

# 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).

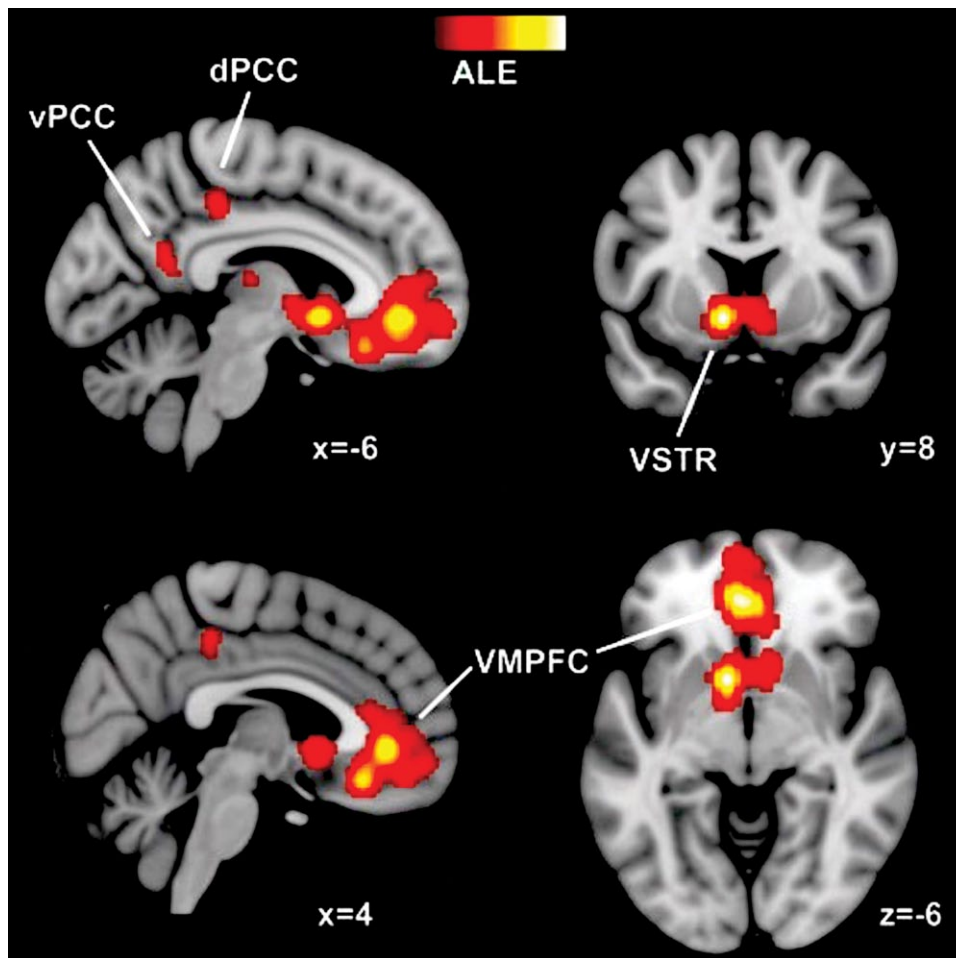
The basic premise of the present framework is that creative cognition is similarly supported by value-based decision-making processes. Creative cognition could be just another form of value-based decision making because it is underwritten by the same neural systems that drive value computations in the 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, Maysless, 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).

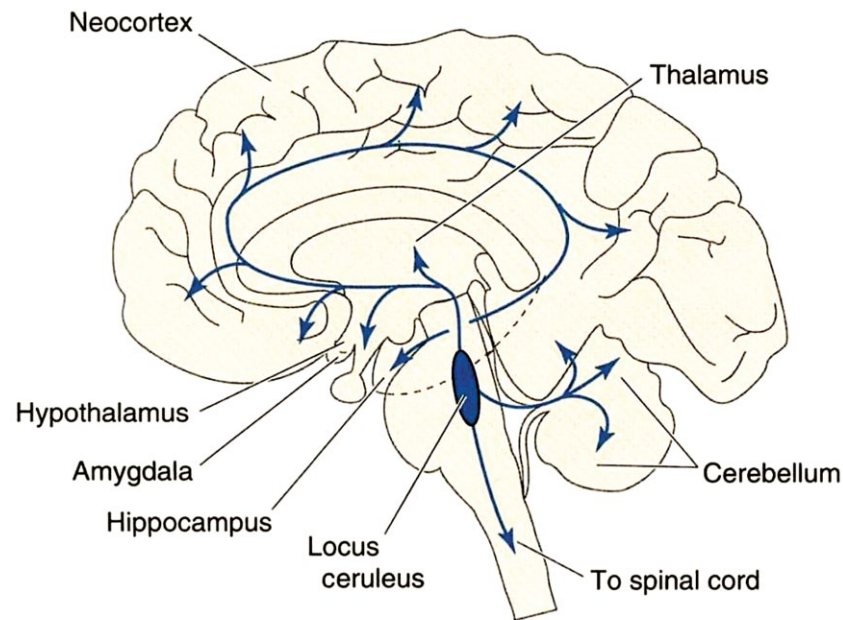
Creative cognition appears to rely on abilities to exploit and explore ideas, as well as to switch between these two modes of cognition (Monechi, Ruiz-Serrano, Tria, & Loreto, 2017). When people are initially trying to find inspiration or ideas for tackling a new problem, they are attempting to explore 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 responsiveness) 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 (Beverdors, 2013, 2018; Heilman, 2016; Heilman, Nadeau, & Beverdors, 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  $\alpha$ -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  $\alpha$ -adrenergic receptors facilitates set shifting, reducing norepinephrine via  $\beta$ -adrenergic receptors (e.g., using propranolol, a  $\beta$ -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; Beverdors, Hughes, Steinberg, Lewis, & Heilman, 1999; Beverdors, White, Chever, Hughes, & Bornstein, 2002; H. L. Campbell, Tivarus, Hillier, & Beverdors, 2008; Hecht, Will, Schachtman, Welby, & Beverdors, 2014). These opposing effects suggest that  $\alpha$ - and  $\beta$ -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  $\alpha$ -2A receptors,  $\beta$ -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  $\alpha$ - and  $\beta$ -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  $\beta$ -adrenergic-receptor blockers are most apparent under stressful conditions (Alexander, Hillier, Smith, Tivarus, & Beverdors, 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  $\alpha$ - and  $\beta$ -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  $\alpha$ -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 D<sub>2</sub> 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 (Beatty, 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, Boebel, & 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 (Beatty et al., 2015; Beatty, 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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## Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

## References

- Abraham, A. (2013). The promises and perils of the neuroscience of creativity. *Frontiers in Human Neuroscience*, *7*, Article 246. doi:10.3389/fnhum.2013.00246
- Alexander, J. K., Hillier, A., Smith, R. M., Tivarus, M. E., & Beversdorf, D. Q. (2007). Beta-adrenergic modulation of cognitive flexibility during stress. *Journal of Cognitive Neuroscience*, *19*, 468–478. doi:10.1162/jocn.2007.19.3.468
- Alsene, K. M., & Bakshi, V. P. (2011). Pharmacological stimulation of locus coeruleus reveals a new antipsychotic-responsive pathway for deficient sensorimotor gating. *Neuropsychopharmacology*, *36*, 1656–1667. doi:10.1038/npp.2011.47
- Amaral, D. G., & Sinnamon, H. M. (1977). The locus coeruleus: Neurobiology of a central noradrenergic nucleus. *Progress in Neurobiology*, *9*, 147–196. doi:10.1016/0301-0082(77)90016-8
- Andrews-Hanna, J. R., Reidler, J. S., Sepulcre, J., Poulin, R., & Buckner, R. L. (2010). Functional-anatomic fractionation of the brain's default network. *Neuron*, *65*, 550–562. doi:10.1016/j.neuron.2010.02.005
- Andrews-Hanna, J. R., Smallwood, J., & Spreng, R. N. (2014). The default network and self-generated thought: Component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*, *1316*, 29–52. doi:10.1111/nyas.12360
- Ansburg, P. I., & Hill, K. (2003). Creative and analytic thinkers differ in their use of attentional resources. *Personality and Individual Differences*, *34*, 1141–1152. doi:10.1016/S0191-8869(02)00104-6
- Arnsten, A. F. T. (2000). Through the looking glass: Differential noradrenergic modulation of prefrontal cortical function. *Neural Plasticity*, *7*, 133–146. doi:10.1155/np.2000.133
- Arnsten, A. F. T. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nature Reviews Neuroscience*, *10*, 410–422. doi:10.1038/nrn2648
- Aston-Jones, G., & Bloom, F. E. (1981). Norepinephrine-containing locus coeruleus neurons in behaving rats exhibit pronounced responses to non-noxious environmental stimuli. *Journal of Neuroscience*, *1*, 887–900.
- Aston-Jones, G., & Cohen, J. D. (2005a). Adaptive gain and the role of the locus coeruleus-norepinephrine system in optimal performance. *Journal of Comparative Neurology*, *493*, 99–110. doi:10.1002/cne.20723
- Aston-Jones, G., & Cohen, J. D. (2005b). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*, *28*, 403–450. doi:10.1146/annurev.neuro.28.061604.135709
- Aston-Jones, G., Rajkowski, J., & Cohen, J. (1999). Role of locus coeruleus in attention and behavioral flexibility. *Biological Psychiatry*, *46*, 1309–1320. doi:10.1016/s0006-3223(99)00140-7
- Aston-Jones, G., & Waterhouse, B. (2016). Locus coeruleus: From global projection system to adaptive regulation of behavior. *Brain Research*, *1645*, 75–78. doi:10.1016/j.brainres.2016.03.001
- Baas, M., Nijstad, B. A., Boot, N. C., & De Dreu, C. K. W. (2016). Mad genius revisited: Vulnerability to psychopathology, biobehavioral approach-avoidance, and creativity. *Psychological Bulletin*, *142*, 668–692. doi:10.1037/bul0000049
- Bar, M., & Neta, M. (2006). Humans prefer curved visual objects. *Psychological Science*, *17*, 645–648. doi:10.1111/j.1467-9280.2006.01759.x
- Bar, M., & Neta, M. (2007). Visual elements of subjective preference modulate amygdala activation. *Neuropsychologia*, *45*, 2191–2200. doi:10.1016/j.neuropsychologia.2007.03.008



- Barack, D. L., Chang, S. W. C., & Platt, M. L. (2017). Posterior cingulate neurons dynamically signal decisions to disengage during foraging. *Neuron*, *96*, 339–347. doi:10.1016/j.neuron.2017.09.048
- Bartra, O., McGuire, J. T., & Kable, J. W. (2013). The valuation system: A coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *NeuroImage*, *76*, 412–427. doi:10.1016/j.neuroimage.2013.02.063
- Basadur, M., Graen, G. B., & Green, S. G. (1982). Training in creative problem solving: Effects on ideation and problem finding and solving in an industrial research organization. *Organizational Behavior and Human Performance*, *30*, 41–70. doi:10.1016/0030-5073(82)90233-1
- Beatty, R. E., Benedek, M., Kaufman, S. B., & Silvia, P. J. (2015). Default and executive network coupling supports creative idea production. *Scientific Reports*, *5*, Article 10964. doi:10.1038/srep10964
- Beatty, R. E., Benedek, M., Silvia, P. J., & Schacter, D. L. (2016). Creative cognition and brain network dynamics. *Trends in Cognitive Sciences*, *20*, 87–95. doi:10.1016/j.tics.2015.10.004
- Benedek, M., Jauk, E., Sommer, M., Arendasy, M., & Neubauer, A. C. (2014). Intelligence, creativity, and cognitive control: The common and differential involvement of executive functions in intelligence and creativity. *Intelligence*, *46*, 73–83. doi:10.1016/j.intell.2014.05.007
- Beninger, R. J., & Miller, R. (1998). Dopamine D1-like receptors and reward-related incentive learning. *Neuroscience & Biobehavioral Reviews*, *22*, 335–345. doi:10.1016/s0149-7634(97)00019-5
- Berke, J. D. (2018). What does dopamine mean? *Nature Neuroscience*, *21*, 787–793. doi:10.1038/s41593-018-0152-y
- Berkman, E. T. (2018). Value-based choice: An integrative, neuroscience-informed model of health goals. *Psychology & Health*, *33*, 40–57. doi:10.1080/08870446.2017.1316847
- Berkman, E. T., Hutcherson, C., Livingston, J. L., Kahn, L. E., & Inzlicht, M. (2017). Self-control as value-based choice. *Current Directions in Psychological Science*, *26*, 422–428. doi:10.1177/0963721417704394
- Berridge, C. W., & Waterhouse, B. D. (2003). The locus coeruleus–noradrenergic system: Modulation of behavioral state and state-dependent cognitive processes. *Brain Research Reviews*, *42*, 33–84. doi:10.1016/S0165-0173(03)00143-7
- Beversdorf, D. Q. (2013). Pharmacological effects on creativity. In O. Vartanian, A. S. Bristol, & J. C. Kaufman (Eds.), *Neuroscience of creativity* (pp. 159–173). Cambridge, MA: MIT Press.
- Beversdorf, D. Q. (2018). Stress, pharmacology, and creativity. In R. E. Jung & O. Vartanian (Eds.), *The Cambridge handbook of the neuroscience of creativity* (pp. 73–91). New York, NY: Cambridge University Press.
- Beversdorf, D. Q., Hughes, J. D., Steinberg, B. A., Lewis, L. D., & Heilman, K. M. (1999). Noradrenergic modulation of cognitive flexibility in problem solving. *NeuroReport*, *10*, 2763–2767. doi:10.1097/00001756-199909090-00012
- Beversdorf, D. Q., White, D. M., Chever, D. C., Hughes, J. D., & Bornstein, R. A. (2002). Central  $\beta$ -adrenergic modulation of cognitive flexibility. *NeuroReport*, *13*, 2505–2507. doi:10.1097/00001756-200212200-00025
- Birrell, J. M., & Brown, V. J. (2000). Medial frontal cortex mediates perceptual attentional set shifting in the rat. *Journal of Neuroscience*, *20*, 4320–4324.
- Boccia, M., Piccardi, L., Palermo, L., Nori, R., & Palmiero, M. (2015). Where do bright ideas occur in our brain? Meta-analytic evidence from neuroimaging studies of domain-specific creativity. *Frontiers in Psychology*, *6*, Article 1195. doi:10.3389/fpsyg.2015.01195
- Bogacz, R., Brown, E., Moehlis, J., Holmes, P., & Cohen, J. D. (2006). The physics of optimal decision making: A formal analysis of models of performance in two-alternative forced-choice tasks. *Psychological Review*, *113*, 700–765. doi:10.1037/0033-295X.113.4.700
- Boot, N., Baas, M., van Gaal, S., Cools, R., & De Dreu, C. K. W. (2017). Creative cognition and dopaminergic modulation of fronto-striatal networks: Integrative review and research agenda. *Neuroscience & Biobehavioral Reviews*, *78*, 13–23. doi:10.1016/j.neubiorev.2017.04.007
- Boureau, Y.-L., & Dayan, P. (2011). Opponency revisited: Competition and cooperation between dopamine and serotonin. *Neuropsychopharmacology*, *36*, 74–97. doi:10.1038/npp.2010.151
- Bouret, S., & Sara, S. J. (2005). Network reset: A simplified overarching theory of locus coeruleus noradrenaline function. *Trends in Neurosciences*, *28*, 574–582. doi:10.1016/j.tins.2005.09.002
- Braff, D. L., Geyer, M. A., & Swerdlow, N. R. (2001). Human studies of prepulse inhibition of startle: Normal subjects, patient groups, and pharmacological studies. *Psychopharmacology*, *156*, 234–258. doi:10.1007/s002130100810
- Braff, D. L., Greenwood, T. A., Swerdlow, N. R., Light, G. A., & Schork, H. J. (2008). Advances in endophenotyping schizophrenia. *World Psychiatry*, *7*, 11–18. doi:10.1002/j.2051-5545.2008.tb00140.x
- Breedlove, S. M., Watson, N. V., & Rosenzweig, M. R. (2010). *Biological psychology* (6th ed.). Sunderland, MA: Sinauer Associates.
- Brown, S., Gao, X., Tisdelle, L., Eickhoff, S. B., & Liotti, M. (2011). Naturalizing aesthetics: Brain areas for aesthetic appraisal across sensory modalities. *NeuroImage*, *58*, 250–258. doi:10.1016/j.neuroimage.2011.06.012
- Buckley, M. J., Mansouri, F. A., Hoda, H., Mahboubi, M., Browning, P. G. F., Kwok, S. C., . . . Tanaka, K. (2009). Dissociable components of rule-guided behavior depend on distinct medial and prefrontal regions. *Science*, *325*, 52–58. doi:10.1126/science.1172377
- Calhoun, A. J., & Hayden, B. Y. (2015). The foraging brain. *Current Opinion in Behavioral Sciences*, *5*, 24–31. doi:10.1016/j.cobeha.2015.07.003
- Camerer, C. F. (2013). Goals, methods, and progress in neuroeconomics. *Annual Review of Economics*, *5*, 425–455. doi:10.1146/annurev-economics-082012-123040

- Camille, N., Griffiths, C. A., Vo, K., Fellows, L. K., & Kable, J. W. (2011). Ventromedial frontal lobe damage disrupts value maximization in humans. *Journal of Neuroscience*, *31*, 7527–7532. doi:10.1523/JNEUROSCI.6527-10.2011
- Campbell, D. T. (1960). Blind variation and selective retentions in creative thought as in other knowledge processes. *Psychological Review*, *67*, 380–400. doi:10.1037/h0040373
- Campbell, H. L., Tivarus, M. E., Hillier, A., & Beversdorf, D. Q. (2008). Increased task difficulty results in greater impact of noradrenergic modulation of cognitive flexibility. *Pharmacology Biochemistry & Behavior*, *88*, 222–229. doi:10.1016/j.pbb.2007.08.003
- Carson, S. H. (2011). Creativity and psychopathology: A shared vulnerability model. *Canadian Journal of Psychiatry*, *56*, 144–153.
- Carson, S. H. (2014). Cognitive disinhibition, creativity, and psychopathology. In D. K. Simonton (Ed.), *The Wiley handbook of genius* (pp. 198–221). Oxford, England: Wiley.
- Carson, S. H. (2018). Creativity and psychopathology: A relationship of shared neurocognitive vulnerabilities. In R. E. Jung & O. Vartanian (Eds.), *The Cambridge handbook of the neuroscience of creativity* (pp. 136–158). New York, NY: Cambridge University Press.
- Carson, S. H., Peterson, J. B., & Higgins, D. M. (2003). Decreased latent inhibition is associated with increased creative achievement in high-functioning individuals. *Journal of Personality and Social Psychology*, *85*, 499–506. doi:10.1037/0022-3514.85.3.499
- Carson, S. H., Peterson, J. B., & Higgins, D. M. (2005). Reliability, validity, and factor structure of the Creative Achievement Questionnaire. *Creativity Research Journal*, *17*, 37–50. doi:10.1207/s15326934crj1701\_4
- Chatterjee, A., & Vartanian, O. (2014). Neuroaesthetics. *Trends in Cognitive Sciences*, *18*, 370–375. doi:10.1016/j.tics.2014.03.003
- Chatterjee, A., & Vartanian, O. (2016). Neuroscience of aesthetics. *Annals of the New York Academy of Sciences*, *1369*, 172–194. doi:10.1111/nyas.13035
- Chmielewski, W. X., Mückschel, M., Ziemssen, T., & Beste, C. (2017). The norepinephrine system affects specific neurophysiological subprocesses in the modulation of inhibitory control by working memory demands. *Human Brain Mapping*, *38*, 68–81. doi:10.1002/hbm.23344
- Christian, B., & Griffiths, T. (2016). *Algorithms to live by: The computer science of human decisions*. New York, NY: Macmillan.
- Christoff, K., Irving, Z. C., Fox, K. C., Spreng, R. N., & Andrews-Hanna, J. R. (2016). Mind-wandering as spontaneous thought: A dynamic framework. *Nature Reviews Neuroscience*, *17*, 718–731. doi:10.1038/nrn.2016.113
- Churchland, A. K., Kiani, R., & Shadlen, M. N. (2008). Decision-making with multiple alternatives. *Nature Neuroscience*, *11*, 693–702. doi:10.1038/nn.2123
- Clarke, H. F., Dalley, J. W., Crofts, H. S., Robbins, T. W., & Roberts, A. C. (2004). Cognitive inflexibility after prefrontal serotonin depletion. *Science*, *304*, 878–880. doi:10.1126/science.1094987
- Clarke, H. F., Walker, S. C., Crofts, H. S., Dalley, J. W., Robbins, T. W., & Roberts, A. C. (2005). Prefrontal serotonin depletion affects reversal learning but not attentional set shifting. *Journal of Neuroscience*, *25*, 532–538. doi:10.1523/JNEUROSCI.3690-04.2005
- Clithero, J. A., & Rangel, A. (2014). Informatic parcellation of the network involved in the computation of subjective value. *Social Cognitive and Affective Neuroscience*, *9*, 1289–1302. doi:10.1093/scan/nst106
- Cocchi, L., Zalesky, A., Fornito, A., & Mattingley, J. B. (2013). Dynamic cooperation and competition between brain systems during cognitive control. *Trends in Cognitive Sciences*, *17*, 493–501. doi:10.1016/j.tics.2013.08.006
- Cohen, J. D., McClure, S. M., & Yu, A. J. (2007). Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 933–942. doi:10.1098/rstb.2007.2098
- Cools, R., Nakamura, K., & Daw, N. D. (2011). Serotonin and dopamine: Unifying affective, activational, and decision functions. *Neuropsychopharmacology*, *36*, 98–113. doi:10.1038/npp.2010.121
- Cools, R., Robinson, O. J., & Sahakian, B. (2008). Acute tryptophan depletion in healthy volunteers enhances punishment prediction but does not affect reward prediction. *Neuropsychopharmacology*, *33*, 2291–2299. doi:10.1038/sj.npp.1301598
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron*, *58*, 306–324. doi:10.1016/j.neuron.2008.04.017
- Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., & Dolan, R. J. (2006). Cortical substrates for exploratory decisions in humans. *Nature*, *441*, 876–879. doi:10.1038/nature04766
- De Dreu, C. K. W., Nijstad, B. A., Baas, M., Wolsink, I., & Roskes, M. (2012). Working memory benefits creative insight, musical improvisation, and original ideation through maintained task-focused attention. *Personality and Social Psychology Bulletin*, *38*, 656–669. doi:10.1177/0146167211435795
- Diedrich, J., Benedek, M., Jauk, E., & Neubauer, A. C. (2015). Are creative ideas novel and useful? *Psychology of Aesthetics, Creativity, and the Arts*, *9*, 35–40. doi:10.1037/a0038688
- Dietrich, A., & Haider, H. (2016). A neurocognitive framework for human creative thought. *Frontiers in Psychology*, *7*, Article 2078. doi:10.3389/fpsyg.2016.02078
- Dixon, M. L., Andrews-Hanna, J. R., Spreng, R. N., Irving, Z. C., & Christoff, K. (2017). Interactions between the default network and dorsal attention network vary across default subsystems, time, and cognitive states. *NeuroImage*, *147*, 632–649.
- Dorfman, L., Martindale, O., Gassimova, V., & Vartanian, O. (2008). Creativity and speed of information processing: A double dissociation involving elementary versus inhibitory cognitive tasks. *Personality and Individual Differences*, *44*, 1382–1390. doi:10.1016/j.paid.2007.12.006

- Eldar, E., Cohen, J. D., & Niv, Y. (2013). The effects of neural gain on attention and learning. *Nature Neuroscience*, *16*, 1146–1153. doi:10.1038/nn.3428
- Eldar, E., Niv, Y., & Cohen, J. D. (2016). Do you see the forest or the tree? Neural gain and breadth versus focus in perceptual processing. *Psychological Science*, *27*, 1632–1643. doi:10.1177/0956797616665578
- Ellamil, M., Dobson, C., Beeman, M., & Christoff, K. (2012). Evaluative and generative modes of thought during the creative process. *NeuroImage*, *59*, 1783–1794. doi:10.1016/j.neuroimage.2011.08.008
- Eysenck, H. J. (1995). *Genius: The natural history of creativity*. Cambridge, England: Cambridge University Press.
- Floresco, S. B., Magyar, O., Ghods-Sharifi, S., Vexelman, C., & Tse, M. T. (2006). Multiple dopamine receptor subtypes in the medial prefrontal cortex of the rat regulate set-shifting. *Neuropsychopharmacology*, *31*, 297–309. doi:10.1038/sj.npp.1300825
- Foote, S. L., Berridge, C. W., Adams, L. M., & Pineda, J. A. (1991). Electrophysiological evidence for the involvement of the locus coeruleus in alerting, orienting, and attending. *Progress in Brain Research*, *88*, 521–532. doi:10.1016/S0079-6123(08)63831-5
- Foote, S. L., & Morrison, J. H. (1987). Extrathalamic modulation of cortical function. *Annual Review of Neuroscience*, *10*, 67–95. doi:10.1146/annurev.ne.10.030187.000435
- Frank, M. J., Doll, B. B., Oas-Terpstra, J., & Moreno, F. (2009). Prefrontal and striatal dopaminergic genes predict individual differences in exploration and exploitation. *Nature Neuroscience*, *12*, 1062–1068. doi:10.1038/nn.2342
- Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annual Review of Neuroscience*, *30*, 535–574. doi:10.1146/annurev.neuro.29.051605.113038
- Goldfarb, E. V., Froböse, M. I., Cools, R., & Phelps, E. A. (2017). Stress and cognitive flexibility: Cortisol increases are associated with enhanced updating but impaired switching. *Journal of Cognitive Neuroscience*, *29*, 14–24. doi:10.1162/jocn\_a\_01029
- Gonen-Yaacovi, G., de Souza, L. C., Levy, R., Urbanski, M., Josse, G., & Volle, E. (2013). Rostral and caudal prefrontal contribution to creativity: A meta-analysis of functional imaging data. *Frontiers in Human Neuroscience*, *7*, Article 465. doi:10.3389/fnhum.2013.00465
- Goschke, T. (2000). Intentional reconfiguration and involuntary persistence in task set switching. In S. Monsell & J. Driver (Eds.), *Attention and performance XVIII: Control of cognitive processes* (pp. 331–355). Cambridge, MA: MIT Press.
- Grueschow, M., Polania, R., Hare, T. A., & Ruff, C. C. (2015). Automatic versus choice-dependent value representations in the human brain. *Neuron*, *85*, 874–885. doi:10.1016/j.neuron.2014.12.054
- Guedj, C., Meunier, D., Meunier, M., & Hadj-Bouziane, F. (2017). Could LC-NE-dependent adjustment of neural gain drive functional brain network reorganization? *Neural Plasticity*. Article 4328015. doi:10.1155/2017/4328015
- Gvirts, H. Z., Mayseless, N., Segev, A., Lewis, D. Y., Feffer, K., Barnea, Y., . . . Shamay-Tsoory, S. G. (2017). Novelty-seeking trait predicts the effect of methylphenidate on creativity. *Journal of Psychopharmacology*, *31*, 599–605. doi:10.1177/0269881116667703
- Hamid, A. A., Pettibone, J. R., Mabrouk, O. S., Hetrick, V. L., Schmidt, R., Vander Weele, C. M., . . . Berke, J. D. (2016). Mesolimbic dopamine signals the value of work. *Nature Neuroscience*, *19*, 117–126. doi:10.1038/nn.4173
- Hao, N., Ku, Y., Liu, M., Hu, Y., Grabner, R. H., & Fink, A. (2016). Reflection enhances creativity: Beneficial effects of idea evaluation on idea generation. *Brain and Cognition*, *103*, 30–37. doi:10.1016/j.bandc.2016.01.005
- Hare, T. A., Camerer, C. F., & Rangel, A. (2009). Self-control in decision-making involves modulation of the vmPFC valuation system. *Science*, *324*, 646–648. doi:10.1126/science.1169957
- Hare, T. A., Malmaud, J., & Rangel, A. (2011). Focusing attention on the health aspects of foods changes value signals in vmPFC and improves dietary choice. *Journal of Neuroscience*, *31*, 11077–11087. doi:10.1523/JNEUROSCI.6383-10.2011
- Harrington, D. M. (2018). On the usefulness of “value” in the definition of creativity: A commentary. *Creativity Research Journal*, *30*, 118–121. doi:10.1080/10400419.2018.1411432
- Harris, A., Adolphs, R., Camerer, C., & Rangel, A. (2011). Dynamic construction of stimulus values in the ventromedial prefrontal cortex. *PLOS ONE*, *6*(6), Article e21074. doi:10.1371/journal.pone.0021074
- Harris, A., Clithero, J. A., & Hutcherson, C. A. Accounting for taste: A multi-attribute neurocomputational model explains the neural dynamics of choices for self and others. *Journal of Neuroscienc*, *38*, 7952–7968 (2018). doi: 10.1523/JNEUROSCI.3327-17.2018
- Hassall, C. D., Holland, K., & Krigolson, O. E. (2013). What do I do now? An electroencephalographic investigation of the explore/exploit dilemma. *Neuroscience*, *228*, 361–370. doi:10.1016/j.neuroscience.2012.10.040
- Hasselmo, M. E., Linster, C., Patil, M., Ma, D., & Cekic, M. (1997). Noradrenergic suppression of synaptic transmission may influence cortical signal-to-noise ratio. *Journal of Neurophysiology*, *77*, 3326–3339. doi:10.1152/jn.1997.77.6.3326
- Hecht, P. M., Will, M. J., Schachtman, T. R., Welby, L. M., & Beversdorf, D. Q. (2014). Beta-adrenergic antagonist effects on a novel cognitive flexibility task in rodents. *Behavioural Brain Research*, *260*, 148–154. doi:10.1016/j.bbr.2013.11.041
- Heilbronner, S. R., & Hayden, B. Y. (2016). Dorsal anterior cingulate cortex: A bottom-up view. *Annual Review of Neuroscience*, *39*, 149–170. doi:10.1146/annurev-neuro-070815-013952
- Heilman, K. M. (2016). Possible brain mechanisms of creativity. *Archives of Clinical Neuropsychology*, *31*, 285–296. doi:10.1093/arclin/acw009
- Heilman, K. M., Nadeau, S. E., & Beversdorf, D. O. (2003). Creative innovation: Possible brain mechanisms. *Neurocase*, *9*, 369–379. doi:10.1076/neur.9.5.369.16553
- Hervé-Minvielle, A., & Sara, S. J. (1995). Rapid habituation of auditory responses of locus coeruleus cells in

- anaesthetized and awake rats. *NeuroReport*, 6, 1363–1368. doi:10.1097/00001756-199507100-00001
- Hills, T. T., Todd, P. M., Lazer, D., Redish, A. D., Couzin, I. D., & the Cognitive Search Research Group. (2015). Exploration versus exploitation in space, mind, and society. *Trends in Cognitive Sciences*, 19, 46–54. doi:10.1016/j.tics.2014.10.004
- Hogeveen, J., Hauner, K. K., Chau, A., Krueger, F., & Grafman, J. (2017). Impaired valuation leads to increased apathy following ventromedial prefrontal cortex damage. *Cerebral Cortex*, 27, 1401–1408. doi:10.1093/cercor/bhv317
- Hutcherson, C. A., Bushong, B., & Rangel, A. (2015). A neurocomputational model of altruistic choice and its implications. *Neuron*, 87, 451–462. doi:10.1016/j.neuron.2015.06.031
- Hutcherson, C. A., Montaser-Kouhsari, L., Woodward, J., & Rangel, A. (2015). Emotional and utilitarian appraisals of moral dilemmas are encoded in separate areas and integrated in ventromedial prefrontal cortex. *Journal of Neuroscience*, 35, 12593–12605. doi:10.1523/JNEUROSCI.3402-14.2015
- Ikeda, T., Matsuyoshi, D., Sawamoto, N., Fukuyama, H., & Osaka, N. (2015). Color harmony represented by activity in the medial orbitofrontal cortex and amygdala. *Frontiers in Human Neuroscience*, 9, Article 382. doi:10.3389/fnhum.2015.00382
- Ishizu, T., & Zeki, S. (2011). Toward a brain-based theory of beauty. *PLOS ONE*, 6(7), Article e21852. doi:10.1371/journal.pone.0021852
- Jacobsen, T., Schubotz, R. I., Höfel, L., & Cramon, D. Y. (2006). Brain correlates of aesthetic judgment of beauty. *NeuroImage*, 29, 276–285. doi:10.1016/j.neuroimage.2005.07.010
- Jauk, E., Benedek, M., Dunst, B., & Neubauer, A. C. (2013). The relationship between intelligence and creativity: New support for the threshold hypothesis by means of empirical breakpoint detection. *Intelligence*, 41, 212–221. doi:10.1016/j.intell.2013.03.003
- Jauk, E., Benedek, M., & Neubauer, A. C. (2014). The road to creative achievement: A latent variable model of ability and personality predictors. *European Journal of Personality*, 28, 95–105. doi:10.1002/per.1941
- Jepma, M., & Nieuwenhuis, S. (2011). Pupil diameter predicts changes in the exploration-exploitation trade-off: Evidence for the adaptive gain theory. *Journal of Cognitive Neuroscience*, 23, 1587–1596. doi:10.1162/jocn.2010.21548
- Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, 89, P221–P234. doi:10.1016/j.neuron.2015.11.028
- Jung, R. E., & Vartanian, O. (Eds.). (2018). *The Cambridge handbook of the neuroscience of creativity*. New York, NY: Cambridge University Press.
- Kable, J. W., & Glimcher, P. W. (2007). The neural correlates of subjective value during intertemporal choice. *Nature Neuroscience*, 10, 1625–1633. doi:10.1038/nn2007
- Kable, J. W., & Glimcher, P. W. (2009). The neurobiology of decision: Consensus and controversy. *Neuron*, 63, 733–745. doi:10.1016/j.neuron.2009.09.003
- Karpinski, R. I., Kinase Kolb, A. M., Tetreault, N. A., & Borowski, T. B. (2018). High intelligence: A risk factor for psychological and physiological overexcitabilities. *Intelligence*, 66, 8–23. doi:10.1016/j.intell.2017.09.001
- Kehagia, A. A., Murray, G. K., & Robbins, T. W. (2010). Learning and cognitive flexibility: Frontostriatal function and monoaminergic modulation. *Current Opinion in Neurobiology*, 20, 199–204. doi:10.1016/j.conb.2010.01.007
- Kidd, C., & Hayden, B. Y. (2015). The psychology and neuroscience of curiosity. *Neuron*, 88, 449–460. doi:10.1016/j.neuron.2015.09.010
- Kim, H., Adolphs, R., O'Doherty, J. P., & Shimojo, S. (2007). Temporal isolation of neural processes underlying face preference decisions. *Proceedings of the National Academy of Sciences, USA*, 104, 18253–18258. doi:10.1073/pnas.0703101104
- Kolling, N., Behrens, T. E. J., Mars, R. B., & Rushworth, M. F. S. (2012). Neural mechanisms of foraging. *Science*, 336, 95–98. doi:10.1126/science.1218004
- Konovalov, A., & Krajbich, I. (2016). Over a decade of neuroeconomics: What have we learned? *Organizational Research Methods*. Advance online publication. doi:10.1177/1094428116644502
- Kounios, J., Frymiare, J. L., Bowden, E. M., Fleck, J. I., Subramaniam, K., Parrish, T. B., & Jung-Beeman, M. (2006). The prepared mind: Neural activity prior to problem presentation predicts subsequent solution by sudden insight. *Psychological Science*, 17, 882–890. doi:10.1111/j.1467-9280.2006.01798.x
- Kranz, G. S., Kasper, S., & Lanzenberger, R. (2010). Reward and the serotonergic system. *Neuroscience*, 166, 1023–1035. doi:10.1016/j.neuroscience.2010.01.036
- Kyaga, S., Lichtenstein, P., Boman, M., Hultman, C., Långström, N., & Landén, M. (2011). Creativity and mental disorder: Family study of 300,000 people with severe mental disorder. *The British Journal of Psychiatry*, 199, 373–379. doi:10.1192/bjp.bp.110.085316
- Lapiz, M. D., Bondi, C. O., & Morilak, D. A. (2007). Chronic treatment with desipramine improves cognitive performance of rats in an attentional set-shifting test. *Neuropsychopharmacology*, 32, 1000–1010. doi:10.1038/sj.npp.1301235
- Lapiz, M. D., & Morilak, D. A. (2006). Noradrenergic modulation of cognitive function in rat medial prefrontal cortex as measured by attentional set shifting capability. *Neuroscience*, 137, 1039–1049. doi:10.1016/j.neuroscience.2005.09.031
- Lee, T.-H., Greening, S. G., Ueno, T., Clewett, D., Ponzio, A., Sakaki, M., & Mather, M. (2018). Arousal increases neural gain via the locus coeruleus–noradrenaline system in younger adults but not in older adults. *Nature Human Behaviour*, 2, 356–366. doi:10.1038/s41562-018-0344-1
- Levy, D. J., & Glimcher, P. W. (2012). The root of all value: A neural common currency for choice. *Current*

- Opinion in Neurobiology*, 22, 1027–1038. doi:10.1016/j.conb.2012.06.001
- Lin, H., Saunders, B., Hutcherson, C. A., & Inzlicht, M. (2018). Midfrontal theta and pupil dilation parametrically track subjective conflict (but also surprise) during intertemporal choice. *NeuroImage*, 172, 838–852. doi:10.1016/j.neuroimage.2017.10.055
- Liu, S., Erkkinen, M. G., Healey, M. L., Xu, Y., Swett, K. E., Chow, H. M., & Braun, A. R. (2015). Brain activity and connectivity during poetry composition: Toward a multi-dimensional model of the creative process. *Human Brain Mapping*, 36, 3351–3372. doi:10.1002/hbm.22849
- Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature*, 453, 869–878. doi:10.1038/nature06976
- Lubart, T. I., & Sternberg, R. J. (1995). An investment approach to creativity: Theory and data. In S. M. Smith, T. B. Ward, & R. A. Finke (Eds.), *The creative cognition approach* (pp. 269–302). Cambridge, MA: MIT Press.
- MacCabe, J. H., Sariaslan, A., Almqvist, C., Lichtenstein, P., Larsson, H., & Kyaga, S. (2018). Artistic creativity and risk for schizophrenia, bipolar disorder and unipolar depression: A Swedish population-based case-control study and sib-pair analysis. *The British Journal of Psychiatry*, 212, 370–376. doi:10.1192/bjp.2018.23
- Marner, L., Søborg, C., & Pakkenberg, B. (2005). Increased volume of the pigmented neurons in the locus coeruleus of schizophrenic subjects: A stereological study. *Journal of Psychiatric Research*, 39, 337–345. doi:10.1016/j.jpsy.chires.2004.10.008
- Martindale, C. (1977). Creativity, consciousness, and cortical arousal. *Journal of Altered States of Consciousness*, 3, 69–87.
- Martindale, C. (1984). The pleasures of thought: A theory of cognitive hedonics. *The Journal of Mind and Behavior*, 5, 49–80.
- Martindale, C., Anderson, K., Moore, K., & West, A. N. (1996). Creativity, oversensitivity, and rate of habituation. *Personality and Individual Differences*, 20, 423–427. doi:10.1016/0191-8869(95)00193-X
- Martindale, C., & Armstrong, J. (1974). The relationship of creativity to cortical activation and its operant control. *The Journal of Genetic Psychology*, 124, 311–320. doi:10.1080/00221325.1974.10532293
- Martindale, C., & Greenough, J. (1973). The differential effect of increased arousal on creative and intellectual performance. *The Journal of Genetic Psychology*, 123, 329–335. doi:10.1080/00221325.1973.10532692
- Martindale, C., & Hasenpus, N. (1978). EEG differences as a function of creativity, stage of the creative process, and effort to be original. *Biological Psychology*, 6, 157–167. doi:10.1016/0301-0511(78)90018-2
- Mather, M., Clewett, D., Sakaki, M., & Harley, C. W. (2015). Norepinephrine ignites local hot spots of neuronal excitation: How arousal amplifies selectivity in perception and memory. *Behavioral & Brain Sciences*, 39, Article e200. doi:10.1017/S0140525X15000667
- Mather, M., & Harley, C. W. (2016). The locus coeruleus: Essential for maintaining cognitive function and the aging brain. *Trends in Cognitive Sciences*, 20, 214–226. doi:10.1016/j.tics.2016.01.001
- Mather, M., Joo Yoo, H., Clewett, D. V., Lee, T. H., Greening, S. G., Ponzio, A., . . . Thayer, J. F. (2017). Higher locus coeruleus MRI contrast is associated with lower parasympathetic influence over heart rate variability. *NeuroImage*, 150, 329–335. doi:10.1016/j.neuroimage.2017.02.025
- Mayseless, N., Aharon-Peretz, J., & Shamay-Tsoory, S. (2014). Unleashing creativity: The role of left temporoparietal regions in evaluating and inhibiting the generation of creative ideas. *Neuropsychologia*, 64, 157–168. doi:10.1016/j.neuropsychologia.2014.09.022
- McClure, S. M., Gilzenrat, M. S., & Cohen, J. D. (2006). An exploration-exploitation model based on norepinephrine and dopamine activity. In Y. Weiss, B. Schölkopf, & J. Platt (Eds.), *Advances in Neural Information Processing Systems 18* (pp. 867–974). Cambridge, MA: MIT Press.
- McClure, S. M., Laibson, D. I., Loewenstein, G., & Cohen, J. D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Science*, 306, 503–507. doi:10.1126/science.1094492
- McClure, S. M., Li, J., Tomlin, D., Cypert, K. S., Montague, L. M., & Montague, P. R. (2004). Neural correlates of behavioral preference for culturally familiar drinks. *Neuron*, 44, 379–387. doi:10.1016/j.neuron.2004.09.019
- Mendelsohn, G. A., & Griswold, B. B. (1964). Differential use of incidental stimuli in problem solving as a function of creativity. *Journal of Abnormal and Social Psychology*, 68, 431–436. doi:10.1037/h0040166
- Menon, V. (2015). Salience network. In A. W. Toga (Ed.), *Brain mapping: An encyclopedic reference* (Vol. 2, pp. 597–611). Amsterdam, The Netherlands: Academic Press.
- Miner, L. H., Jedema, H. P., Moore, F. W., Blakely, R. D., Grace, A. A., & Sesack, S. R. (2006). Chronic stress increases the plasmalemmal distribution of the norepinephrine transporter and the coexpression of tyrosine hydroxylase in norepinephrine axons in the prefrontal cortex. *Journal of Neuroscience*, 26, 1571–1578. doi:10.1523/JNEUROSCI.4450-05.2006
- Mittner, M., Hawkins, G. E., Boekel, W., & Forstmann, B. U. (2016). A neural model of mind wandering. *Trends in Cognitive Sciences*, 20, 570–578. doi:10.1016/j.tics.2016.06.004
- Mobbs, D., Trimmer, P. C., Blumstein, D. T., & Dayan, P. (2018). Foraging for foundations in decision neuroscience: Insights from ethology. *Nature Reviews Neuroscience*, 19, 419–427. doi:10.1038/s41583-018-0010-7
- Monechi, B., Ruiz-Serrano, A., Tria, F., & Loreto, V. (2017). Waves of novelties in the expansion into the adjacent possible. *PLOS ONE*, 12(6), Article e0179303. doi:10.1371/journal.pone.0179303
- Monsell, S. (2003). Task switching. *Trends in Cognitive Sciences*, 7, 134–140. doi:10.1016/S1364-6613(03)00028-7
- Montague, P. R., Hyman, S. E., & Cohen, J. D. (2004). Computational roles for dopamine in behavioural control. *Nature*, 431, 760–767. doi:10.1038/nature03015
- Moore, R. Y., & Bloom, F. E. (1979). Central catecholamine neuron systems: Anatomy and physiology of the norepinephrine and epinephrine systems. *Annual Review*

- of *Neuroscience*, 2, 113–168. doi:10.1146/annurev.ne.02.030179.000553
- Morilak, D. A., Barrera, G., Echevarria, D. J., Garcia, A. S., Hernandez, A., Ma, S., & Petre, C. O. (2005). Role of brain norepinephrine in the behavioral response to stress. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*, 29, 1214–1224. doi:10.1016/j.pnpbp.2005.08.007
- Murphy, P. R., O'Connell, R. G., O'Sullivan, M., Robertson, I. H., & Balsters, J. H. (2014). Pupil diameter covaries with BOLD activity in human locus coeruleus. *Human Brain Mapping*, 35, 4140–4154. doi:10.1002/hbm.22466
- Murphy, P. R., Robertson, I. H., Balsters, J., & O'Connell, R. G. (2011). Pupillometry and P3 index the locus coeruleus-noradrenergic arousal function in humans. *Psychophysiology*, 48, 1532–1543. doi:10.1111/j.1469-8986.2011.01226.x
- Nakamura, K., Matsumoto, M., & Hikosaka, O. (2008). Reward-dependent modulation of neuronal activity in the primate dorsal raphe nucleus. *Journal of Neuroscience*, 28, 5331–5343. doi:10.1523/JNEUROSCI.0021-08.2008
- Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus-norepinephrine system. *Psychological Bulletin*, 131, 510–532. doi:10.1037/0033-2909.131.4.510
- Niv, Y., Daw, N. D., Joel, D., & Dayan, P. (2007). Tonic dopamine: Opportunity costs and the control of response vigor. *Psychopharmacology*, 191, 507–520. doi:10.1007/s00213-006-0502-4
- Nusbaum, E. C., & Silvia, P. J. (2011). Are intelligence and creativity really so different? Fluid intelligence, executive processes, and strategy use in divergent thinking. *Intelligence*, 39, 36–45. doi:10.1016/j.intell.2010.11.002
- O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, 41, 147–155. doi:10.1016/S0028-3932(02)00145-8
- O'Doherty, J. P., Cockburn, J., & Pauli, W. M. (2017). Learning, reward, and decision making. *Annual Review of Psychology*, 68, 73–100. doi:10.1146/annurev-psych-010416-044216
- Padoa-Schioppa, C. (2011). Neurobiology of economic choice: A good-based model. *Annual Review of Neuroscience*, 34, 333–359. doi:10.1146/annurev-neuro-061010-113648
- Padoa-Schioppa, C., & Assad, J. A. (2006). Neurons in the orbitofrontal cortex encode economic value. *Nature*, 441, 223–226. doi:10.1038/nature04676
- Padoa-Schioppa, C., & Cai, X. (2011). The orbitofrontal cortex and the computation of subjective value: Consolidated concepts and new perspectives. *Annals of the New York Academy of Sciences*, 1239, 130–137. doi:10.1111/nyas.2011.1239.issue-1
- Padoa-Schioppa, C., & Conen, K. E. (2017). Orbitofrontal cortex: A neural circuit for economic decisions. *Neuron*, 96, 736–754. doi:10.1016/j.neuron.2017.09.031
- Pearce, M. T., Zaidel, D. W., Vartanian, O., Skov, M., Leder, H., Chatterjee, A., & Nadal, M. (2016). Neuroaesthetics: The cognitive neuroscience of aesthetic experience. *Perspectives on Psychological Science*, 11, 265–279. doi:10.1177/1745691615621274
- Pearson, J. M., Hayden, B. Y., Raghavachari, S., & Platt, M. L. (2009). Neurons in posterior cingulate cortex signal exploratory decisions in a dynamic multioption choice task. *Current Biology*, 19, 1532–1537. doi:10.1016/j.cub.2009.07.048
- Pearson, J. M., Heilbronner, S. R., Barack, D. L., Hayden, B. Y., & Platt, M. L. (2011). Posterior cingulate cortex: Adapting behavior to a changing world. *Trends in Cognitive Sciences*, 15, 143–151. doi:10.1016/j.tics.2011.02.002
- Pearson, J. M., Watson, K. K., & Platt, M. L. (2014). Decision making: The neuroethological turn. *Neuron*, 82, 950–965. doi:10.1016/j.neuron.2014.04.037
- Porrino, L. J., & Goldman-Rakic, P. S. (1982). Brainstem innervation of prefrontal and anterior cingulate cortex in the rhesus monkey revealed by retrograde transport of HRP. *Journal of Comparative Neurology*, 205, 63–76. doi:10.1002/cne.902050107
- Rangel, A., Camerer, C., & Montague, P. R. (2008). A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience*, 9, 545–556. doi:10.1038/nrn2357
- Rangel, A., & Hare, T. (2010). Neural computations associated with goal-directed choice. *Current Opinion in Neurobiology*, 20, 262–270. doi:10.1016/j.conb.2010.03.001
- Ratcliff, R., Smith, P. L., Brown, S. D., & McKoon, G. (2016). Diffusion decision model: Current issues and history. *Trends in Cognitive Sciences*, 20, 260–281. doi:10.1016/j.tics.2016.01.007
- Reimer, J., McGinley, M. J., Liu, Y., Rodenkirch, C., Wang, Q., McCormick, D. A., & Tolia, A. S. (2016). Pupil fluctuations track rapid changes in adrenergic and cholinergic activity in cortex. *Nature Communications*, 7, Article 13289. doi:10.1038/ncomms13289
- Reuter, M., Roth, S., Holve, K., & Hennig, J. (2006). Identification of first candidate genes for creativity: A pilot study. *Brain Research*, 1069, 190–197. doi:10.1016/j.brainres.2005.11.046
- Rich, E. L., & Wallis, J. D. (2016). Decoding subjective decisions from orbitofrontal cortex. *Nature Neuroscience*, 19, 973–980. doi:10.1038/nn.4320
- Robbins, T. W., & Arnsten, A. F. (2009). The neuropsychopharmacology of fronto-executive function: Monoaminergic modulation. *Annual Review of Neuroscience*, 32, 267–287. doi:10.1146/annurev.neuro.051508.135535
- Robbins, T. W., & Roberts, A. C. (2007). Differential regulation of fronto-executive function by the monoamines and acetylcholine. *Cerebral Cortex*, 17, i151–i160. doi:10.1093/cercor/bhm066
- Roesch, M. R., Calu, D. J., & Schoenbaum, G. (2007). Dopamine neurons encode the better option in rats deciding between differently delayed or sized rewards. *Nature Neuroscience*, 10, 1615–1624. doi:10.1038/nn2013
- Ruff, C. C., & Fehr, E. (2014). The neurobiology of rewards and values in social decision making. *Nature Reviews Neuroscience*, 15, 549–562. doi:10.1038/nrn3776
- Runco, M. A., & Jaeger, G. J. (2012). The standard definition of creativity. *Creativity Research Journal*, 24, 92–96. doi:10.1080/10400419.2012.650092

- Russell, J. (1976). Utilization of irrelevant information by high and low creatives. *Psychological Reports*, *39*, 105–106. doi:10.2466/pr0.1976.39.1.105
- Sadacca, B. F., Wikenheiser, A. M., & Schoenbaum, G. (2017). Toward a theoretical role for tonic norepinephrine in the orbitofrontal cortex in facilitating flexible learning. *Neuroscience*, *345*, 124–129. doi:10.1016/j.neurosci.2016.04.017
- Salamone, J. D., & Correa, M. (2002). Motivational views of reinforcement: Implications for understanding the behavioral functions of nucleus accumbens dopamine. *Behavioural Brain Research*, *137*, 3–25. doi:10.1016/S0166-4328(02)00282-6
- Salimpoor, V. N., Benovoy, M., Larcher, K., Dagher, A., & Zatorre, R. J. (2011). Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nature Neuroscience*, *14*, 257–262. doi:10.1038/nn.2726
- Salimpoor, V. N., van den Bosch, I., Kovacevic, N., McIntosh, A. R., Dagher, A., & Zatorre, R. J. (2013). Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science*, *340*, 216–219. doi:10.1126/science.1231059
- Salimpoor, V. N., & Zatorre, R. J. (2013). Neural interactions that give rise to musical pleasure. *Psychology of Aesthetics, Creativity, and the Arts*, *7*, 62–75. doi:10.1037/a0031819.supp
- Samuels, E. R., & Szabadi, E. (2008). Functional neuroanatomy of the noradrenergic locus coeruleus: Its roles in the regulation of arousal and autonomic function Part I: Principles of functional organisation. *Current Neuropharmacology*, *6*, 235–253.
- Sara, S. J. (2009). The locus coeruleus and noradrenergic modulation of cognition. *Nature Reviews Neuroscience*, *10*, 211–223. doi:10.1038/nrn2573
- Sara, S. J., & Bouret, S. (2012). Orienting and reorienting: The locus coeruleus mediates cognition through arousal. *Neuron*, *76*, 130–141. doi:10.1016/j.neuron.2012.09.011
- Schultz, W. (2007). Multiple dopamine functions at different time courses. *Annual Review of Neuroscience*, *30*, 259–288. doi:10.1146/annurev.neuro.28.061604.135722
- Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, *275*, 1593–1599. doi:10.1126/science.275.5306.1593
- Shadlen, M. N., & Kiani, R. (2013). Decision making as a window on cognition. *Neuron*, *80*, 791–806. doi:10.1016/j.neuron.2013.10.047
- Shadlen, M. N., & Shohamy, D. (2016). Decision making and sequential sampling from memory. *Neuron*, *90*, 927–939. doi:10.1016/j.neuron.2016.04.036
- Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, *79*, 217–240. doi:10.1016/j.neuron.2013.07.007
- Shrivastava, D., Ahmed, S., Laha, A., & Sankaranarayanan, K. (2017). *A machine learning approach for evaluating creative artifacts*. Retrieved from <https://arxiv.org/abs/1707.05499>
- Simonton, D. K. (1999). Creativity as blind variation and selective retention: Is the creative process Darwinian? *Psychological Inquiry*, *10*, 309–328. doi:10.1207/S15327965PLI1004\_4
- Simonton, D. K. (2012). Quantifying creativity: Can measures span the spectrum? *Dialogues in Clinical Neuroscience*, *14*, 100–104.
- Simonton, D. K. (2013). Creative thought as blind variation and selective retention: Why sightedness is inversely related to creativity. *Journal of Theoretical & Philosophical Psychology*, *33*, 253–266.
- Simonton, D. K. (2014). The mad-genius paradox: Can creative people be more mentally healthy but highly creative people more mentally ill? *Perspectives on Psychological Science*, *9*, 470–480. doi:10.1177/1745691614543973
- Simonton, D. K. (2016). Creativity, automaticity, irrationality, fortuity, fantasy, and other contingencies: An eightfold response typology. *Review of General Psychology*, *20*, 194–204.
- Simonton, D. K. (2018). Creative ideas and the creative process: Good news and bad news for the neuroscience of creativity. In R. E. Jung & O. Vartanian (Eds.), *The Cambridge handbook of the neuroscience of creativity* (pp. 9–18). New York, NY: Cambridge University Press.
- Smallwood, J., Brown, K. S., Baird, B., Mrazek, M. D., Franklin, M. S., & Schooler, J. W. (2012). Insulation for daydreams: A role for tonic norepinephrine in the facilitation of internally guided thought. *PLOS ONE*, *7*(4), Article e33706. doi:10.1371/journal.pone.0033706
- Smallwood, J., & Schooler, J. W. (2015). The science of mind wandering: Empirically navigating the stream of consciousness. *Annual Review of Psychology*, *66*, 487–518. doi:10.1146/annurev-psych-010814-015331
- Smith, A., Bernheim, B. D., Camerer, C., & Rangel, A. (2014). Neural activity reveals preferences without choices. *American Economic Journal: Microeconomics*, *6*, 1–36. doi:10.1257/mic.6.2.1
- Smith, P. L., & Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends in Neurosciences*, *27*, 161–168. doi:10.1016/j.tins.2004.01.006
- Spee, B., Ishizu, T., Leder, H., Mikuni, J., Kawabata, H., & Pelowski, M. (2018). Neuropsychopharmacological aesthetics: A theoretical consideration of pharmacological approaches to causative brain study in aesthetics and art. *Progress in Brain Research*, *237*, 343–372. doi:10.1016/bs.pbr.2018.03.021
- Sternberg, R. J. (1999). *Handbook of creativity*. Cambridge, England: Cambridge University Press.
- Sternberg, R. J. (2006). The nature of creativity. *Creativity Research Journal*, *18*, 87–98. doi:10.1207/s15326934crj1801\_10
- Sternberg, R. J. (2012). The assessment of creativity: An investment-based approach. *Creativity Research Journal*, *24*, 3–12. doi:10.1080/10400419.2012.652925
- Sullivan, N., Hutcherson, C., Harris, A., & Rangel, A. (2015). Dietary self-control is related to the speed with which attributes of healthfulness and tastiness are processed. *Psychological Science*, *26*, 122–134. doi:10.1177/0956797614559543



- Suzuki, S., Cross, L., & O'Doherty, J. P. (2017). Elucidating the underlying components of food valuation in the human orbitofrontal cortex. *Nature Neuroscience*, *20*, 1780–1786. doi:10.1038/s41593-017-0008-x
- Tajima, S., Drugowitsch, J., & Pouget, A. (2016). Optimal policy for value-based decision-making. *Nature Communications*, *7*, Article 12400. doi:10.1038/ncomms12400
- Tervo, D. G. R., Proskurin, M., Manakov, M., Kabra, M., Vollmer, A., Branson, K., & Karpova, A. Y. (2014). Behavioral variability through stochastic choice and its gating by anterior cingulate cortex. *Cell*, *159*, 21–32. doi:10.1016/j.cell.2014.08.037
- Toussay, X., Basu, K., Lacoste, B., & Hamel, E. (2013). Locus coeruleus stimulation recruits a broad cortical neuronal network and increases cortical perfusion. *Journal of Neuroscience*, *33*, 3390–3401. doi:10.1523/JNEUROSCI.3346-12.2013
- Tsukahara, J. S., Harrison, T. L., & Engle, R. W. (2016). The relationship between baseline pupil size and intelligence. *Cognitive Psychology*, *91*, 109–123. doi:10.1016/j.cogpsych.2016.10.001
- Tusche, A., Bode, S., & Haynes, J. D. (2010). Neural responses to unattended products predict later consumer choices. *Journal of Neuroscience*, *30*, 8024–8031. doi:10.1523/JNEUROSCI.0064-10.2010
- Tusche, A., & Hutcherson, C. A. (2018). Cognitive regulation alters social and dietary choice by changing attribute representations in domain-general and domain-specific brain circuits. *eLife*, *7*, Article e31185. doi:10.7554/eLife.31185.001
- Uddin, L. Q. (2015). Salience processing and insular cortical function and dysfunction. *Nature Reviews Neuroscience*, *16*, 55–61. doi:10.1038/nrn3857
- Unsworth, N., & Robison, M. K. (2016). Pupillary correlates of lapses of sustained attention. *Cognitive, Affective, & Behavioral Neuroscience*, *16*, 601–615. doi:10.3758/s13415-016-0417-4
- Usher, M., Cohen, J. D., Servan-Schreiber, D., Rajkowski, J., & Aston-Jones, G. (1999). The role of locus coeruleus in the regulation of cognitive performance. *Science*, *283*, 549–554. doi:10.1126/science.283.5401.549
- van der Wel, P., & van Steenbergen, H. (2018). Pupil dilation as an index of effort in cognitive control tasks: A review. *Psychonomic Bulletin & Review*. Advance online publication. doi:10.3758/s13423-018-1432-y
- Van Slooten, J. C., Jahfari, S., Knapen, T., & Theeuwes, J. (2018). Pupil responses as indicators of value-based decision-making. *bioRxiv*. doi:10.1101/302166
- Varazzani, C., San-Galli, A., Gilardeau, S., & Bouret, S. (2015). Noradrenaline and dopamine neurons in the reward/effort trade-off: A direct electrophysiological comparison in behaving monkeys. *Journal of Neuroscience*, *35*, 7866–7877. doi:10.1523/JNEUROSCI.0454-15.2015
- Vartanian, O. (2009). Variable attention facilitates creative problem solving. *Psychology of Aesthetics, Creativity, and the Arts*, *3*, 57–59. doi:10.1037/a0014781
- Vartanian, O. (2011). Decision junctures in the creative process. In O. Vartanian & D. R. Mandel (Eds.), *Neuroscience of decision making* (pp. 311–327). New York, NY: Psychology Press.
- Vartanian, O., Bristol, A., & Kaufman, J. C. (Eds.). (2013). *Neuroscience of creativity*. Cambridge, MA: MIT Press.
- Vartanian, O., Martindale, C., & Kwiatkowski, J. (2007). Creative potential, attention, and speed of information processing. *Personality and Individual Differences*, *43*, 1470–1480. doi:10.1016/j.paid.2007.04.027
- Vartanian, O., & Skov, M. (2014). Neural correlates of viewing paintings: Evidence from a quantitative meta-analysis of functional magnetic resonance imaging data. *Brain and Cognition*, *87*, 52–56. doi:10.1016/j.bandc.2014.03.004
- Volf, N. V., Kulikov, A. V., Bortsov, C. U., & Popova, N. K. (2009). Association of verbal and figural creative achievement with polymorphism in the human serotonin transporter gene. *Neuroscience Letters*, *463*, 154–157. doi:10.1016/j.neulet.2009.07.070
- Wang, X.-J. (2002). Probabilistic decision making by slow reverberation in cortical circuits. *Neuron*, *36*, 955–968. doi:10.1016/S0896-6273(02)01092-9
- Wu, X., Yang, W., Tong, D., Sun, J., Chen, Q., Wei, D., . . . Qiu, J. (2015). A meta-analysis of neuroimaging studies on divergent thinking using activation likelihood estimation. *Human Brain Mapping*, *36*, 2703–2718.
- Yamamoto, K., & Hornykiewicz, O. (2004). Proposal for a noradrenaline hypothesis of schizophrenia. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*, *28*, 913–922. doi:10.1016/j.pnpbp.2004.05.033
- Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of Comparative Neurology and Psychology*, *18*, 459–482. doi:10.1002/cne.920180503
- Yu, A. J., & Dayan, P. (2005). Uncertainty, neuromodulation, and attention. *Neuron*, *46*, 681–692. doi:10.1016/j.neuron.2005.04.026
- Zabelina, D. L., & Andrews-Hanna, J. R. (2016). Dynamic network interactions supporting internally-oriented cognition. *Current Opinion in Neurobiology*, *40*, 86–93. doi:10.1016/j.conb.2016.06.014
- Zabelina, D. L., Colzato, L., Beeman, M., & Hommel, B. (2016). Dopamine and the creative mind: Individual differences in creativity are predicted by interactions between dopamine genes DAT and COMT. *PLOS ONE*, *11*(1), Article e0146768. doi:10.1371/journal.pone.0146768
- Zabelina, D. L., O'Leary, D., Pornpattananangkul, N., Nusslock, R., & Beeman, M. (2015). Creativity and sensory gating indexed by the P50: Selective versus leaky sensory gating in divergent thinkers and creative achievers. *Neuropsychologia*, *69*, 77–84. doi:10.1016/j.neuropsychologia.2015.01.034
- Zabelina, D. L., Saporta, A., & Beeman, M. (2016). Flexible or leaky attention in creative people? Distinct patterns of attention for different types of creative thinking. *Memory & Cognition*, *44*, 488–498. doi:10.3758/s13421-015-0569-4
- Zhang, S., Zhang, M., & Zhang, J. (2014). An exploratory study on DRD2 and creative potential. *Creativity Research Journal*, *26*, 115–123. doi:10.1080/10400419.2014.874267