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Chapter:

Curiosity and Learning: A Neuroscientific Perspective

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Abstract

Curiosity – the intrinsic desire to acquire new information – is a key factor for learning and memory in every-day life. To date, there has been very little research on curiosity and, therefore, our understanding of how curiosity impacts learning is relatively poor. In this chapter, we will give an overview of psychological theories of curiosity and how initial research has focused on curiosity as a specific personality characteristic (i.e. trait curiosity). We will then review recent findings on curiosity emerging in experimental psychology and cognitive neuroscience. Rather than examining trait curiosity, this recent line of research explores how temporary states of curiosity affect cognitive processes. Recent findings suggest that curiosity states elicit activity in the brain's dopaminergic circuit and thereby enhance hippocampus-dependent learning for information associated with high curiosity but also for incidental information encountered during high-curiosity states. We will speculate how this new line of curiosity research could help to better understand the mechanisms underlying curiosity-related learning and potentially lead to a fruitful avenue of translating laboratory-based findings on curiosity into educational settings.

I have no special talents. I am only passionately curious.

-- Albert Einstein

Introduction

Epistemic curiosity – the intrinsic desire to acquire new knowledge – enhances learning (for a review, see Hidi, 2016), and it is a strong predictor of academic achievement and job performance (Mussel, 2013; von Stumm, Hell, & Chamorro-Premuzic, 2011). Despite the importance of curiosity to everyday learning, until recently, the topic has been largely ignored in experimental psychology and cognitive neuroscience, and we lack an understanding of the cognitive and neural processes underlying the nebulous concept of curiosity. Fortunately, new experimental research has begun to shed some light on how curiosity modulates brain activity and memory processes. In this chapter, we will give an overview of what is known about curiosity. We will start by reviewing theories of curiosity and early research on curiosity as personality trait (part 1). Subsequently, we will review research from experimental psychology and cognitive neuroscience showing how momentary states of curiosity affect learning and memory processes (part 2). Finally, we will propose how a neuroscience-based framework of curiosity can stimulate hypothesis-driven research on curiosity and we will speculate about how future findings could be used for educational settings (part 3).

Part 1: Psychological theories on curiosity and curiosity as a personality trait

In 1891, William James (1891) was the first to describe curiosity as an instinct that evolved to facilitate survival and adaptation through active exploration of the environment. However, it was not until the 1950s, when the behaviourist D.E. Berlyne started the first series of experimental research on curiosity. Berlyne categorised curiosity along several dimensions: "epistemic and perceptual curiosity", where the former refers to the drive and desire for knowledge, and perceptual curiosity which refers to exploratory behaviour that enhances perception of the environment (Berlyne, 1954). Another dimension introduced by Berlyne (1960) was "specific and diversive curiosity", where specific curiosity relates to the desire to reduce uncertainty by searching for a particular piece of information that is lacking. In contrast, diversive curiosity refers to the seeking of information or stimulation that is novel, complex or surprising in order to reduce feelings of boredom and increase arousal (Berlyne, 1960, 1966). Berlyne (1960) suggested that complexity, surprise, uncertainty and novelty, activate the 'curiosity drive' and subsequently increase aversive arousal levels. The desire to resolve uncertainty is thought to be fulfilled through information-seeking, a behaviour that is proposed to reduce arousal and satisfy curiosity. A limitation of this theory by Berlyne is that it poses a paradox between the assertion that curiosity is aversive, and the fact that people frequently and intentionally look for opportunities that spark their curiosity. If curiosity merely raises levels of aversiveness, it would be sensible to avoid exposure to situations that spark such curiosity.

Alternate accounts, such as incongruity theory, define curiosity as the propensity to make sense of the environment instigated by violated expectations (Loewenstein, 1994). Along the same lines, optimal arousal theory (Berlyne, 1967; Hebb, 1949, 1955) proposed the existence of an 'optimal level of incongruity,' such that slight expectancy violations stimulate curiosity, whilst higher states of incongruity create a fear-like response. In contrast to drive theories, the optimal arousal account argues that 'moderate levels of curiosity' are sought out as they are 'more pleasurable' than high and low levels which are more aversive. However, this idea fails to explain why, if pleasurable levels of curiosity are preferred, people try to resolve their curiosity (Loewenstein, 1994). Therefore, Loewenstein (1994) proposed the information-gap theory to better explain voluntary exposure to curiosity and its situational determinants. He characterized specific epistemic curiosity as a "cognitively induced deprivation that results from the perception of a gap in one's knowledge" (p.76). Like drive theories, information-gap theory frames curiosity as a motivation to seek information in order to eliminate an aversive state. However, Loewenstein (1994) additionally proposed that, "satisfying curiosity is in itself pleasurable," and that pleasure, "compensates for the aversiveness of the curiosity itself" (Loewenstein, 1994, p. 90) (for other related theoretical accounts, see Spielberger & Starr, 1994; Litman, 2005).

Adopting these early ideas on dissociating between various underlying factors of epistemic curiosity (Berlyne, 1954; Loewenstein, 1994), subsequent research focused on developing various personality questionnaires to measure different facets of trait curiosity. Most questionnaires include general self-report statements about an individual's curiosity. One of the most prominent questionnaires, the Epistemic Curiosity Scale (ECS) developed by Litman and Spielberger (2003) measured the two constructs of Diversive and Specific Epistemic Curiosity that were originally introduced by Berlyne (1960). Furthermore, extending beyond contemporary models of curiosity (Loewenstein, 1994; Spielberger & Starr, 1994), Litman and Jimerson (2004) suggested that curiosity and our intent to seek out information could be elicited both by aversive feelings of deprivation and positive emotional feelings of interest which led to the 2-factor Interest-/ Deprivation-type Epistemic Curiosity scale (Litman, 2008).

Contrary to the research investigating different factors that induce curiosity, Kashdan and colleagues have focused on the nature and processes underlying trait curiosity. Kashdan, Gallagher, Silvia, Breen, and Steger (2009) developed the Curiosity and Exploration Inventory-II (CEI-II) that measures two processes underlying curiosity: (i) stretching: the initial desire to obtain information and seek out new opportunities; and (ii) embracing: the actual willingness and readiness to embrace unpredictable and novel situations (Kashdan et al., 2009; for an earlier version of the inventory, see Kashdan, Rose & Fincham, 2004). Interestingly, this line of research has shown how trait curiosity is positively related to well-being and personal growth (e.g. Kashdan & Steger, 2007).

In addition to refine how to measure specific aspects of trait curiosity, it has also been recently suggested that trait curiosity can be understood as a critical component of the 'Openness to Experience' trait – one of the Big Five personality traits (i.e. Neuroticism, Agreeableness, Extraversion, Conscientiousness and Openness to Experience) (Deyoung, 2014; Woo et al., 2014). In particular, Woo et al. (2014) developed a hierarchical measure of the Openness to Experience Scale that attempt to dissociate the multiple factors that contribute to the global trait Openness to Experience. The scale highlights curiosity as an important factor within 'Openness to intellectual experiences' which contains the facets 'Intellectual efficiency', 'Ingenuity' and 'Curiosity' (for further measures of curiosity, e.g., see the Ontario Test of Intrinsic Motivation (OTIM; Day, 1971) and Melbourne Curiosity Inventory (MCI; Naylor, 1981).

In addition to understanding the various concepts underlying trait curiosity, a crucial question is whether there is any relationship between trait curiosity and learning abilities. As expected, some studies that investigate the association between personality traits and learning mostly support positive relationships. For example, Hassan, Bashir, and Mussel (2015) found a mediating role of epistemic curiosity on learning. Additionally, Mussel (2013) showed that trait curiosity positively correlated with performance in work settings, potentially suggesting a facilitating role of curiosity on learning. Similarly, curiosity measures that are applicable to educational settings have also been shown to influence learning (Grossnickle, 2016; Hidi, 2016; von Stumm et al., 2011). For example, Kashdan and Yuen (2007) studied the relationship between perceived school qualities, school grades and trait curiosity using the CEI. The authors found that Chinese students scoring high in trait curiosity outperformed students who were low in trait curiosity, but only when they believed their school provided a challenging environment to learn. Highly curious individuals showed greater academic success in more challenging environments, but critically they performed more poorly in less challenging environments (Kashdan & Yuen, 2007).

In conclusion, several theories have highlighted different types of curiosity and speculated how curiosity is accompanied by aversive and positive feelings. Questionnaires measuring trait curiosity have attempted to dissociate different types and factors underlying curiosity. Critically, initial studies that have shown that trait curiosity positively correlates with learning success stress the importance to better harness curiosity in the classroom (Ainley, Hidi, & Berndorff, 2002; Grossnickle, 2016; Hidi, 2016; Mussel, 2013).

Part 2: The neural mechanisms underlying curiosity states

Instead of focusing on curiosity traits, a recent series of studies have started to investigate how momentary states of curiosity can affect learning and memory. In this part, we will describe the current research on such curiosity states and explain how their findings are consistent with the large literature on how extrinsic rewards affect learning and memory.

Epistemic curiosity states

Kang and colleagues (2009) conducted the first study that investigated the neural mechanisms underlying curiosity states. In order to manipulate curiosity in a lab setting, participants were presented with a set of trivia questions that elicited either high or low epistemic curiosity. Participants' brain activation underlying curiosity was measured via functional magnetic resonance imaging (fMRI)[1]. During the fMRI phase of the experiment, participants were required to read the trivia questions, silently guess the answer and rate their curiosity, and then rate their confidence in knowing the answer. Each trivia question was subsequently shown again, this time followed by the correct answer. After participants had completed the fMRI task, they reported their initial answers to the trivia questions. Based on previous findings showing that activation in the striatum signals reward anticipation (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Knutson, Adams, Fong, & Hommer, 2001) (see Figure 1), the authors speculated that activation in the striatum could correlate with curiosity. Consistent with

[1] fMRI is a non-invasive technique that allows to indirectly measure neural activity throughout the whole brain, while participants perform a task or rest inside an MRI scanner. Compared to other methods in cognitive neuroscience, fMRI has a very high spatial resolution allowing to make inferences about the contribution of specific brain areas in certain tasks.

this idea, Kang et al. (2009) found that when trivia questions were presented for the first time, increased activity for high- compared to low-curiosity questions were observed in the prefrontal cortex (PFC), the parahippocampal gyri (PHG) and importantly the caudate nucleus – a region within the striatum. Kang et al. (2009) suggested that the relationship between activity in the caudate nucleus and participants' reported curiosity is consistent with Loewenstein's (1994) information-gap theory that proposes that curiosity is associated with the anticipation of rewarding information (i.e. satisfying a knowledge gap). The assumption that curiosity satisfaction is rewarding led Kang et al. (2009) to conduct another behavioural study in which they demonstrated that participants were willing to sacrifice 'scarce resources', such as 'waiting time' or 'limited tokens', to learn answers to questions that piqued their curiosity (see also Marvin & Shohamy, 2016).

The fMRI findings by Kang et al. (2009) suggest that high curiosity is related to the rewarding value of information, which in turn facilitates learning of the new information. To test this prediction, Kang and colleagues conducted a follow-up experiment in which a memory test for answers to previously seen trivia questions was administered 1 to 2 weeks after learning. Results showed that increased curiosity was associated with increased recollection of answers to trivia questions that were initially unknown. The authors speculated that the findings imply that curiosity might stimulate brain regions associated with memory in response to unknown answers and thereby enhance memory for correct, previously unknown, trivia answers (Kang et al., 2009).

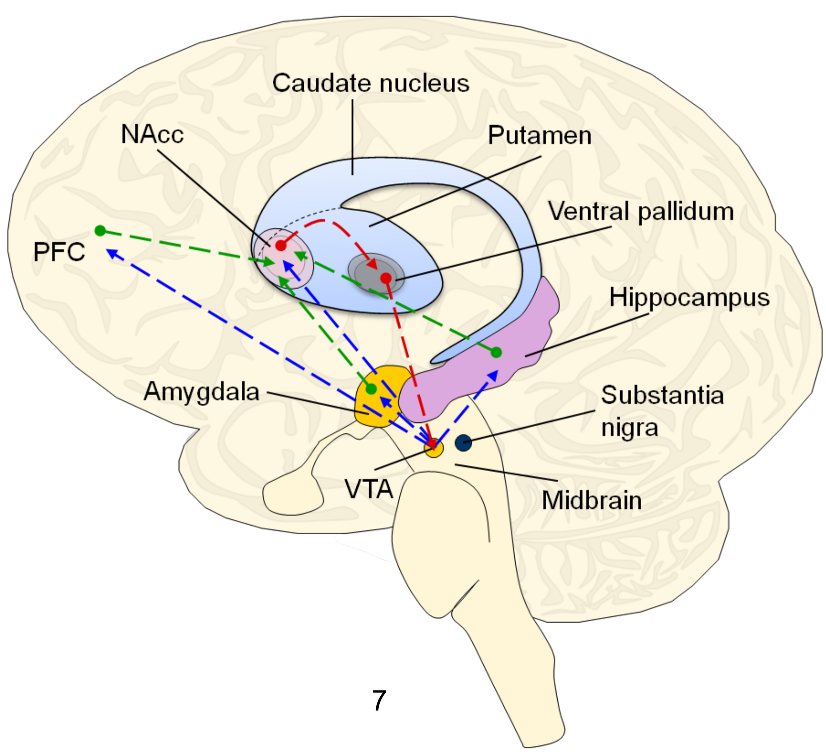

Figure 1. Mesolimbic pathway. Blue lines indicate dopaminergic input from the ventral tegmental area (VTA) to the hippocampus, amygdala, prefrontal cortex (PFC) and nucleus accumbens (NAcc). Green lines indicate glutamatergic input from the hippocampus, amygdala and PFC to the NAcc. Red lines indicate inhibitory GABAergic inputs that subsequently stimulate dopaminergic neurons in the midbrain (VTA). (See Lisman & Grace, 2005; Shohamy & Adcock, 2010).

In addition, a growing literature on extrinsic motivation and memory has shown that motivational states by itself can facilitate learning and memory (Shohamy & Adcock, 2010). More specifically, the hippocampus – a critical area in the brain's memory circuit – together with two critical reward-related regions, the nucleus accumbens (NAcc) and the substantia nigra/ ventral tegmental area (SN/VTA) complex, have been found to be highly connected, and are thought to form a functional loop that regulates learning (Kahn & Shohamy, 2013; Lisman & Grace, 2005). Thereby, VTA dopaminergic neurons enhance long-term potentiation (LTP) in the hippocampus, which then leads to enhanced memory consolidation (for reviews, see Lisman & Grace, 2005; Lisman et al., 2011; Otmakhova, Duzel, Deutch, & Lisman, 2013; Shohamy & Adcock, 2010). A seminal fMRI study by Adcock et al. (2006) tested for the first time how such reward- and memory-related regions affect memory retention. In their study, cues signalled either a high or low monetary reward for successfully memorizing upcoming neutral visual stimuli. Participants showed increased memory performance for visual scenes that followed high- compared to low-reward cues. During the encoding phase, high-reward cues predictive of later remembered scenes showed increased activity in the hippocampus and brain regions receptive to reward anticipation such as the NAcc and the SN/VTA (for converging findings, see Murty & Adcock, 2014; Wittmann et al., 2005; Wolosin, Zeithamova, & Preston, 2012). Crucially, these findings illustrate that activity (elicited by reward cues) *prior* to the encoding of upcoming information leads to reward-related memory enhancements, specifically, via activity and interactions between the SN/VTA and hippocampus (Adcock et al., 2006).

The findings on the relationship between reward states and memory by Adcock et al. (2006) together with the findings by Kang et al. (2009) on the involvement of the reward-related areas during states of epistemic curiosity raise the question whether curiosity states enhance long term memory similar to reward states (Gruber, Gelman, & Ranganath, 2014). Therefore, we followed up the initial findings by Kang et al. (2009) and addressed the question whether this specific functional loop supporting reward-related memory benefits involving the hippocampus, NAcc and SN/VTA predicted memory enhancements for upcoming information during states of curiosity (Gruber et al., 2014). The experimental procedure was adopted from Kang et al. (2009) and involved an initial screening phase, a study phase, and a surprise memory test. In the screening phase, participants rated the likelihood of knowing the correct answer to each trivia question and their curiosity about the answer to each question. Trivia questions for which the answers were unknown were included in the remaining phases of the experiment. In the study phase in which we used fMRI to measure brain activity, a trial began with the presentation of a selected trivia question and participants had to wait for 14 seconds until the correct answer was revealed. During this anticipation period, a neutral image was also presented (for further details, see below). During the final phase, memory for the trivia answers and neutral images was tested after a short delay in this fMRI experiment and after a one-day delay in a behavioural follow-up experiment.

In both same-day and one-day-delayed memory tests, we found that participants exhibited better memory for answers to questions that they were more curious about (in line with Kang et al., 2009). The fMRI results indicated that when trivia questions were presented, activity in the critical reward-related regions (i.e. SN/VTA and NAcc) linearly increased with participants' curiosity ratings. This suggests that key regions of the dopaminergic circuit involved during extrinsic reward anticipation also correlate with the level of curiosity (cf. Adcock et al., 2006; Knutson et al., 2001). In contrast, however, once curiosity had been satisfied (i.e. when the answer was shown), these two regions no longer showed an increase of activation for high- compared to low-curiosity states. The findings underscore the role of anticipatory activity during curiosity states ahead of upcoming information. To further extend the findings by Kang et al. (2009), we then asked whether activity during curiosity states (i.e. activity elicited by the trivia questions) predicts later memory for upcoming high- or low-curiosity information. We found that activation in the right hippocampus and bilateral NAcc during the presentation of high- compared to low-curiosity questions predicted later memory improvements for answers to high- compared to low-curiosity questions (Gruber et al., 2014). In contrast, activity *during* the presentation of high- and low-curiosity answers did not predict the curiosity-related memory improvements. These findings are consistent with studies on extrinsic reward anticipation and demonstrate that anticipatory activity elicited in the NAcc and the hippocampus during states of high curiosity facilitate the learning of the upcoming information associated with high curiosity.

Investigating how the characteristics of the anticipation period enhance memory for upcoming high-curiosity information, Mullaney, Carpenter, Grotenhuis and Burianek (2014) hypothesized that the duration and unpredictability of waiting periods ahead of upcoming high-curiosity information could increase participants' anticipation about information and subsequently facilitate learning. In line with their predictions, answers presented after a fixed 4-second delay and after a random delay compared to no-delay condition increased memory performance for answers to high-curiosity questions (Mullaney et al., 2014). In addition, Baranes, Oudeyer and Gottlieb (2015) recorded eye movements during curiosity states and found that states of high curiosity, elicited by the presentation of a trivia question, were associated with participants' anticipatory gaze towards the location of the answer. In another recent study, Marvin and Shohamy (2016) found that the positive relationship between curiosity and willingness to wait for the associated answer to a high-curiosity trivia question is independent of the valence of the trivia question (i.e. information associated with negative, neutral, or positive emotions). Together, these findings suggest that harnessing states of high curiosity via anticipating information leads to memory enhancements for high-curiosity information.

Perceptual curiosity states and uncertainty

In addition to studies on epistemic curiosity states, Jepma and colleagues explored the neural mechanisms underlying perceptual curiosity (Jepma, Verdonschot, van Steenbergen, Rombouts, & Nieuwenhuis, 2012). The authors used blurred visual stimuli as compared to clear visual stimuli in order to induce perceptual curiosity. They found that blurred compared to clear visual stimuli increased activation in conflict and arousal regions including the anterior insular cortex and anterior cingulate cortex. The authors therefore speculated that this finding is in line with early drive theories (Berlyne, 1954, 1960, 1966) that assume curiosity is an aversive state that subsequently increases arousal. During relief of perceptual curiosity, Jepma et al. (2012) found increased activation in the striatum (i.e., caudate nucleus, putamen and NAcc) for conditions in which visual stimuli disambiguated blurred images compared to visual stimuli that failed to resolve the identity of blurred images. This latter finding suggests that reducing perceptual uncertainty, through access to information that resolves uncertainty, might be in itself rewarding. The results by Jepma et al (2012) might seem contradictory to our study on epistemic curiosity (Gruber et al., 2014) that show increased activity in the striatum and hippocampus during anticipation rather than during processing of the actual (uncertainty reducing) information. However, these differences in findings might potentially not be driven by the type of curiosity but might be due to different levels of uncertainty about the anticipated information in the two studies. In the study by Jepma et al. (2012), the correct information (i.e., clear image) was not often revealed leading to high uncertainty whether curiosity might be satisfied. Contrary, in our study (Gruber et al., 2014), trivia questions were followed by the correct answer in most cases leading to high certainty that curiosity will be satisfied. In line with theoretical accounts and non-human animal findings on dopamine functions (Lisman et al., 2011; Shohamy & Adcock, 2010), high certainty to receive upcoming information is likely to drive dopaminergic activity during anticipatory states whereas high uncertainty about presentation of upcoming information might drive dopaminergic activity during processing of the actual awaited information via resolving uncertainty and leading to surprise (cf. Chiew, Stanek, & Adcock, 2016; Marvin & Shohamy, 2016). Future studies need to systematically address the role of uncertainty in curiosity, and how uncertainty affects learning and memory for high-curiosity information. Interestingly, a nascent line of curiosity research in non-human animals suggests that resolving uncertainty activates dopaminergic neurons in the midbrain associated with reward. For example, Bromberg-Martin and Hikosaka (2009) found that advance information elicits dopaminergic activity in a similar way as primary rewards (e.g., food, water). In addition, Daddaoua, Lopes, and Gottlieb (2016) showed that intrinsically motivated behaviours are, in part, elicited by events associated with uncertainty that needs to be resolved.

Importantly, while recent findings suggest that curiosity-inducing information might stimulate dopaminergic regions in a similar fashion as primary rewards, it is conceivable that other brain regions and networks might code the differential attributes of secondary rewards (e.g., information) and primary rewards (cf., Blanchard, Hayden & Bromberg-Martin, 2015; Bouret & Richmond, 2010). Although curiosity research in humans has started to demonstrate broad commonalities between curiosity and reward processes, the dissociations between them and their unique contributions to learning and memory still remain to be explored.

Curiosity states benefit learning of incidental information

In our fMRI experiment, we showed that hippocampal activity during high-curiosity states predicts the memory advantage for upcoming high-curiosity information (Gruber et al., 2014). Furthermore, we explored whether a high-curiosity state could even facilitate learning for incidentally encoded information that is presented during a high-curiosity state. To address this question, we presented a neutral, incidental image of a face during the 14-seconds long anticipation period. Participants had to make an incidental encoding judgment on the face image in order to ensure similar levels of encoding throughout the experiment. Finally, as a surprise to participants, we tested their memory not only for the trivia answers but also for the incidental face images. Interestingly, we found that neutral face stimuli were better recognised when these faces were presented during states of high compared to low curiosity. Because participants did not expect the later surprise memory test, it is unlikely that participants used deeper encoding strategies for faces presented during high- compared to low-curiosity states. In line with this speculation, activity following faces did not differ between high- and low-curiosity states suggesting that a memory enhancement for incidental faces might not be purely driven by stimulus-related factors (Gruber et al., 2014).

We therefore further investigated whether it is the activation when curiosity is elicited (via a trivia question) that might predict the later memory advantage for incidental faces encountered during states of high curiosity. Although, brain activation across all participants did not predict the memory improvement for incidental faces, we found that *individual variations* in question-related activity showed a positive correlation with the later memory advantage for incidental faces. Specifically, the level of activation in the SN/VTA and hippocampus predicted the magnitude of the curiosity-driven memory enhancements for incidental faces. In addition, between-participants variations in the level of communication (i.e. functional connectivity) between the SN/VTA and hippocampus also predicted the magnitude of the memory enhancement for incidental faces. Importantly, this suggests that curiosity activates critical regions within the dopaminergic circuit and the hippocampus in preparation for upcoming information, *regardless* of whether this is information that a participant was initially curious about or whether it is other information that is presented when anticipating high-curiosity information.

Importantly, we replicated the curiosity-driven memory advantage for incidental faces when faces were tested in a recognition test one day later (Gruber et al., 2014), suggesting that curiosity-driven memory enhancements for incidental information might be persistent across time and might potentially undergo enhanced memory consolidation (cf. Kang et al., 2009; Marvin & Shohamy, 2016) (for further elaboration of this finding, see below). In addition, unpublished data from our laboratory indicates that curiosity-driven memory enhancements for incidental faces are not evident for all types of recognition memory, but these memory enhancements seem to be specific for recollection that is accompanied by retrieving contextualspatial details (Gruber, Yonelinas, & Ranganath, 2015). In addition, unpublished data from our laboratory also suggests that curiosity-driven memory enhancements are especially pronounced when the incidental information is presented early during the anticipation period. That is, we found curiosity-driven memory enhancements for incidental faces when the face images were presented directly after the presentation of the trivia question (i.e. early in the anticipation period) but not when face images were presented directly prior to the presentation of the trivia answer (i.e. late in the anticipation period) (Gruber et al., 2015). These findings again are in line with the idea that incidental information might show memory enhancements that are driven by processes related to eliciting a curiosity state (i.e. temporally contiguous to the trivia question), but not necessarily driven by processes related to satisfying a curiosity state (i.e. temporally contiguous to the trivia answer). Although these initial findings of how curiosity states benefit learning of incidental information are intriguing, future research is needed to better understand the generalizability of these findings and how they can potentially translate to educational settings (see below).

Similarities between how curiosity and reward states benefit learning of neutral information

Consistent with the curiosity-related memory advantage for incidental information, studies that investigate how other types of salient states influence memory have shown converging findings. For example, several studies that elicit reward states via monetary incentives also demonstrated memory enhancements of temporally contiguous neutral or non-rewarded information. In a study by Mather and Schoeke (2011), the authors showed that reward-related memory enhancements in young and old adults spread from rewarded to neighbouring, non-rewarded trials. Furthermore, in an elegant design by Murayama and Kitagami (2014), the authors showed that neutral images of objects showed memory enhancements when these images preceded an unrelated rewarded reaction time task. In addition, Loh et al. (2016) demonstrated that memory enhancements for rewarded information presented during representationally rich contexts also led to memory enhancements of neutral, non-rewarded information presented in the same high-reward context. Together, the findings on how curiosity and reward states enhance memory for temporally contiguous information are in line with rodent studies that have shown that mere novelty exposure – a different type of salience that activates the dopaminergic circuit – can enhance memory retention for originally weakly encoded information (Moncada & Viola, 2007; Wang, Redondo, & Morris, 2010; Redondo & Morris, 2011). In addition, two recent studies in humans have shown that memory enhancements for rewarded information can also spread to semantically related, non-rewarded information even if the semantically associated information is not temporally contiguous (Oyarzún, Packard, de Diego-Balaguer, & Fuentemilla, 2016; Patil, Murty, Dunsmoor, Phelps, & Davachi, 2016). It would be highly relevant to investigate whether this spreading of memory enhancements via semantically associated information would also be evident when curiosity (instead of rewards) facilitates learning (e.g. whether memory enhancements are evident for neutral, low-curiosity information that is semantically linked to information associated with high curiosity).

Curiosity states and memory consolidation

One important point about how curiosity might benefit memory is that curiosity states seem to lead to better memory retention. Recent studies have suggested that information associated with high curiosity is still better remembered a day and up to at least two weeks after it has been studied (Gruber et al., 2014; Kang et al., 2009; Marvin & Shohamy, 2016; McGillivray, Murayama, & Castel, 2015). While only one study by McGillivray et al. (2015) investigated memory performance after both immediate and delayed memory tests, their results seem to indicate that the magnitude of curiosity-driven memory enhancements does not change over time. These findings are in line with our own findings showing memory benefits for high-curiosity trivia answers and incidental faces presented during high-curiosity states in an immediate but also 1-day delayed memory test (Gruber et al., 2014). Critically, these findings suggest that curiosity does not lead to a mere immediate short-lived memory benefit but seems to enhance memory retention across time.

Although future research on curiosity and memory would need to investigate the underlying neural processes associated with enhanced memory retention, theories and work in rodents suggest that rewards lead to increased memory consolidation processes via dopaminergic modulation of hippocampal functions (for further reading, see Düzel et al., 2009; Lisman & Grace, 2005; Shohamy & Adcock, 2010). Furthermore, recent human fMRI studies on reward and memory that investigated neural activity during *post*-learning rest periods or during sleep have shown that increases in *post*-learning neural dynamics predict later memory advantages for high-reward information (Gruber, Ritchey, Wang, Doss, & Ranganath, 2016; Igloi, Gaggioni, Sterpenich, & Schwartz, 2015; Murty, Tompary, Adcock, & Davachi, 2017). The findings on reward and memory suggest that neural processes that happen *after* learning facilitate memory consolidation to build strong and more permanent memory traces for highly salient information (for further reviews, see: Miendlarzewska, Bavelier, & Schwartz, 2016; Murty & Dickerson, 2016); [chapter XX in this book by Alison Adcock ?]). Future research would need to address whether curiosity enhances neural consolidation mechanisms in a similar way and how enhanced consolidation for high-curiosity information can be optimally harnessed in educational settings.

Curiosity-based learning might not require any additional extrinsic rewards

Another important factor in our understanding of how curiosity increases memory retention concerns its relationship to extrinsic rewards. Research suggests that it is still widely believed that rewards might help to foster intrinsic motivation (Murayama, Kitagami, Tanaka, & Raw, 2017). However, research suggests that the opposite is likely to be the case (Murayama, Matsumoto, Izuma, & Matsumoto, 2010). Most relevant, Murayama and Kuhbandner (2011) conducted a study in which they investigated how the interplay between reward and curiosity influences memory retention. Participants received high and low monetary incentives in order to successfully encode answers to trivia questions. Importantly, when the trivia material was associated with low curiosity, participants indeed remembered low-curiosity trivia answers better for which they received high compared to low reward. In contrast, however, high-curiosity trivia material did not benefit from the additional high-reward incentive. The findings suggest that when learning is driven by curiosity, additional extrinsic motivation might not be effective and necessary. It might also be the case that in some circumstances, reward might undermine the beneficial effects of curiosity (Murayama et al., 2010). Further research is needed to better understand how curiosity and reward interact in order to facilitate learning and memory retention.

Part 3: Future directions and implications for education

A neuromodulatory framework of curiosity

Despite the importance of curiosity and learning in real-life, research on curiosity research has never been a widely-studied topic. As we reviewed here, psychological theories on curiosity primarily sparked initial research on trait curiosity. However, studies in experimental psychology and cognitive neuroscience on curiosity states provide promising findings that might help to develop an increased interest in hypothesis-driven curiosity research. In this chapter, we focused on recent findings that have started to uncover how curiosity states shape learning and memory (for alternative reviews and current models on the influence of curiosity on information-seeking, see Gottlieb et al., 2013; Kidd & Hayden, 2015; Oudeyer & Kaplan, 2009).

The recent findings on curiosity and memory seem to support the idea that the neurocognitive mechanisms of curiosity states resemble mechanisms associated with reward anticipation that depend on the dopaminergic circuit and thereby benefit hippocampal functions to facilitate learning and memory. Such a neural framework of curiosity allows us to generate specific predictions about curiosity and learning. In particular, theories and findings in humans and non-human animals on the neural mechanisms of reward anticipation can guide the generation of hypotheses about how curiosity might influence learning and memory (cf. Marvin & Shohamy, 2016). In addition to reward anticipation, it has recently been shown that there is a variety of other extrinsically and intrinsically salient processes that affect hippocampal functions via dopaminergic modulation: for example, novelty, exploration, and choice (Düzel, Bunzeck, Guitart-Masip, & Düzel, 2010; Lisman & Grace, 2005; Murty, DuBrow, & Davachi, 2015). Importantly, these processes are strongly linked to curiosity and a systematic investigation of how these processes share commonalities might hold the promise to elucidate the underlying factors of how curiosity affects memory. In addition, it is highly conceivable that other neuromodulators such as noradrenaline or acetylcholine that are thought to affect hippocampal functions via arousal and novelty (Mather, Clewett, Sakaki, & Harley, in press; Ranganath & Rainer, 2003) might potentially underlie the neural mechanisms of how curiosity facilitates learning. Importantly, future research on curiosity states could borrow from theories and findings on how neuromodulation affects hippocampus-dependent learning.

Future directions

The neuromodulatory framework of how curiosity might affect hippocampus-dependent learning has the potential to guide further research on curiosity and memory. Here, we propose several potential future directions that would help to better understand the neural mechanisms of curiosity and their impact on learning and memory specifically in educational settings.

First, what are the neurocognitive processes that overlap or dissociate between the various types of curiosity? As reviewed above, over the last decades, theories on curiosity have proposed different types (e.g., epistemic vs. perceptual curiosity; Berlyne, 1960) and different facets of curiosity (e.g., interest-based vs. deprivation-based curiosity; Litman, 2008). It is not known, however, to what degree these different types and facets of curiosity potentially share the same cognitive and neural mechanisms and whether these different types of curiosity facilitate learning and memory processes in a similar way. In order to refine our understanding of the commonalities and differences between curiosity types and their underlying facets, future research in cognitive neuroscience can elucidate the extent to which these various hypothesised types of curiosity differ or share similar neural mechanisms, and how they ultimately benefit memory in potentially different ways.

Second, how does curiosity interact with other processes in support of learning? Initial evidence has suggested that when curiosity is satisfied, other processes that are either independent of curiosity or interact with curiosity might benefit memory (e.g. valence and the actual interestingness of or surprise about the information, or interest and expert knowledge about a topic) (cf., Marvin & Shohamy, 2016; McGillivray et al., 2015). Again, in line with a neuromodulatory framework of curiosity, predictions about the interactions between curiosity and other related processes (e.g. interestingness, surprise) could be derived from the human and non-human animal literature investigating the interactions between reward anticipation and other reward-related processes (e.g. reward consumption or reward-prediction errors) (cf. Marvin & Shohamy, 2016; McGillivray et al., 2015). In addition, educational research has suggested that the concepts of curiosity and interest can be differentiated and are not interchangeable terms (Grossnickle et al., 2016; Hidi, 2016). The four-phase model of interest development by Hidi and Renninger (2006) proposes how initial situational interest stimulated by curiosity can lead to a 'well-developed individual interest' in a topic. Therefore, it would be highly relevant for educational settings to understand how the neural mechanisms between curiosity and interest differ and how these two factors may differentially influence learning and memory.

Third, are the beneficial effects of curiosity states influenced by trait curiosity?
It has been shown that individual variations in curiosity traits might show relationships with learning and academic success (e.g., Kashdan & Yuen, 2007; von Stumm, 2011). In our initial fMRI experiment (Gruber et al., 2014), we found large individual variations in the extent to which curiosity states facilitated learning of incidental information. These individual variations were driven by activation in the SN/VTA and hippocampus. It is unclear whether these variations might have been driven by variations in individuals' general trait curiosity. To date, there is very little evidence on the relationship between curiosity states and trait curiosity (Spielberger & Starr, 1994). In other words, it is not clear whether somebody who scores high on a curiosity trait questionnaire might also benefit the most from a high-curiosity state during learning. Initial studies using EEG and eye-tracking (Baranes et al., 2015; Begus, Gliga & Southgate, 2016; Mussel, Ulrich, Allen, Osinsky & Hewig, 2016) suggest that curiosity traits and their states could

show a relationship. However, future research would need to elucidate to what extent curiosity traits and states share similar structural and functional neural mechanisms, and how the interplay between curiosity traits and states facilitate learning. This research would be important for educational settings in order to understand how students who show generally low or high trait curiosity might benefit in the best way from being in high-curiosity states when they learn new material.

Fourth, how do curiosity-related memory enhancements spread across incidental, non-curiosity-related information?

States associated with curiosity and reward enhance memory for incidental information presented during such salient states. Furthermore, it has been shown that reward enhances memory for non-rewarded information that is semantically associated with rewarded information (Oyarzún et al., 2016; Patil, Murty et al., 2016). It would be crucial to better understand the temporal characteristics of how curiosity states can benefit memory for neutral or semantically associated information. For example, what is the maximum duration for a curiosity state in order to benefit memory for incidental information encountered during a curiosity state? Do curiosity-related memory benefits spread to information that is semantically associated with high-curiosity information? How does initial curiosity for a topic develop into interest for a given topic (cf. Hidi & Renninger, 2006)? Translating those findings into educational settings could potentially be very fruitful. For example, in the classroom, if curiosity is sparked at the start of a lesson, is this sufficient to accelerate learning for specific types of incidental information encountered throughout the lesson? It would be interesting to explore how often curiosity needs to be sparked within a lesson in order to maximize the influence of curiosity on learning.

Conclusion

Recent promising developments in our understanding of the neurocognitive mechanisms of curiosity suggest that curiosity seems to recruit the dopaminergic circuit similar to reward anticipation processes and thereby facilitates hippocampus-dependent learning. Our proposed neuromodulatory framework of curiosity provides a fruitful approach to stimulate and guide further research on the neural and cognitive components of curiosity. The recent resurgence of research on curiosity has started to shed light on how curiosity benefits learning and memory. For education, a better understanding of the mechanisms underlying curiosity-based learning might help to (i) inform teachers and policy makers of *why* curiosity is important for learning, (ii) *how* curiosity can be harnessed in the most effective way in the classroom, and (iii) to improve educational training on the role of curiosity and learning in the classroom. Ultimately, a potentially very promising translational research avenue will be to further test laboratory-based findings in the classroom in order to test the generalizability of the beneficial effects of curiosity in applied settings. Such applied research findings can then in turn inform theories and guide future laboratory-based research on curiosity. Developing such a ‘closed-loop’ approach between curiosity research in the laboratory and applied settings could be a very promising way to increasingly harness the benefits of curiosity in today’s classrooms and thereby improve teaching strategies and guide educational policy making.

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