses in those regions correlate positively with the perceived creativeness of ideas (the weighted sum, product, or both of novelty and usefulness) generated during creative cognition. For example, when participants perform divergent-thinking tasks such as the alternate-uses task, their self-reported ratings of their responses' creativity should correlate positively with activity in regions such as the mPFC, OFC, and PCC. Finally, given that neural responses in these valuation regions can predict economic choices (A. Smith, Bernheim, Camerer, & Rangel, 2014; Tusche, Bode, & Haynes, 2010), it might be possible to use these neural responses (combined with machine learning; see Shrivastava, Ahmed, Laha, & Sankaranarayan, 2017) to predict which idea, out of all the options generated, an individual will eventually select as the best idea.

What makes something creative?

Neuroeconomics can help to explain creative cognition by providing computational models that specify which decision variables (e.g., attributes such as novelty and usefulness) are included during value computation, how those computations are carried out in distinct brain regions and networks, and how these computations lead to choices (Rangel & Hare, 2010; Ratcliff, Smith, Brown, & McKoon, 2016; Shadlen & Kiani, 2013; P. L. Smith & Ratcliff, 2004). These models have proven fruitful in various domains, such as perceptual decision making (Churchland, Kiani, & Shadlen, 2008; Gold & Shadlen, 2007), memory (Shadlen & Shohamy, 2016), self-control (Berkman, 2018; Berkman et al., 2017; Hare et al., 2009), and social decision making (Ruff & Fehr, 2014). We believe that this computational

approach can also be useful for explaining creative cognition.

Most neurocomputational models assume that a noisy relative-value signal accumulates over time, and that decisions are made once the accumulated information about one option becomes sufficiently strong to drive choice. For example, one study showed that individuals chose between altruistic and selfish options by assigning to each option an overall value computed as the weighted sum of two attributes: reward for self and reward for the other person (Hutcherson, Bushong, & Rangel, 2015). Information about the two attributes was computed independently in distinct brain regions before being integrated and represented as an overall value signal in the vmPFC, and these processes could be described using extensions of standard computational models of decision making (e.g., Ratcliff et al., 2016). Given that judgments of creative ideas are assumed to depend on the integration of multiple attributes, in what follows we outline how neurocomputational models may provide insights into such integration during creative cognition.

The assumptions underlying computational models of multiattribute integration during choice resemble those in models of aesthetic experiences. Chatterjee and Vartanian (2014, 2016) suggested that distinct neural systems underlie different aspects of aesthetic experiences (e.g., emotional, perceptual) and that different weights might be assigned to the different systems that underlie those aspects. For example, studies have shown that humans prefer curved over sharp objects (Bar & Neta, 2006) and that sharp objects tend to increase activity in the amygdala (Bar & Neta, 2007), presumably a reflection of increased arousal, salience, or sense of threat associated with sharp objects. Neurocomputational models would thus predict that activity in the amygdala reflects one of the many attributes (e.g., sense of threat) that an individual might consider when computing overall liking for a sharp or curved object (computed within the brain's valuation system). Because creative ideas are also defined along multiple attributes, future work could explore how information about different attributes (perhaps beyond just novelty and usefulness; e.g., surprise) is represented in distinct brain regions, and how these brain regions interact to produce an integrated subjective value that reflects the creativity of an idea or product. These suggestions are consistent with Martindale's (1984) theory of cognitive hedonics, according to which thoughts (e.g., ideas) have evaluative aspects, which in turn can drive preference for and continued pursuit of certain ideas over others. If the common-currency hypothesis is correct, then the evaluation of ideas should occur within the same neural network that computes subjective values for all other stimuli.

The LC-NE System Supports Creative Cognition

Exploiting and exploring ideas

When trying to generate creative ideas, people assign higher subjective value to ideas that are high in both novelty and usefulness than to ideas that are low in these attributes. If an idea has high subjective value (i.e., it is high in both attributes), it is often advantageous to exploit the idea further. In contrast, if an idea has relatively low subjective value (i.e., it is low in one or both attributes), it may be preferable to explore other ideas to find better alternatives. Many decisions in daily life require trade-offs between exploitation and exploration (Christian & Griffiths, 2016; Cohen, McClure, & Yu, 2007; Hills et al., 2015). For example, after having generated a certain number of ideas for a new product, should you start to focus on and develop one of them further, or should you continue developing new ideas? How does the brain choose the best course of action—or the best creative solution?

Our framework suggests that activity in the LC-NE neuromodulatory system plays an essential role in creative cognition by modulating the balance between exploitation and exploration. Our framework focuses mainly on the LC-NE system, but we note that all the major neuromodulatory systems that have been implicated in various decision and valuation processes also underlie creative cognition (e.g., Spee et al., 2018). For example, dopamine is believed to be important for learning the value of objects from prediction errors (Berke, 2018; Montague, Hyman, & Cohen, 2004; Roesch, Calu, & Schoenbaum, 2007; Schultz, 2007), so the dopamine system may be necessary for learning which ideas are rewarding or creative. Serotonin, like dopamine, has also been implicated in reward signaling—specifically, in learning from punishments or negative prediction errors (Boureau & Dayan, 2011; Cools, Nakamura, & Daw, 2011; Cools, Robinson, & Sahakian, 2008; Kranz, Kasper, & Lanzenberger, 2010; Nakamura, Matsumoto, & Hikosaka, 2008). Moreover, acetylcholine and norepinephrine appear to play major roles in flexible learning and decision making; especially relevant to our framework is the proposal that norepinephrine mediates flexible shifts between exploitation and exploration (Aston-Jones & Cohen, 2005b; Kehagia, Murray, & Robbins, 2010; Yu & Dayan, 2005). If creative cognition is mediated by processes that resemble those in classic exploitation-exploration trade-offs (Cohen et al., 2007; Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006), then understanding the relationship between decision making and creative processes will organize and benefit research in various fields (we address the

interplay between various neuromodulatory system further in Interactions With Other Neurotransmitter Systems).

Creative cognition appears to rely on abilities to exploit and explore ideas, as well as to switch between these two modes of cognition (Monechi, Ruiz-Serrano, Tria, & Loreto, 2017). When people are initially trying to find inspiration or ideas for tackling a new problem, they are attempting to explore and generate ideas that satisfy criteria that are often based on relatively abstract goals. The relative importance of each criterion depends on the context, and the subjective value of an idea depends on how well it satisfies those criteria. For example, an artist might be seeking an idea that best conveys a particular meaning, and a scientist might be developing a new experimental procedure that most stringently tests a theoretical prediction. These individuals pursue ideas by exploring the available options and pruning them by assessing their subjective values. Different ideas will have different subjective values, according to how well they satisfy the criteria. Most ideas will likely fail to satisfy the criteria (i.e., they will be assigned low subjective values), and they will be entertained very briefly before being discarded. However, when the artist and scientist land on ideas that satisfy the criteria sufficiently, they will likely stop exploring alternatives because they will want to devote their time and resources to fully exploit the value those ideas provide. We suggest that this creative process reflects an adaptive value-optimization process mediated by activity in the LC-NE system and interconnected brain regions that compute and evaluate the subjective values of various creative ideas and strategies (see Aston-Jones & Cohen, 2005b), while at the same time acknowledging that other neuromodulatory systems likely also contribute to the dynamics of creative cognition.

LC-NE system and function

The locus ceruleus nucleus sits deep in the pons and sends noradrenergic projections to nearly all brain regions (with the notable exception of the basal ganglia and hypothalamus). It is also the only source of norepinephrine (also known as noradrenaline) to the cerebral, cerebellar, and hippocampal cortices (Foote & Morrison, 1987; Moore & Bloom, 1979; Fig. 2). Because the locus ceruleus projects diffusely to cortical regions, early research focused primarily on its role in general cognitive processes, especially in mediating arousal (Amaral & Sinnamon, 1977; Aston-Jones & Waterhouse, 2016; Berridge & Waterhouse, 2003).

Recent work has highlighted the role of the LC-NE system in regulating engagement during tasks that

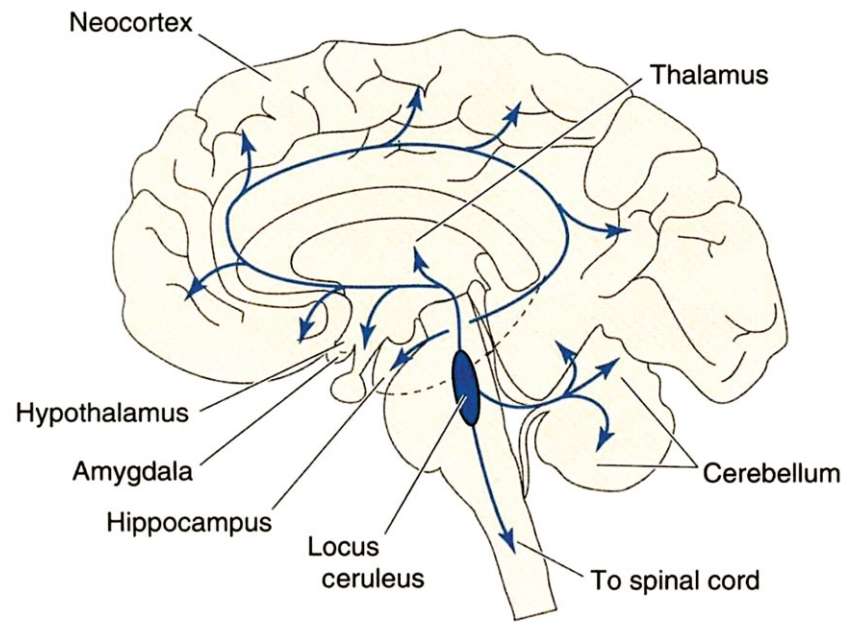


Fig. 2. Projections of the locus ceruleus-norepinephrine (LC-NE) system. Nearly all brain regions, with the exception of the basal ganglia and hypothalamus, receive norepinephrine (also known as noradrenaline). Figure reproduced from *Biological Psychology: An Introduction to Behavioral, Cognitive, and Clinical Neuroscience*, 6th edition, by Breedlove, Watson, and Rosenzweig (2010), p. 92, Fig. 4.4, with permission from Oxford University Press, USA.

require selective attention (Aston-Jones & Cohen, 2005a, 2005b; Chmielewski, Mückschel, Ziemssen, & Beste, 2017). Many studies have shown that salient or task-relevant stimuli reliably elicit *phasic* activation of locus ceruleus neurons and norepinephrine release at cortical target sites (Aston-Jones & Bloom, 1981; Hervé-Minvielle & Sara, 1995). Phasic activity is characterized by short-duration, rapid bursts of locus ceruleus activity and concomitant norepinephrine release at cortical sites, the timing of which correlates strongly with behavioral performance (Usher, Cohen, Servan-Schreiber, Rajkowski, & Aston-Jones, 1999). Such phasic activity is thought to increase neural gain (sensitivity or responsivity) in task-relevant cortical regions, which then focus attention on task-relevant events to improve engagement and performance (Aston-Jones & Cohen, 2005b; Hasselmo, Linster, Patil, Ma, & Cekic, 1997; Lee et al., 2018; Mather, Clewett, Sakaki, & Harley, 2016).

Whereas phasic activity of the locus ceruleus is often tightly coupled with good performance during selective-attention tasks, *tonic* activity of this region also affects engagement and performance (Aston-Jones & Cohen, 2005b). Tonic activity of the locus ceruleus, in contrast to its phasic activity, is characterized by intrinsic, ongoing firing that is unrelated to the task and occurs in the background. Specifically, relative levels

of phasic and tonic locus ceruleus activity relate to performance in a manner that reflects the classic Yerkes-Dodson inverted-U arousal curve (Yerkes & Dodson, 1908): At moderate levels of tonic activity, phasic activity is elevated and performance on selective-attention tasks is optimal, whereas shifts toward lower or higher tonic activity are associated with reduced phasic activity and poorer performance on these tasks. More broadly, the *phasic mode* is characterized by moderate tonic activity but increased phasic activity that facilitates exploitation of options, whereas the *tonic mode* is characterized by reduced phasic activity but higher tonic activity, which is thought to promote exploration of alternatives that could be more rewarding than the available options (Aston-Jones & Cohen, 2005b; Berridge & Waterhouse, 2003; Cohen et al., 2007; Usher et al., 1999).

Here we build on evidence from selective-attention tasks and neuroeconomics to provide an integrative neurobiological framework for creative cognition. We suggest that creative cognition relies on neural value computations that also underlie a range of behaviors, such as choices between material goods, perceptual decisions, memory, and social decisions (e.g., Berkman et al., 2017; Ruff & Fehr, 2014; Shadlen & Kiani, 2013). Drawing on recent theorizing on the role of the

norepinephrine system (Aston-Jones & Cohen, 2005b; Kehagia et al., 2010; Sadacca, Wikenheiser, & Schoenbaum, 2017), we suggest that value-based decision-making processes mediate the fine balance and transitions between the phasic and tonic locus ceruleus modes, which, in turn optimize creativity by facilitating flexible exploitation and exploration of ideas and strategies with varying subjective values. That is, flexible and adaptive fluctuations between the phasic and tonic modes may be critical to creative cognition, and might underlie performance on both laboratory and real-world creative tasks.

Norepinephrine underlies creative cognition

Being creative depends on the ability to both maintain task goals (e.g., exploit specific mental representations of ideas or familiar strategies) and switch between task sets (e.g., explore different mental representations; see Goschke, 2000; Hills et al., 2015; Monsell, 2003). Thus, as is the case for many everyday value-based decisions, the demands on creative cognition seem to imply a delicate balance between exploitative and exploratory processes that are regulated by the phasic and tonic locus ceruleus modes, respectively. Indeed, early work hinted at potential relationships among LC-NE activity, engagement, arousal, and creativity. For example, classic studies showed that states of relaxation and low arousal are associated with increased creativity (Martindale & Greenough, 1973). During creative generation, more creative individuals show stronger EEG alpha-band activity (Martindale & Hasenfus, 1978), which is believed to reflect reduced arousal mediated by norepinephrine from the locus ceruleus (Foote, Berridge, Adams, & Pineda, 1991; Foote & Morrison, 1987).

Pharmacological studies have provided stronger evidence for the role of norepinephrine in creative processes (Beversdorf, 2013, 2018; Heilman, 2016; Heilman, Nadeau, & Beversdorf, 2003). One such process is cognitive flexibility, required in set-shifting tasks in which attention must be shifted from one perceptual dimension to another (Birrell & Brown, 2000). Increasing tonic norepinephrine activity via α -adrenergic receptors in the mPFC improved rats' set-shifting performance (Lapiz, Bondi, & Morilak, 2007; Lapiz & Morilak, 2006), presumably because elevated tonic norepinephrine corresponds to an attentional state that reduces focus on well-established cues or strategies and promotes attention to novel or previously nonsalient cues (Aston-Jones, Rajkowski, & Cohen, 1999; Sadacca et al., 2017). However, the effects of pharmacological interventions might depend on other factors, including personality. For example, administering methylphenidate (a psychostimulant

that increases norepinephrine and dopamine levels in the brain) improves creativity in people low in novelty seeking (i.e., weak exploratory tendencies), but impairs creativity in those high in novelty seeking (Gvirts et al., 2017). These findings suggest that when designing and interpreting norepinephrine intervention studies, one should consider contextual and personality variables that could influence the balance between the phasic and tonic locus ceruleus modes (e.g., stress, age; see also Mather & Harley, 2016).

Although increasing norepinephrine via α -adrenergic receptors facilitates set shifting, reducing norepinephrine via β -adrenergic receptors (e.g., using propranolol, a β -adrenergic-receptor blocker) seems to benefit other forms of cognitive flexibility in tasks that require efficient access to and search throughout neural networks (e.g., anagram problems; Beversdorf, Hughes, Steinberg, Lewis, & Heilman, 1999; Beversdorf, White, Chever, Hughes, & Bornstein, 2002; H. L. Campbell, Tivarus, Hillier, & Beversdorf, 2008; Hecht, Will, Schachtman, Welby, & Beversdorf, 2014). These opposing effects suggest that α - and β -adrenergic receptors might mediate creative cognition via distinct processes, possibly owing to differences in whether the specific receptor in question is excitatory or inhibitory, as well as the receptors' differential affinities for norepinephrine. For example, compared with α -2A receptors, β -adrenergic receptors tend to have lower affinity for norepinephrine and to activate only with relatively high levels of it (Lee et al., 2018; Samuels & Szabadi, 2008). Thus, to elucidate how the phasic and tonic modes mediate creative cognition, future research should investigate and compare the effects of both activating and blocking α - and β -adrenergic receptors in contexts that have been associated with different levels of tonic norepinephrine (e.g., drowsiness, wakeful alertness, and stress are associated with low, moderate, and high norepinephrine levels, respectively).

For example, stress is known to increase norepinephrine, impair prefrontal function, and alter cellular activity in prefrontal norepinephrine neurons (Arnsten, 2009; Goldfarb, Froböse, Cools, & Phelps, 2017; Miner et al., 2006; Morilak et al., 2005). Critically, for certain forms of cognitive flexibility, the benefits of administering β -adrenergic-receptor blockers are most apparent under stressful conditions (Alexander, Hillier, Smith, Tivarus, & Beversdorf, 2007). These findings again suggest that whether pharmacological interventions improve or impair creativity might depend on factors (e.g., personality, context) that affect tonic norepinephrine levels.

Although the studies described thus far have demonstrated the broad effect of norepinephrine on exploitation, exploration, and creative cognition, they have

not shown specifically how phasic and tonic locus ceruleus activities during creative cognition are affected by manipulating norepinephrine levels. Moreover, most of these studies focused on cognitive flexibility in the context of situational stress (e.g., Alexander et al., 2007; H. L. Campbell et al., 2008). This contextual factor is particularly relevant because stress could have increased tonic norepinephrine levels, shifted the baseline balance between exploitation and exploration tendencies, influenced attention and performance, and engaged α - and β -adrenergic receptors differently (Arnsten, 2000, 2009; Berridge & Waterhouse, 2003; Robbins & Arnsten, 2009). As natural phasic activity may be influenced by general changes in tonic activity (e.g., due to stress, receptor agonists), this phasic-tonic duality in firing modes often complicates the interpretation of pharmacological studies (an issue discussed in the context of dopamine by Beninger & Miller, 1998). Nevertheless, these studies have provided strong evidence that the balanced fluctuations in norepinephrine levels are essential to different forms of cognitive flexibility. Future work should be aimed at determining why creative processes sometimes benefit from increasing norepinephrine and other times benefit from reducing norepinephrine. Examining the neurobiological processes and contextual factors that determine changes in norepinephrine levels and transitions between the two locus ceruleus modes will also be crucial to understanding how norepinephrine underlies exploit-explore trade-offs during creative cognition (e.g., Aston-Jones & Cohen, 2005b).

Value-based decision making regulates transitions between exploitation and exploration

The adaptive-gain theory of LC-NE function (Aston-Jones & Cohen, 2005b) may help bridge neuroeconomic findings with research relating norepinephrine to creativity. According to this theory, during selective-attention tasks, the high subjective value associated with the current task triggers the phasic mode, which facilitates exploitation of ongoing behaviors or existing strategies to optimize performance. Low or declining subjective value, however, triggers the tonic mode, which promotes disengagement from the current task and exploration of alternatives that can potentially represent more rewarding opportunities (Aston-Jones & Cohen, 2005b; Cohen et al., 2007).

We suggest that the phasic locus ceruleus mode corresponds to creative processes that involve exploitation of ideas or strategies with high subjective values. For example, when experimental participants are asked to solve anagrams (a standard measure of cognitive flexibility), an

idea or strategy that allows them to generate many solutions within a limited time is likely to have relatively high subjective value. One common anagram strategy involves finding suffixes and adding them to the end of already generated words (e.g., add *-er* to *paint* and *work*). Value-based decision processes will then trigger the phasic mode, which helps exploit this high-value solution through processes such as evaluation and elaboration (e.g., find additional suffixes, such as *-ing*). Thus, at least for laboratory measures of creativity, the phasic mode should increase neural gain and focus attention on task-relevant representations to help generate solutions, in much the same way that it facilitates good performance during selective-attention tasks (Aston-Jones & Cohen, 2005b; Mather et al., 2016).

The tonic mode, however, is associated with processes that facilitate the exploration of alternatives when the subjective values of existing options are relatively low or declining. When an idea or strategy is no longer novel or successful in generating novel and useful solutions, its declining subjective value triggers shifts toward the tonic mode, which promotes exploration of alternatives. Although this mode might temporarily impair immediate performance by causing increased distractibility and temporary disengagement from the currently salient task representations (e.g., finding suffixes), it encourages individuals to widen their attentional focus to explore alternatives that might provide better long-term payoffs despite the short-term costs of exploration (Aston-Jones & Cohen, 2005b; Sadacca et al., 2017; Tervo et al., 2014; Usher et al., 1999). For example, if a participant has exhausted all possible suffixes for a given anagram, the shift from the phasic to the tonic mode might trigger changes in strategy, causing the participant to start considering prefixes instead and adding them to the beginning of generated words (e.g., add *re-* to *paint* and *work*). Thus, the tonic mode might be required—at least temporarily—to mentally explore alternatives. Moreover, because creative cognition appears to resemble solutions the brain has evolved to solve basic ecological problems in real-world environments (e.g., exploitation-exploration dilemmas, foraging in patchy environments; Cohen et al., 2007; Kidd & Hayden, 2015; Mobbs, Trimmer, Blumstein, & Dayan, 2018; Pearson et al., 2014), this account has the potential to explain not only creativity in the laboratory, but also real-world creativity.

Critically, the adaptive-gain theory suggests that whether LC-NE activity is in the phasic or tonic mode depends on value computations in cortical regions such as the OFC (Padoa-Schioppa & Assad, 2006) and the anterior cingulate cortex (ACC; Calhoun & Hayden, 2015; Heilbronner & Hayden, 2016; Shenhav, Botvinick, & Cohen, 2013)—both of which project densely to the

locus ceruleus (Aston-Jones & Cohen, 2005a; Porrino & Goldman-Rakic, 1982). We suggest that during creative cognition, activity in the neural valuation regions (e.g., OFC) drives and produces the transitions between the phasic and tonic locus ceruleus modes.

According to our framework, when a newly generated idea is novel and useful, the valuation regions assign a high subjective value to it, triggering the phasic mode, which promotes exploitation of that idea. But when ideas are not or are no longer useful or novel, the valuation regions register low overall subjective value, which temporarily triggers shifts toward the tonic mode, which increases baseline norepinephrine release, facilitating exploring and sampling of other ideas that might provide higher long-term subjective value (Aston-Jones & Cohen, 2005b). In sum, the subjective values assigned to ideas or strategies (according to how well they satisfy criteria such as novelty and usefulness) are hypothesized to flexibly balance the transitions between the phasic and tonic modes. These transitions, in turn, help maximize long-term payoff by optimizing the trade-off between exploitation and exploration.

Integrating existing findings, new predictions, and new measures

By extending the adaptive-gain theory of LC-NE function to creative cognition, the present framework is useful for reinterpreting and integrating existing findings and also for making new predictions that can be tested with various behavioral and neurophysiological measures. First, because the LC-NE system is hypothesized to drive exploitation-exploration processes that underlie creative cognition, one would expect the phasic and tonic locus ceruleus modes to correspond, respectively, to exploiting ideas with high subjective value (e.g., evaluation, elaboration) and exploring alternative options (e.g., switching to a different strategy). These predictions can be tested in the laboratory by tracking participants' behavioral performance and strategy use in tasks involving creative thinking while measuring fMRI BOLD activity in the locus ceruleus and valuation regions (Kolling, Behrens, Mars, & Rushworth, 2012; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014).

Measures such as pupil diameter can also be used to study how creative processes unfold in real time because they track LC-NE activity and elucidate the processes underlying value-based decision making (Hassall, Holland, & Krigolson, 2013; Lin, Saunders, Hutcherson, & Inzlicht, 2018; Murphy, Robertson, Balsters, & O'Connell, 2011; Van Slooten, Jahfari, Knapen, & Theeuwes, 2018). For example, phasic LC-NE activity correlates with the P3, a positive potential that peaks about 350 ms following stimulus

onset and is observed over central-parietal midline EEG electrodes (Nieuwenhuis, Aston-Jones, & Cohen, 2005); changes in locus ceruleus firing rates also correspond remarkably well to changes in pupil dilation responses (Joshi, Li, Kalwani, & Gold, 2016; Murphy et al., 2014; Reimer et al., 2016; Varazzani, San-Galli, Gilardeau, & Bouret, 2015). Results from gambling tasks designed to specifically investigate exploitation-exploration trade-offs have shown that high baseline pupil diameter (elevated tonic activity) predicts disengagement and exploration of alternative rewards, whereas low baseline pupil diameter predicts task engagement and exploitation of the current reward (Jepma & Nieuwenhuis, 2011). If value computation and exploitative-exploratory processes also underlie creative cognition, then incorporating electroencephalography and pupillometry in future research may provide insights into creative cognition and related processes (see Smallwood et al., 2012; Unsworth & Robison, 2016; van der Wel & van Steenbergen, 2018). For example, one could pharmacologically manipulate norepinephrine and then track changes in tonic and phasic pupil diameter while participants perform cognitive-flexibility tasks. These examples further highlight the usefulness of the present framework for suggesting measures that might profitably be used to investigate the processes participants rely on while engaging in creative cognition (e.g., pupil diameter, locus ceruleus BOLD activity, P3; see also Mather et al., 2017, for a relevant discussion of heart rate variability).

Second, the present framework suggests that instead of focusing solely on behavioral outcome measures, such as response latency or responses generated during creativity tasks (e.g., fluency, defined as the number of ideas), one can gain more insights into creative cognition by also investigating the underlying processes that lead to the observed outcomes. For example, although two individuals may have generated the same number of responses on a cognitive-flexibility task, one cannot automatically infer that they relied on the same strategies and underlying processes to arrive at those solutions. For example, they might have relied differentially on exploitative and explorative strategies, despite having generated the same number of responses.

With its focus on the underlying processes, our framework could explain why laboratory measures of creativity (e.g., divergent thinking) at times correlate only weakly with real-world creative achievement (e.g., Zabelina, Saporta, & Beeman, 2016), which is often measured using the Creative Achievement Questionnaire (Carson, Peterson, & Higgins, 2005). Laboratory measures of creativity often require participants to generate many solutions within a limited amount of time. This emphasis on responding under time pressure in fact characterizes the demands of selective-attention

tasks, which are best met by the phasic locus ceruleus mode (Aston-Jones & Cohen, 2005b; Usher et al., 1999). Real-world creative achievement, however, is often more protracted (i.e., involves less immediate time pressure) and might ultimately require different dynamics than laboratory-based creativity tasks do. In addition, the criteria defining the “correctness” of any given solution or idea might be relatively unclear and could even change over time. In this sense, discovering and stumbling upon better alternatives through exploration (triggered by the tonic mode) might be a particularly apt characterization of real-world creativity (Monechi et al., 2017). Consistent with these ideas, studies have shown that divergent thinking in the laboratory is associated with selective attention, whereas creative real-world achievement is associated with wider attentional focus and failures to inhibit seemingly irrelevant stimuli (Carson, Peterson, & Higgins, 2003; Zabelina, Colzato, Beeman, & Hommel, 2016; Zabelina, O’Leary, Pornpattananangkul, Nusslock, & Beeman, 2015; Zabelina, Saporta, & Beeman, 2016). More broadly, creativity in laboratory and real-world tasks might be predicted by distinct patterns of exploitation-exploration tendencies, an idea that will have to be tested in future experiments.

Third, people with greater real-world creative achievement appear to have wider attentional focus, which can in turn distract them from their primary tasks. Although distractibility usually impairs task performance, it might allow individuals to consider and generate more alternative ideas (e.g., Carson et al., 2003; Zabelina et al., 2015; Zabelina, Saporta, & Beeman, 2016) and might be associated with increased exploratory tendencies that are driven by relatively high tonic locus ceruleus activity and norepinephrine levels (but see the last two paragraphs of this subsection for stress and psychological dysfunction). Our framework therefore has the potential to explain not only the neurobiological bases of creativity, but also individual differences in creativity. Although there is no direct evidence for the hypothesized relationship between tonic activity and creativity, the locus ceruleus has been associated with individual differences in cognitive function and abilities (Mather & Harley, 2016). Indeed, a recent study found that baseline pupil diameter (a proxy for tonic activity) correlates with intelligence (Tsukahara, Harrison, & Engle, 2016), which predicts individual differences in creativity (Benedek, Jauk, Sommer, Arendasy, & Neubauer, 2014; Jauk, Benedek, Dunst, & Neubauer, 2013; Jauk, Benedek, & Neubauer, 2014; Nusbaum & Silvia, 2011). But given that blocking norepinephrine has also been shown to benefit certain types of creative processes (e.g., Alexander et al., 2007; Hecht et al., 2014), increased tonic activity and

norepinephrine might benefit only specific forms of creativity in certain contexts.

Fourth, increased tonic locus ceruleus activity could predispose creative people to increased distractibility, primarily because higher tonic activity increases intrinsic background neural activity and reduces attentional selectivity, which in turn allows a wider range of seemingly irrelevant mental representations to be sampled (Eldar, Cohen, & Niv, 2013; Hasselmo et al., 1997; Usher et al., 1999). However, whether these effects lead to better or worse creativity may depend on which norepinephrine receptors are activated and which specific creative process is under consideration (e.g., Alexander et al., 2007; Lapiz & Morilak, 2006). Nevertheless, these effects suggest that more creative people may be more likely to experience sensory overstimulation because of their overinclusive attention. Consistent with this prediction, many studies have shown that more creative people tend to exhibit greater sensitivity to sensory stimuli. For example, compared with less creative people, they rate electrical shocks as being more painful and register higher-amplitude skin potential responses to tones (e.g., Martindale, 1977; Martindale, Anderson, Moore, & West, 1996; Martindale & Armstrong, 1974). Presently, the precise relationships among the locus ceruleus modes, norepinephrine receptor types, and individual differences in creativity remain unclear, and we believe our framework could offer insights into the interplay among these variables, as well as the relation between locus ceruleus activity and sensory overstimulation in laboratory and real-world studies.

Real-world creative achievement has also been associated with “leaky” attention, which is reflected in reduced sensory gating as indexed by the P50 event-related potential (Zabelina et al., 2015). These findings suggest that real-world creative achievers might be less able than other people to filter out irrelevant information—a process mediated by the phasic locus ceruleus mode—and that leaky sensory gating (mediated by the tonic locus ceruleus mode) might be one of the processes that benefit creativity by focusing attention on more stimuli regardless of their immediate relevance (Mendelsohn & Griswold, 1964; Russell, 1976). In addition, more creative people are hypothesized to connect distantly related concepts or ideas more easily, presumably because the tonic mode increases noise and leaky sensory gating, allowing them to sample a wider range of stimuli (Ansburg & Hill, 2003).

Support for the relationship between the tonic mode and leaky sensory gating comes from recent work showing that pupil diameter reflects locus ceruleus-driven neural gain and sensory processing, such that higher gain (i.e., phasic mode) is associated with

narrow attentional focus, whereas lower gain (i.e., tonic mode) is associated with broader attentional focus (Eldar et al., 2013; Eldar, Niv, & Cohen, 2016). Despite the evidence linking the tonic mode with creativity, it could be that creative people are also better than non-creative people at balancing and switching between the phasic and tonic modes. Our framework suggests that by incorporating valuation processes, researchers can better understand how creative people excel at switching between different modes of cognition in the service of creative problem solving, which remains one of the open questions in the field (see Dorfman, Martindale, Gassimova, & Vartanian, 2008; Vartanian, 2009; Vartanian, Martindale, & Kwiatkowski, 2007).

Finally, if the LC-NE system plays a central role in creative cognition, it follows that disturbances in this system might affect creative cognition. For example, the LC-NE system has been implicated in highly overlapping sets of clinical disorders associated with either enhanced or impaired creativity (e.g., schizophrenia, bipolar disorder; Baas, Nijstad, Boot, & De Dreu, 2016; Kyaga et al., 2011; MacCabe, Sariaslan, Almqvist, Lichtenstein, Larsson, & Kyaga, 2018; Simonton, 2014). Some evidence suggests that schizophrenic patients have increased locus ceruleus cell volumes (Marner, Søborg, & Pakkenberg, 2005), and Type 1 (positive symptoms) schizophrenia has been associated with elevated norepinephrine and metabolites in the brain (Yamamoto & Hornykiewicz, 2004). Patients with schizophrenia often show sensory-gating deficits, in that they fail to filter out potentially irrelevant stimuli (Braff, Geyer, & Swerdlow, 2001; Braff, Greenwood, Swerdlow, Light, & Schork, 2008). Moreover, increasing tonic activity leads to sensory-gating deficits in rats, whereas reducing tonic activity via α -adrenergic receptors prevents these deficits (Alsene & Bakshi, 2011). Together, these findings suggest that the LC-NE system underlies gating deficits and mental disorders, but whether it explains changes in creativity related to these abnormalities and, if so, how it explains those changes, remain open questions. Similarly, hypersensitivity to environmental stimuli—as reflected in increased rates of food allergies, asthma, and autoimmune diseases—have also been observed in people with high intelligence (Karpinski, Kinase-Kolb, Tetreault, & Borowski, 2017), a trait that has been associated with increased creativity (e.g., Benedek et al., 2014). Given these potential links among LC-NE activity, sensory gating, real-world creative achievement (Zabelina et al., 2015; Zabelina, Saporta, & Beeman, 2016), and flexible decision making (Aston-Jones & Cohen, 2005b; Sadacca et al., 2017), we suggest that a fruitful topic for future research would be how value-based decision-making and LC-NE processes might explain the relationship between creativity and certain clinical disorders.

Viewing our framework from the perspective of Carson's (2011, 2014, 2018) shared-vulnerabilities model could also help elucidate the relationships among the LC-NE system, creativity, and psychopathology. According to this model, creative people and those with psychopathology share certain vulnerabilities, including novelty seeking, cognitive disinhibition, and neural hyperconnectivity. For example, both creative people and those with schizophrenia or schizotypy have been shown to exhibit low levels of latent inhibition—defined as the ability to screen from current attentional focus stimuli previously experienced as irrelevant (see Carson et al., 2003; see also Eysenck, 1995). If unchecked, reduced latent inhibition could lead to disturbances in cognition that are caused by a reduced ability to discriminate between task-relevant and task-irrelevant information. However, what distinguishes creative people from those with psychopathology is the additional presence of protective factors, including high intelligence, large working memory capacity, and ego strength. In turn, the presence of these protective factors enables creative people to utilize their vulnerabilities in the service of goal-directed behavior. For example, large working memory capacity might enable a person to systematically use and combine stimuli previously experienced as irrelevant to generate creative solutions (e.g., De Dreu, Nijstad, Baas, Wolsink, & Roskes, 2012). Within this framework, individual differences in LC-NE system activity might interact with vulnerability and protective factors to modulate creativity. However, to the best of our knowledge, there is no direct evidence linking different psychopathologies to different levels of tonic and phasic LC-NE activity, the examination of which remains an open question.

Interactions with other neurotransmitter systems

Although we have focused on the LC-NE system, much evidence suggests that other neuromodulatory systems—especially the dopamine system—also support creative cognition (e.g., Spee et al., 2018). For example, converging evidence suggests that moderate (but not low or high) levels of dopamine in the striatum and prefrontal cortex facilitate various types of creative processes (Boot, Baas, van Gaal, Cools, & De Dreu, 2017). Various dopamine receptor subtypes in the mPFC and different genes—for example, dopamine D₂ receptor (*DRD2*) and catechol-*O*-methyltransferase (*COMT*)—have been associated with cognitive flexibility and divergent thinking (Floresco, Magyar, Ghods-Sharifi, Vexelman, & Tse, 2006; Reuter, Roth, Holve, & Hennig, 2006; Zabelina, Colzato, et al., 2016; Zhang, Zhang, & Zhang, 2014). In addition, given dopamine's role in

reward and reinforcement learning (O'Doherty, Cockburn, & Pauli, 2017; Schultz, Dayan, & Montague, 1997), dopamine might be critical to learning what is creative and which actions or strategies lead to greatest creativity. Serotonin genes have also been associated with creativity (Reuter et al., 2006; Volf, Kulikov, Bortsov, & Popova, 2009), and serotonin has been implicated in specific forms of cognitive flexibility (e.g., reversal learning) that are mediated primarily by the OFC (Clarke, Dalley, Crofts, Robbins, & Roberts, 2004; Clarke et al., 2005). Similarly, acetylcholine has been associated with reversal learning (Robbins & Roberts, 2007; see also Yu & Dayan, 2005). A discussion of the theories about and functions of these systems is beyond the scope of this article, but these findings, together with work indicating that dopamine and serotonin play major roles in learning and valuation (e.g., Boureau & Dayan, 2011; Cools et al., 2011; Montague et al., 2004; Schultz, 2007), are consistent with our suggestion that valuation processes may underlie creative cognition.

Norepinephrine assumes a central role in our framework because of its proposed role in mediating the balance between exploitation and exploration during creative cognition, but some evidence suggests that dopamine and serotonin also modulate the phasic and tonic locus ceruleus modes (e.g., McClure, Gilzenrat, & Cohen, 2006). Specifically, tonic dopamine and serotonin activities have been proposed to track average levels of reward and punishment (Boureau & Dayan, 2011; Cools et al., 2011; Niv, Daw, Joel, & Dayan, 2007), which might in turn determine the threshold for exploring alternatives (Hills et al., 2015). For instance, higher average reward rates, reflected in relative increases in tonic dopamine, might increase phasic activity in the LC-NE system, which corresponds to exploitative behaviors such as fast and vigorous responding (e.g., Hamid et al., 2016; Salamone & Correa, 2002). Further evidence for the role of dopamine in governing these behaviors comes from a genetic study, which found that the *DRD2* and *COMT* genes were associated with exploitation and exploration (Frank, Doll, Oas-Terpstra, & Moreno, 2009). Together, these findings suggest that conceptualizing creative processes as involving valuation and exploitation-exploration trade-offs can potentially elucidate the roles of both norepinephrine and the other neurotransmitters during creative cognition.

Valuation Processes and LC-NE Activity Mediate Creative-Cognition Network Dynamics

Recent neuroimaging work has converged on the view that creative cognition involves dynamic interactions within and between large-scale brain networks,

especially the default-mode network (DMN) and the executive-control network (Beaty, Benedek, Kaufman, & Silvia, 2015; Ellamil et al., 2012; Liu et al., 2015). The DMN and executive-control network are engaged by different types of tasks. Specifically, the DMN is activated by tasks that involve internally directed processes, such as self-generated thought, simulation of future events, and spontaneous thought, and it exhibits decreased activation during tasks that involve attention to external stimuli (Andrews-Hanna, Smallwood, & Spreng, 2014; Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016; Mittner, Hawkins, Boekel, & Forstmann, 2016; Smallwood & Schooler, 2015; Zabelina & Andrews-Hanna, 2016). In contrast, the executive-control network is part of a “task positive” set of regions, and the activation of these regions increases during tasks that require attention to external stimuli (Dixon, Andrews-Hanna, Spreng, Irving, & Christoff, 2017, p. 633). The observation of their joint activation during creative cognition has led to the idea that the two networks support different aspects of creativity: Whereas the DMN supports the generation of creative ideas, the executive-control network modulates activity in the DMN to ensure that task goals are met (Beaty et al., 2015; Beaty, Benedek, Silvia, & Schacter, 2016). Although these brain networks are clearly implicated in creative cognition, it remains unclear what factors engage these networks and drive interactions and transitions among these networks. We speculate that network dynamics observed during creative cognition are driven by value computations in regions within the brain's valuation system and by activity in the LC-NE system, which jointly optimize the trade-off between idea exploitation and exploration.

The core brain regions that assign, represent, and evaluate subjective value during value-based decision making are the OFC, vmPFC, and PCC (Bartra et al., 2013; Clithero & Rangel, 2014). Coincidentally, the mPFC and PCC form the core of the DMN (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Zabelina & Andrews-Hanna, 2016). These anatomical (and related functional) overlaps suggest that DMN activity might in part reflect the neural value computations that we propose underlie creative cognition. For example, multiple lines of work suggest that the PCC might play an important role during creative cognition. In addition to being implicated in value-based decision making (Barack, Chang, & Platt, 2017; Bartra et al., 2013; Grueschow et al., 2015) and internally oriented cognition (Christoff et al., 2016; Zabelina & Andrews-Hanna, 2016), the PCC might mediate functional coupling and transitions between different brain networks. For example, during early phases of divergent thinking, the PCC strongly couples with regions of the salience network, such as the insula and ACC, whereas during

later phases, it couples with regions of the executive-control network (e.g., dorsolateral PFC; Beaty et al., 2015). The salience network helps to focus the spotlight of attention on relevant stimuli in the service of goal-directed behavior, as well as to initiate the switch between the DMN and the executive-control network (Cocchi, Zalesky, Fornito, & Mattingley, 2013; Menon, 2015; Uddin, 2015). These findings suggest that in conjunction with the salience network, the PCC might be critical for engaging different brain networks, as well as mediating network interactions and transitions in the service of creativity.

Indeed, neuroeconomic studies have demonstrated that the PCC mediates shifts between networks and corresponding transitions in exploitation and exploration (Barack et al., 2017; Pearson, Hayden, Raghavachari, & Platt, 2009; Pearson, Heilbronner, Barack, Hayden, & Platt, 2011). Kounios et al. (2006) reported increased activity in the PCC during the period leading up to an insightful solution. PCC activity during this period might reflect processes that mediate the shift from exploration (i.e., finding alternative solutions) to exploitation (i.e., focusing on an insightful solution). Given that the PCC is involved in detecting changes in the environment and mediating subsequent changes in behavior (Pearson et al., 2011), it may be that the PCC helps detect changes in the overall value of ideas during creative cognition (see Barack et al., 2017) and, in response, mediates shifts between different brain networks.

The insula, ACC, OFC, and locus ceruleus nucleus are highly interconnected, which suggests that transitions between the phasic and tonic LC-NE modes could be associated with activity in the salience network (ACC and insula). The OFC and ACC send major cortical inputs to the locus ceruleus (Aston-Jones & Cohen, 2005a; Porrino & Goldman-Rakic, 1982); the OFC also projects to the insula (Aston-Jones & Cohen, 2005a), which projects to the OFC and ACC (Aston-Jones & Cohen, 2005a, 2005b). These neuroanatomical interconnections raise the possibility that value computations drive LC-NE activity, which, in turn, mediates interactions and transitions between various brain networks. That is, the diffuse projections of the LC-NE system through cortical regions might play a central role in governing network dynamics that have typically been observed in neuroimaging experiments (Guedj, Meunier, Meunier, & Hadj-Bouziane, 2017; Logothetis, 2008; Toussay, Basu, Lacoste, & Hamel, 2013).

The idea that LC-NE activity might drive network dynamics is also consistent with other models of LC-NE function. LC-NE activity has been proposed to facilitate network resetting, such that when the LC-NE system is activated, it interrupts and resets existing functional networks, facilitating the emergence of new ones

(Bouret & Sara, 2005; Guedj et al., 2017; Sara, 2009; see also Mittner et al., 2016). For example, it may be that norepinephrine released by the locus ceruleus resets the attention networks to promote adaptive shifts in attention and changes in behavioral responses (Corbetta, Patel, & Shulman, 2008; Sara & Bouret, 2012). During creative cognition, such attention resetting might facilitate the transition from exploration to exploitation. Integrating these theories of LC-NE function is beyond the scope of the current article, but we hope our framework will stimulate future work that bridges LC-NE function, creative cognition, and value-based decision making.

Limitations and Future Directions

By synthesizing ideas and findings from multiple fields, the present framework offers a novel account of creative cognition. However, several issues remain to be addressed. First, our framework assumes that creative cognition is not qualitatively different from normal cognition, in that decision processes that underlie everyday choices are assumed to also support creative processes. However, creative and normal cognition could rely on completely different, partially overlapping, or completely overlapping processes (see Abraham, 2013). Our framework clearly suggests overlapping processes, but future work should explore whether the processes underlying creative cognition, normal cognition, and economic choice are partially or completely overlapping. Second, in its current conceptualization, this framework does not distinguish between the various aspects or types of creativity (e.g., divergent thinking, solving insight problems, combining remote semantic associations; see also constrained vs. unconstrained cognitive flexibility: Alexander et al., 2007; Hecht et al., 2014). It assumes that the same value-based decision-making processes are involved in all creative tasks, although the extent of their involvement could vary across tasks. Future work is required to test this assumption. Third, our framework has the potential to provide an integration that explains not only creative processes within an individual, but also individual differences in creativity. Clearly, more work is needed to test this aspect of the model. Fourth, we have discussed creative generation and evaluation as though these two processes occur largely independently. However, just as LC-NE phasic and tonic activity fall on a continuum, generative and evaluative processes might also fall on a continuum. In addition, it could be that the transitions between these processes occur too rapidly to be measured using tools that have relatively low temporal resolution (e.g., fMRI). Thus, other neuroimaging methods with greater temporal resolution might be better suited

to test some of the framework's predictions—including the prediction that generation and evaluation are distinct stages in the creative process.


Conclusion

Recently, several frameworks have been proposed to account for the neural mechanisms that underlie creativity (Boot et al., 2017; Dietrich & Haider, 2016). Unlike previous accounts, ours draws heavily on neuroeconomics to describe how creative cognition occurs in the brain. By treating creative cognition as an adaptive value-maximization process supported by activity in the LC-NE neuromodulatory system, it offers a different way to think about the creative process and provides a novel perspective for reinterpreting and integrating existing findings. It also is highly testable and falsifiable, because it offers many new hypotheses. Although we have outlined only the key hypotheses, many additional nuanced predictions can be derived from our framework. We believe that this framework can significantly improve understanding of not just creative cognition, but also the relationships among decision making, neuromodulation, and large-scale brain network dynamics.

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