Individual differences in structural-functional brain connections underlying curiosity

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Thesis Summary

Curiosity motivates us to learn yet varies strikingly between individuals. This thesis aims to answer the following research questions: What are the brain networks associated with curiosity traits? How does curiosity benefit memory for information related and unrelated to the object of curiosity? How do curiosity traits and curiosity states interact to benefit memory? And how do variations in structural-functional brain connections relate to individual differences in curiosity-related memory?

Chapters 2 and 3 investigate the neural mechanisms underlying trait curiosity, first examining its structural correlates followed by its functional correlates. In Chapter 2, inter-individual variations in the microstructure of the fornix related to Interest Epistemic Curiosity (EC), and inter-individual variation in the microstructure of the inferior longitudinal fasciculus related to both Interest and Deprivation EC. Furthermore, posterior hippocampal fornix microstructure was associated with Specific Perceptual Curiosity. These findings were not replicated in a follow-up experiment potentially due to several differences in the design. Next, Chapter 3 indicated that trait curiosity is associated with functional connectivity between the ventral tegmental area (VTA), hippocampus, and nucleus accumbens (NAcc); regions involved in the mesolimbic dopaminergic pathway. Chapter 4 transitions the focus of the thesis from trait curiosity to state curiosity, where states of high curiosity were found to predict later memory for trivia answers but not incidental information preceding curiosity elicitation. This chapter also suggests that trait curiosity does not interact with the positive effects of curiosity on later memory. Finally, a three-way relationship between white matter microstructure, resting-state functional connectivity and curiosity-related behaviours was examined. A mediation analysis revealed that functional communication between the VTA and NAcc mediates the relationship between fornix microstructure and curiosity-related memory benefit.

Together, these results provide a better understanding into the underlying relationship between structural and functional connectivity in the brain and how they support curiosity-related behaviours.

Declaration and Statements

DECLARATION

This work has not been submitted in substance for any other degree or award at this or any other university or place of learning, nor is it being submitted concurrently for any other degree or award (outside of any formal collaboration agreement between the University and a partner organisation).

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This thesis is being submitted in partial fulfilment of the requirements for the degree of *PhD.*

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This thesis is the result of my own independent work/investigation, except where otherwise stated, and the views expressed are my own. Other sources are acknowledged by explicit references. The thesis has not been edited by a third party beyond what is permitted by Cardiff University's Use of Third Party Editors by Research Degree Students Procedure.

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I hereby give consent for my thesis, if accepted, to be available in the University's Open Access repository (or, where approved, to be available in the University's library and for inter-library loan), and for the title and summary to be made available to outside organisations, subject to the expiry of a University-approved bar on access if applicable.

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Preface

The structure across parts of Chapter 1 are in line with the published book chapter:

- Gruber, M. J., Valji, A., & Ranganath, C. (2019). Curiosity and learning: a neuroscientific perspective. In K. A. Renninger & S. E. Hidi (Eds.), *The Cambridge Handbook of Motivation and Learning* (pp. 397–417). Cambridge: Cambridge University Press.

The results of Chapter 2, Experiment 1 are available as a pre-print:

- Valji, A., Priemysheva, A., Hodgetts, C. J., Costigan, A. G., Parker, G. D., Graham, K. S., Lawrence, A. D., & Gruber, M. J. (2019). Curious connections: white matter pathways supporting individual differences in epistemic and perceptual curiosity. *bioRxiv*, 642165.

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List of Abbreviations

ACC	Anterior cingulate cortex
BOLD	Blood oxygen level dependent
CEI	Curiosity and Exploration Inventory
DTI	Diffusion tensor imaging
DWI	Diffusion weighted imaging
EC	Epistemic Curiosity
EPI	Echo planar imaging
FA	Fractional anisotropy
fMRI	Functional magnetic resonance imaging
HARDI	High angular resolution diffusion imaging
HMOA	Hindrance Modulated Orientational Anisotropy
LTP	Long-term potentiation
MD	Mean diffusivity
MRI	Magnetic resonance imaging
MTL	Medial temporal lobe
NAcc	Nucleus accumbens
NODDI	Neurite Orientation Dispersion and Density Imaging
PC	Perceptual Curiosity
PFC	Prefrontal cortex
ROI	Region of interest
RSFC	Resting-state functional connectivity

SN	Substantia nigra
T	Tesla
TE	Echo time
TI	Inversion time
TR	Repetition time
VTA	Ventral tegmental area

Chapter 1: General Introduction

1.1 Psychological theories of curiosity

Have you ever spent hours studying material for an exam that fails to pique your curiosity, then later felt that you failed to remember the relevant information needed to answer the question on an exam paper? We have all experienced something like this at some point in our lives, whether it be at school, a work-related setting or at home in conversation about a particular topic. Eleanor Roosevelt once said, “I think, at a child's birth, if a mother could ask a fairy godmother to endow it with the most useful gift, that gift should be curiosity”. This statement suggests that curiosity arises within an individual and is something that cannot be taught. More commonly, curiosity is described as a form of intrinsic motivation, “the doing of an activity for its inherent satisfaction rather than for some separable consequence” (Ryan & Deci, 2000, p.56). Curiosity was first introduced by William James (1891) as an instinct evolved to aid our survival and adaptation to the environment through active exploration. However, our fear of new environments and experiences were also considered to be adaptive given they held the potential to be harmful to our survival. Therefore, curiosity and fear were regarded as responses elicited by the same stimulus (James, 1890; McDougall, 1918). Other philosophers describe curiosity as a “passion for learning” (Cicero, as cited in Loewenstein, 1994), appetitive, and an observable exploratory behaviour. In the 1960s, the research into curiosity focussed on its underlying cause (Berlyne, 1966), why individuals voluntarily sought out situations known to induce curiosity, and finally the situational determinants of curiosity (Loewenstein, 1994). This first wave of research quickly subsided and then resurfaced in the mid 1970s when researchers began investigating ways of measuring curiosity, cross-validating curiosity-based scales, and correlating them with behaviours and individual characteristics (Loewenstein, 1994).

D.E. Berlyne (1954), a pioneer in the field of curiosity research, was interested in the motivation underlying knowledge acquisition. He questioned why people spent valuable time and effort in their acquisition of knowledge and why only specific pieces of information were more eagerly pursued and subsequently better remembered, given

there being an infinite number of knowable items that could be pursued instead (Berlyne, 1954). Importantly, curiosity was categorised by Berlyne as having two dimensions. The first dimension defines Perceptual and Epistemic Curiosity, where the former describes exploratory behaviours that result in increased perception of the environment, whilst the latter relates to the desire for knowledge and drive to know (Berlyne, 1954). The second dimension consisted of Diversive and Specific Curiosity, where the former describes the seeking of information and/or stimulation as a means to reduce feelings of boredom and increase arousal, whilst Specific Curiosity refers to the desire to reduce uncertainty by searching for a particular piece of information that is lacking (Berlyne, 1960, 1966).

During the early to mid 20th century, similar to early philosophers' ideas, curiosity drive theories referred to curiosity as an aversive state where subsequent unpleasant experiences and feelings of uncertainty could only be reduced through exploratory behaviours (Loewenstein, 1994). Berlyne (1960) believed stimuli that were complex, surprising, held uncertainty and/or were novel, triggered a person's 'curiosity drive', consequently increasing levels of aversive arousal. According to drive theories that viewed curiosity as a primary drive (Thorndike, as cited in Hunt, 1963; Dashiell, 1925), an individual's intrinsic desire to resolve any uncertainty is achieved through information seeking behaviours that ultimately reduces arousal levels and satisfies their curiosity (Loewenstein, 1994). However, one limitation to this theory is the paradox it poses between the claim that curiosity is aversive, and the consistent observation that individuals regularly and intentionally seek out opportunities that pique their curiosity. For instance, if curiosity simply raises levels of aversiveness, then it is logical to just evade these types of situations to begin with.

Alternatively, the incongruity theory viewed curiosity as the tendency for a person to make sense of their environment when faced with violations to their expectations (Loewenstein, 1994). Similarly, the optimal arousal theory (Berlyne, 1967; Hebb, 1949, 1955) suggests there being an 'optimal level of incongruity' in which moderate levels of curiosity are pursued as they are more pleasurable in comparison to high and low levels of curiosity which are more aversive. Nevertheless, this assertion fails to explain why people attempt to resolve their curiosity if pleasurable levels of curiosity are preferred (Loewenstein, 1994). For instance, as opposed to putting a book down before finding out what happens next, why do people continue to read past a cliff-hanger in a book? This notion that people seek out curiosity because it is pleasurable reverts us back to the

earlier question of why one attempts to satisfy their curiosity in the first place (Loewenstein, 1994).

As a means to better explain this voluntary exposure to curiosity as well as its situational determinants, Loewenstein (1994) introduced the information-gap theory that described epistemic curiosity as a "cognitively induced deprivation that results from the perception of a gap in one's knowledge" (p.76). This is where individuals voluntarily expose themselves to situations that pique their curiosity in order to resolve uncertainty or 'gaps' in their knowledge. However, if this knowledge gap is too big or the gap in one's knowledge is too little, curiosity appears to diminish (Baranes, Oudeyer, & Gottlieb, 2015; Kang et al., 2009). This theory of curiosity relates to the traditional drive theories as it proposes that reducing feelings of deprivation (i.e., by acquiring information that one is lacking) is the primary motive for exploratory behaviours and information seeking. However, Loewenstein's (1994) information-gap theory further emphasises that understanding our self-exposure to situations that stimulate curiosity "lies in recognizing that the processes of satisfying curiosity is itself pleasurable... [*and*] compensates for the aversiveness of the curiosity itself" (Loewenstein, 1994, p.90). Finally, the information-gap theory, unlike other accounts, considers the role of curiosity's situational determinants such as environments that elicit surprise, hold importance or salience, that subsequently amplify gaps in our knowledge and subsequently stimulate states of curiosity (Loewenstein,1994; Markey & Loewenstein, 2014).

In contrast, similar to drive theories that postulate curiosity as a primary drive, Marvin and Shohamy (2016) define the 'information-as-reward hypothesis' that suggests curiosity follows the basic principles associated with reward motivated behaviour, where information-gaps (Loewenstein, 1994) can be viewed as eliciting a prediction error that subsequently plays a role in learning and memory. A prediction error is referred to when an outcome differs from what was predicted, where rewards exercise their effects via dopaminergic reward prediction errors (Schultz & Dickinson, 2000; Schultz, 2006; Schultz, Dayan, & Montague, 1997). Curiosity, being a form of intrinsic motivation, may function similarly to the processes and neural mechanisms underlying extrinsic motivation (Gruber, Gelman, & Ranganath, 2014). Lisman and Grace (2005) propose the existence of a functional loop between the hippocampus and midbrain dopaminergic neurons of the ventral tegmental area (VTA), where long-term potentiation (LTP) in the hippocampus is dependent on dopaminergic input from the substantia nigra (SN) and

VTA. In addition to this, there is also a polysynaptic pathway where the accumbens, a major output of excitatory input from the subiculum, relays information from the hippocampus to the VTA. Similar to rewarding stimuli (Schultz, 1998), novel experiences have also been found to activate dopamine neurons that subsequently enhance LTP (Lisman & Grace, 2005). For example, Legault and Wise (2001) had rats enter a previously restricted part of their cage, in which this novel experience resulted in VTA activation as evidenced by dopamine release in the nucleus accumbens (NAcc). The authors injected tetrodotoxin into the subiculum to test whether dopamine release in the NAcc was dependent on the hippocampus, where it was found that the tetrodotoxin injection subsequently blocked the novelty-dependent release of dopamine (Lagault & Wise, 2001). Similar to the finding in rats, human functional magnetic resonance imaging (fMRI) data indicate that the SN/VTA are activated by reward and/or novelty (Adcock et al., 2006; Knutson, Adams, Fong, & Hommer, 2001; Schott et al., 2004; Wittmann et al., 2005). Düzel, Bunzeck, Guitart-Masip, and Düzel (2010) further suggested through the 'NOvelty-related Motivation of Anticipation and exploration by Dopamine' (NOMAD) framework how dopaminergic activity enhances hippocampus-dependent memory formation. This framework predicts that dopaminergic dysfunction results in an impairment of episodic memory consolidation and diminishes a person's motivational drive that consequently results in reduced exploration of novelty in the environment (Düzel et al., 2010). Such theories of dopamine suggest that reward and novelty modulate activity in the dopaminergic circuit, and subsequently affect exploratory behaviours of rewarding and/or novel stimuli.

The theories of curiosity discussed thus far offer a stage to investigate the effects of curiosity on future behaviours. However, one problem facing research when experimentally investigating curiosity is defining what this concept is and what it is not. One perspective put forward by Kidd and Hayden (2015) suggests that a widely agreed definition of curiosity is not necessary, and instead for curiosity research to progress, researchers should focus their study on the evolution of curiosity, the development of curiosity, the function of curiosity, and finally the neural mechanisms of curiosity. Similarly, as an alternative to focussing attention to the definitions of curiosity, Murayama, FitzGibbon, and Sakaki (2019) propose the 'reward-learning framework of autonomous knowledge acquisition' that describes how individuals engage in sustainable knowledge acquisition. Importantly, this framework describes the process underlying curiosity, in which knowledge acquisition functions as a reward, where a

person's expected feeling of a reward modulates their subsequent information seeking behaviours. Likewise, the Prediction, Appraisal, Curiosity, and Exploration (PACE) framework (Gruber & Ranganath, 2019) suggests that information-gaps in our knowledge and prediction errors prompt an appraisal process that determines whether a person acts on their curiosity or inhibits further exploration due to an evoked state of anxiety. This model then suggests that if curiosity prevails, information seeking behaviours are employed which result in enhanced learning. From here, once the information-gap is closed, there is a chance that a new prediction error is generated – subsequently starting a new cycle of appraisal, curiosity and exploration (Gruber & Ranganath, 2019). Together, these new insights into the processes behind curiosity enable future research to further investigate and better understand the effects of curiosity.

1.2 Curiosity Traits and their effects on learning

Based on models of curiosity, it is expected that people who display high trait curiosity will be more likely to experience states of curiosity more frequently and intensely than those who score low in trait curiosity (Grossnickle, 2016; Litman, 2005; Litman, Hutchins & Russon, 2005; Mussel, 2013a; Spielberger & Starr, 1994). One of the Big Five Personality Traits that is Openness to Experience can be described as a multifaceted and hierarchically organized concept that mirrors a person's cognitive exploration and their ability to deal with novel information (DeYoung, 2014; John, Naumann, & Soto, 2008; Woo et al., 2014). Curiosity, described as an attraction to novel intellectual concepts, is believed to mirror qualities of the Openness global trait, where one Openness to Experience scale that includes curiosity as an Openness facet was developed by Woo et al. (2014). This scale comprises of 6 Openness facets whereby Intellectual Efficiency, Ingenuity and Curiosity reflects a person's openness to intellectual experiences, whilst Aesthetics, Tolerance and Depth relates to a person's openness to cultural experiences. Alternative measures to this broader aspect of curiosity include measures of specific constructs of curiosity. Embracing earlier notions on dissociating between aspects of epistemic curiosity (Berlyne, 1954; Loewenstein, 1994), Litman and Spielberger (2003) developed the 10-item Epistemic Curiosity Scale (EC) scale that described two constructs of curiosity: Specific EC, describing a person's motivation to reduce uncertainty by searching for a particular piece of information that is lacking; and

Diversive EC, the motivation to reduce boredom and increase arousal through seeking uncertainty. Extending the ideas put forward by contemporary models of curiosity (Loewenstein, 1994; Spielberger & Starr, 1994), Litman and Jimerson (2004) proposed that an individual's desire to seek out information was perhaps elicited by both positive emotional feelings of interest and aversive feelings of deprivation. Focusing on the latter, Litman & Jimerson (2004) developed the 15-item Curiosity as a Feeling of Deprivation (CFD) scale measuring three different facets (i.e. CFD-Competence, the CFD-Intolerance and CFD-Persistence), where together they represented Loewenstein's (1994) understanding of curiosity. Investigating the extent to which both the EC and CFD scales differentiated between specific subsets of Epistemic Curiosity, resulted in the two-factor Interest-/Deprivation-type EC scale (Litman, 2008). This measure utilised 5-items that reflected Interest-type EC (i.e., items reflecting Diversive-EC from Litman & Spielberger, 2003; e.g. "I enjoy learning about subjects that are unfamiliar to me".) and 5-items that reflected Deprivation-type EC (i.e., items reflecting CFD/Persistence from Litman & Jimerson, 2004; e.g. "I can spend hours on a single problem because I just can't rest without knowing the answer".). Litman (2008) provides evidence for convergent and discriminant validity of the Interest-/Deprivation-type EC scale, and that Interest-type and Deprivation-type EC had acceptable internal consistency (alpha ≥ 0.76). Furthermore, it is proposed that Deprivation and Interest-type curiosity extend the concepts of Specific and Diversive Curiosity, respectively (Litman, 2008). With regards to measuring perceptual curiosity, Collins, Litman, and Spielberger (2004) developed the 12-item Perceptual Curiosity Scale (PC). Centred on Berlyne's (1960, 1966) ideas of curiosity, this scale comprised of 6 Diversive-based PC items and 6 Specific-based PC items. The former subscale reflected items that describe exploratory behaviours in which one seeks out new places and a broad range of sensory stimulation (e.g. "I like to discover new places to go"), whilst Specific-based PC items described exploration of novel, specific and sensorially stimulating stimuli that is lacking (e.g. "When I hear a strange sound, I usually try to find out what caused it"). To assess discriminant and convergent validity, these subscales of PC were correlated with other measures of curiosity, personality traits and sensation seeking measures. Here, Collins et al., (2004) found that PC subscales did not significantly correlate with measures of trait anxiety, anger, and depression, providing evidence for divergent validity; and instead correlated with Sensation Seeking and Epistemic Curiosity measures, which suggests evidence for convergent validity. This scale of PC also indicated that the Diversive and Specific subscales had satisfactory internal consistency (alpha >.70). **Figure 1.1** illustrates a

representation of Epistemic and Perceptual Curiosity and their facets. (For additional curiosity measures, see the Ontario Test of Intrinsic Motivation (Day, 1971) and Melbourne Curiosity Inventory (Naylor, 1981)).

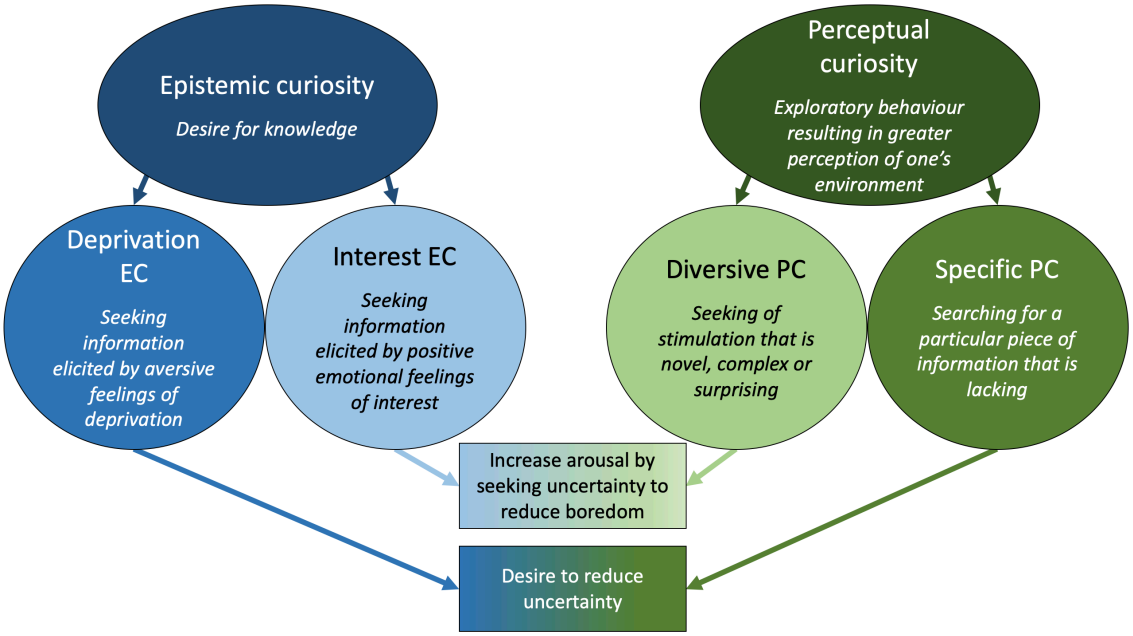


Figure 1.1: Epistemic and Perceptual Curiosity and its subsets, Deprivation/Specific Curiosity and Interest/Diversive Curiosity (see Berlyne, 1954, 1960, 1966, Litman, 2008; Litman & Jimerson, 2004; Litman & Spielberger, 2003).

Building on the proposed ideas from Litman's (2005; 2008) two-dimensional scale of Interest and Deprivation, Kashdan et al. (2018) proposes a multidimensional scale of curiosity that comprises of 5 distinct factors, together forming the 5-Dimensional Curiosity scale. This scale reflects the various ways of experiencing and expressing curiosity and includes dimensions that capture other progressive aspects of curiosity including Stress Tolerance, Social Curiosity, and Thrill Seeking (Kashdan et al., 2018). The first subset of this scale, Joyous Exploration, consists of 5 items that reflects the preference for novel experiences and information, where feeling curious and any subsequent exploratory behaviours are deemed pleasurable (e.g. "I view challenging situations as an opportunity to grow and learn"). In contrast to this appetitive aspect of curiosity, Kashdan et al's. (2018) second subset, Deprivation Sensitivity, reflects the aversive aspect of curiosity,

in which individuals seek out information as a means to escape the tension elicited from not knowing something (e.g. “I like to try to solve problems that puzzle me”). Extending beyond these two aspects of curiosity that have been previously captured in the literature (Litman, 2005; 2008), Stress Tolerance items were included to capture the perceived ability in coping with anxiety involved in encountering the unknown (e.g. “It is difficult to concentrate when there is a possibility that I will be taken by surprise”). The fourth subset of the 5-Dimensional Curiosity scale consists of Social Curiosity items that describes an individual’s fascination and fixation in how other people think, act and feel (e.g. “I like to learn about the habits of others”). Finally, Thrill Seeking items were included to capture a person’s tendency to seek out adventure and pleasure particularly when significant risks are present (e.g. “I would like to explore a strange city or section of town, even if it means getting lost”). Kashdan et al. (2018) in their development and assessment of this curiosity scale, provide evidence for construct validity and high reliability (alpha ≥ 0.83) of the 5 subscales. This scale further emphasises that curiosity is multidimensional and varies between individuals.

Similar to research on curiosity states, this line of research also suggests that curiosity traits might predict learning in work and educational settings (Hassan, Bashir, & Mussel, 2015; Mussel, 2013b). For example, Kashdan and Yuen (2007) examined whether trait curiosity was related to school grades and perceived school quality in a group of high school students. Here, the authors employed the Curiosity and Exploration Inventory (CEI; Kashdan, Rose, & Fincham, 2004) that assessed two dimensions: exploration, the ability to strive for novel and challenging experiences; and absorption, the ability to fully engage in specific activities. This study found that when students believed their academic environment provided novel and challenging experiences to learn from, those students who scored high in the CEI outperformed their peers scoring low on the CEI in both academic and school-based measures of achievement (Kashdan & Yuen, 2007). In addition to this, students reported their aspirations and predicted achievement test scores. With this, it was found that curious students placed in more challenging learning environments reported greater academic success compared to highly curious individuals placed in less challenging learning environments (Kashdan & Yuen, 2007). This evidence suggests that more challenging learning environments enable highly curious students to access the learning tools and opportunities they intrinsically desire, whilst environments which fail to provide novel and challenging experiences result in highly curious students to disengage from their current environment

(Kashdan & Yuen, 2007). Furthermore, this study indicates that the learning benefits of curiosity are facilitated by a possible interaction between an individual's trait and their learning environment (Kashdan & Yuen, 2007).

Another study examined the relationship between each of the Big Five personality traits and learning, in which Epistemic Curiosity was predicted to mediate such relationships (Hassan et al., 2015). A sample of 150 medical physicians working in Pakistan and currently enrolled onto training programmes on general surgery, were asked to complete questionnaires measuring Epistemic Curiosity and the Big Five personality traits. Learning as an outcome from the medical training programmes was measured through supervisory ratings of trainees' knowledge, in which Conscientiousness was the only Big Five trait to significantly predict trainees' learning from the training programmes. Employing separate mediation analyses, the authors then investigated the mediating effect of work-related Epistemic Curiosity (Mussel, Spengler, Litman, & Schuler, 2012) on the relationship between the remaining Big Five personality traits and learning. Whilst the effect of Neuroticism, Agreeableness and Extraversion on learning were found not to be mediated by Epistemic Curiosity, the effect of Openness to Experience as well as Conscientiousness on learning were mediated by Epistemic Curiosity (Hassan et al., 2015). Here, Epistemic Curiosity is shown to explain the relationship between other personality traits and learning, in particular Conscientiousness that describes the ability to plan ahead, persistence and goal directed behaviour; and Openness to Experience, reflecting creativity, imagination, curiosity, and a liking for the new and different (Hassan et al., 2015).

The effect of curiosity on behaviour can also be applied to the work setting. For example, in jobs that require high demands for learning and coping with uncertainty, it is believed that high curiosity increases developing and learning new skills to help overcome challenges and deal with change in the working environment. One study by Mussel (2013b) that aimed to investigate the role of curiosity in predicting job performance, recruited participants employed in the automotive sector of an industrial company to complete the 10 item Work-Related Curiosity Scale (Mussel et al., 2012), a scale reported to have high convergent validity with the EC Scale (Litman & Spielberger, 2003) and the CEI (Kashdan et al., 2004). Scores on this measure of curiosity were subsequently correlated with job performance that comprised of an aggregate score of supervisor ratings on task performance, goal attainment, and vocational school grades.

The authors confirmed that curiosity significantly predicted job performance, indicating that curiosity not only benefits the individual but can also be used in work related settings such as in recruiting and/or building a more productive team (Mussel, 2013b). In summary, individual differences in trait curiosity appear to have some effect on learning. Given the different types of curiosity that exist, it is possible that individual differences in a particular curiosity trait predicts how well they perform in a particular task. Therefore, further research may want to consider examining how different types of trait curiosity benefit learning.

1.3 Memory and motivation-based behaviours

Existing theories on reward and novelty along with subsequent findings of salience-based memory can help pave the way to better understand the link between curiosity and memory. Theories of dopamine so far suggest that reward and novelty modulate activity in the dopaminergic circuit, subsequently enhancing LTP (Lisman & Grace, 2005; Düzel et al., 2010; Gruber & Ranganath, 2019). The process of consciously bringing to mind factual content and autobiographical events is described as declarative/explicit memory, that in turn forms part of long-term memory (Cohen & Squire, 1980; Squire, 1992; Burgess, Maguire, & O'Keefe, 2002; Davachi, 2006; Eichenbaum et al., 2007; Murray, Wise, & Graham, 2018). Early evidence from human amnesic and monkey lesion studies indicate that the medial temporal lobe (MTL) plays a critical role in recognition memory of declarative memory (Cohen & Squire, 1980; Eichenbaum, Yonelinas, & Ranganath, 2007; Nissen, Willingham, & Hartman, 1989; Zola-Morgan & Squire, 1984). The MTL comprises of the hippocampus and surrounding entorhinal, perirhinal and parahippocampal cortices (collectively known as the parahippocampal region). According to the dual-process theory of recognition memory, the hippocampus is critical for recollection, the retrieval of contextual information experienced during the time of encoding; whilst the perirhinal cortex is involved in familiarity-based memory, the feeling that an event has been encountered without recollection of specific event-related information (Brown & Aggleton, 2001; Eichenbaum et al., 2007; Mandler, 1980).

One form of declarative memory is an individual’s memory for personal experiences from a specific time and place – also known as episodic memory

(Tulving,1993). During learning, the relevant information describing an autobiographical event is thought to be converted into an engram and stored as a memory trace (Tulving, 1984; Tulving & Thomson, 1973). Subsequently, when an effective memory cue is presented, these memory traces are retrieved and the event is remembered (Tulving, 2002; Tulving & Thomson, 1973). Some models of memory suggest that the more salient an event is, the better it is remembered to support adaptive behaviours in the future (Shohamy & Adcock, 2010). For example, associating an event with a reward (or punishment) will enhance its salience and strengthen its memory representation that will subsequently guide later behaviour (Matsumoto & Hikosaka, 2009; Shohamy & Adcock, 2010). Another model further suggests that in addition to the salient event itself, we also tend to remember incidental events which surround it (Frey & Morris, 1997, 1998; Wang, Redondo, & Morris, 2010). According to the synaptic tag-and-capture hypothesis, encoding inconsequential information produces a weak tetanisation at the synapse, inducing early long-term potentiation (LTP) and creating a synaptic tag; that subsequently *captures* plasticity-related proteins associated with LTP of salient or novel experiences that follow it (Frey & Morris, 1997, 1998; Redondo & Morris, 2011; Wang et al., 2010). In line with this hypothesis, behavioural tagging suggests that transient memories for incidental information are strengthened when followed closely by behaviourally salient experiences (Moncada, Ballarini, & Viola, 2015; Moncada & Viola, 2007). Based on the behavioural tagging and the synaptic tag-and-capture hypothesis, recent work in humans show that salience retroactively enhances memory following a delay versus immediately after encoding (Dunsmoor, Murty, Davachi, & Phelps, 2015; Murayama & Kitagami, 2014; Patil, Murty, Dunsmoor, Phelps, & Davachi, 2016). This memory effect observed after a long versus short delay post-learning is suggestive of a possible mechanism of consolidation of memory.

Our behaviour and ability to learn can by influenced by extrinsic and intrinsic motivators. Extrinsic motivation is referred to as motivated behaviour that is dependent on the achievement of some separable goal that has instrumental value such as receiving monetary rewards or evading punishments (Ryan & Deci, 2000; Vallerand, 1997). Based on the literature that suggests LTP in the hippocampus is modulated by midbrain dopaminergic neurons involved in the anticipation and processing of rewards (Lisman & Grace, 2005; Otmakhova, Duzel, Deutch, & Lisman, 2013; Shohamy & Adcock, 2010), one study investigating enhanced memory consolidation used visual cues of living and non-living objects as possible predictors of monetary reward versus

no-reward respectively, as a means to induce activity in dopaminergic regions through reward anticipation (Wittmann et al., 2005). Using fMRI, the authors revealed that the SN and striatum, including the NAcc, were strongly activated during anticipation for reward-predicting cues compared to neutral cues. Additionally, a memory test three weeks later revealed that recollection, as measured by source memory hits, was higher for reward-predicting cues compared to neutral cues (source memory was interrogated if a recognition response was elicited in the delayed memory test, where participants were asked whether the item of interest had been presented at study or in the immediate memory test as a new item). Wittmann et al. (2005) further found increased neural activation in the SN and hippocampus for reward-predicting cues at encoding that were later remembered versus forgotten in the delayed memory test. Importantly, this increased activity in the midbrain and hippocampus was absent for reward-predicting cues that were remembered in the immediate memory test. Although fMRI does not allow a direct measure of dopamine, the authors speculate that activation of dopaminergic areas, including the midbrain, improves hippocampus-dependent consolidation where reward-predicting cues compared to neutral cues are better remembered after a long delay (Frey, Schroeder, & Matthies, 1990; Schultz, 1998; Wittmann et al., 2005). Furthermore, using task-based fMRI and [11C] raclopride positron emission tomography as a measure of reward-related neural activity and dopamine release, respectively, Schott et al. (2008) found that neural activity observed in the SN/VTA during reward anticipation positively correlated with dopamine release in the ventral striatum – the target of dopamine neurotransmission from the SN/VTA. This evidence along with Wittmann et al. (2005) suggests that the neurotransmission of dopamine plays a key role in the reward processing. Additionally, a behavioural study by Murayama and Kitagami (2014) found enhanced memory for incidental information that was followed by an unrelated rewarding experience; suggesting that it is not only the reward cue that is consolidated (Wittmann et al., 2005) but independent events preceding it. This retrograde memory effect observed after a delay versus immediately after learning, highlights the importance of memory consolidation and its underlying mechanism involving dopaminergic activation (Murayama & Kitagami, 2014).

Although Wittman et al. (2005) found that increased activation in the midbrain and hippocampus predicted incidental memory formation, an interaction between the two regions was not established. Alternatively, in an intentional memory encoding paradigm, Adcock, Thangavel, Whitfield-Gabrieli, Knutson, and Gabrieli (2006) presented

participants with cues whilst in the MRI scanner that signalled either a high or low monetary reward for learning upcoming visual scenes that would later be tested in a recognition memory test. Twenty-four hours later, participants significantly remembered more scenes that followed high compared to low monetary reward cues. Adcock et al. (2006) also showed that across participants, high-reward cues presented during the encoding task that later predicted the remembered scenes, activated the hippocampus, VTA and NAcc. Furthermore, within-subject correlations revealed an increased relationship between the VTA and hippocampus that subsequently predicted memory formation. These findings suggest that extrinsic rewards presented prior to learning can have an influential effect on subsequent memory formation, for which we also see interactions between reward-related structures and the hippocampus prior to learning (Adcock et al., 2006).

Given the evidence for the consolidation processes in non-human animals (c.f., Foster & Wilson, 2006; McNamara, Tejero-Cantero, Trouche, Campo-Urriza, & Dupret, 2014; Singer & Frank, 2009), Gruber, Ritchey, Wang, Doss, and Ranganath (2016) investigated the effect of reward motivation on consolidation of incidental information in humans. During post-encoding rest periods, the authors examined the interactions between the hippocampus and SN/VTA midbrain areas involved in memory and reward. Furthermore, Gruber et al. (2016) examined whether these interactions during consolidation predicted a later memory advantage for items encoded in contexts of high- versus low-reward. Interestingly, Gruber et al. (2016) found increased resting-state functional connectivity (RSFC) between the hippocampus and midbrain regions that subsequently predicted better memory for items encoded in contexts of high-reward. This finding illustrates that extrinsic motivation may play a role in modifying the post-learning dynamics between the midbrain and hippocampus, providing evidence in humans for a possible neural mechanism by which reward motivation influences the consolidation of memory (Gruber et al., 2016).

In line with the underlying mechanism of reward and memory, encountering novelty is also believed to be related with increased activity and communication within the mesolimbic dopaminergic pathway (Gruber & Ranganath, 2019; Schultz, 1998). Bunzeck and Düzel (2006) employing fMRI methods found that when participants were presented with novel versus neutral stimuli, there was increased activation in the SN/VTA and hippocampus. Additionally, in a separate behavioural experiment, Bunzeck and

Düzel (2006) manipulated testing delay by asking whether memory for familiar stimuli is enhanced in the context of novel stimuli versus very familiar stimuli when examined after short (20-minute delay) or longer periods of retention (1-day delay). The authors found that familiar pictures presented in context with novel pictures compared to contexts with very familiar pictures resulted in better recognition memory after a 20-minute delay than after a 1-day delay. This research suggests that novelty modulates activity in the dopaminergic circuit which enhances memory tested after a short versus long delay (Bunzeck & Düzel, 2006). The evidence reviewed thus far suggests that extrinsic rewards and stimulus novelty activate the hippocampal SN/VTA loop (Lisman & Grace, 2005). Furthermore, it appears that extrinsic rewards influence dopaminergic memory consolidation that benefits memory after a delay rather than immediately after learning, whilst the effects of novelty appear to perhaps influence dopaminergic activity in the SN/VTA that subsequently benefits memory after a short delay.

1.4 Curiosity states

1.4.1 Neural mechanisms of state curiosity

The research investigating the relationship between novelty/reward and dopaminergic activity reviewed thus far, are in line with popular curiosity theories that consider curiosity as a state that encourages information seeking and active exploration of the environment as a means to close knowledge gaps and reduce uncertainty (Litman et al., 2005; Loewenstein, 1994; Berlyne, 1960; Gruber & Ranganath, 2019). As such, information that satisfies curiosity can be regarded as a reinforcer, similar to rewards such as food, water and monetary gains to which experiencing curiosity can be described as a salient event that subsequently guides later behaviour (Gottlieb, Lopes, & Oudeyer, 2016; Shohamy & Adcock, 2010). One of the first studies to investigate the psychological and neural mechanism of curiosity was by Kang et al. (2009) who conducted several experiments where participants were presented with a set of trivia-based questions as a means of eliciting high and low epistemic curiosity. In one of the experiments that used fMRI, participants were presented with trivia questions to which they had to silently guess the answer. Participants were also asked to rate their curiosity and their confidence in

knowing the answer to the question. Following these self-ratings, the question appeared a second time in which the correct answer was presented shortly after. After the scanning session, participants reported their answers they had guessed earlier when in the scanner. The findings indicated that trivia questions presented for the first-time increased activity in the prefrontal cortex (PFC), parahippocampal gyri and caudate nucleus (a region within the striatum), for high- compared to low-curiosity questions. In line with Loewenstein's (1994) information-gap theory, the relationship between participant's curiosity ratings and activity in the caudate nucleus suggests curiosity may be linked with the process of anticipating rewarding information (Kang et al., 2009). Interestingly, when participants were presented with answers to questions that were guessed incorrectly, the authors found increased neural activity in the midbrain and hippocampus that were modulated by curiosity. This suggests that curiosity along with the rewarding value of information may subsequently enhance learning of new information. Based on this prediction, Kang et al. (2009) next examined the relationship between curiosity and memory performance tested 1 to 2 weeks after encoding, where the authors found that greater levels of curiosity led to better memory recall for correct answers that were initially guessed incorrectly (i.e., the new information). In support of their fMRI findings, this behavioural study suggests that curiosity may stimulate memory regions when a person does not know the answer to a question, subsequently enhancing memory for the correct answers presented afterwards (Kang et al., 2009).

In addition, the hippocampus along with the NAcc and SN/VTA have been found to show high intrinsic connectivity, forming a functional loop involved in regulating learning (Kahn & Shohamy, 2013; Lisman & Grace, 2005) (**Figure 1.2**).

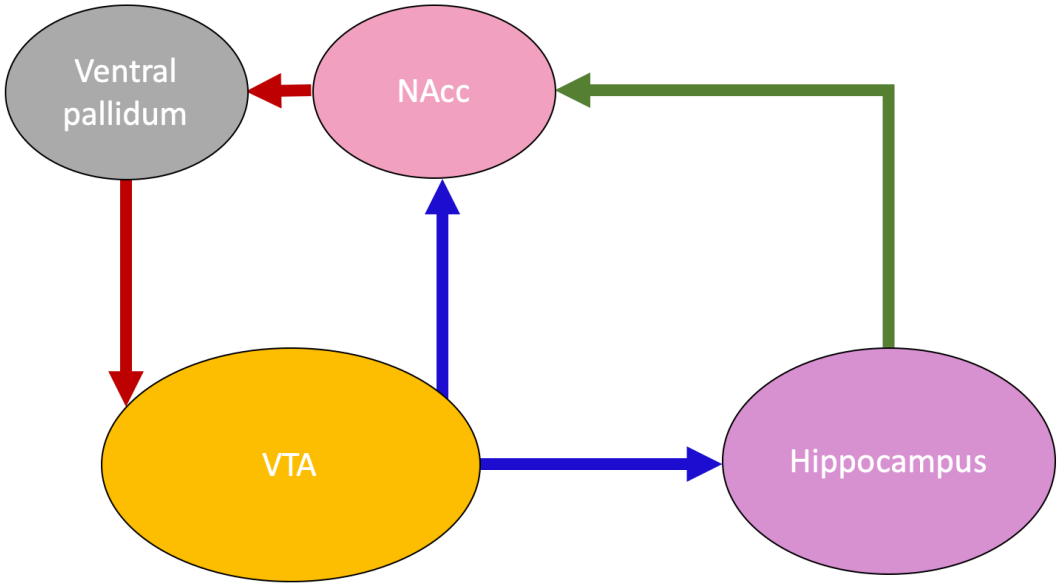


Figure 1.2: Inputs and outputs of the hippocampus, ventral tegmental area (VTA) and nucleus accumbens (NAcc). The VTA provides dopaminergic input (blue arrows) to the hippocampus and NAcc. The hippocampus provides excitatory glutamatergic input (green arrow) to the NAcc. The NAcc projects GABAergic inputs (red arrows) to the ventral pallidum, that in turn reduces GABAergic inhibition to the VTA, subsequently stimulating dopaminergic neurons in the midbrain. (*See Lisman & Grace, 2005; Shohamy & Adcock, 2010; Gruber, Valji, & Ranganath, 2019*).

In order to better understand the relationship between curiosity, reward anticipation and learning, Gruber et al. (2014) examined whether states of curiosity enhanced long-term memory similar to reward anticipation. The authors investigated whether functional activity at the level of the hippocampus, NAcc and SN/VTA would predict memory enhancements for curiosity-related information and incidental information encoded under states of high curiosity. Utilising a modified version of Kang et al's. (2009) fMRI experimental procedure, participants performed a screening phase in which trivia questions were rated on the degree to which they elicited curiosity and how confident participants were in knowing the answer. This phase enabled the researchers to manipulate high and low curiosity levels during the learning phase of the experiment and include only questions that participants did not know the answer to. Throughout the next phase of the experiment, the fMRI scanning phase, questions that elicited high and low curiosity were presented to participants, followed by a fixation period

until the answer was revealed. During this anticipation period, an incidental face was presented in which participants were required to judge whether the person was knowledgeable about the topic. Participants were then given a surprise memory test on the answers to the trivia questions and the incidental faces immediately after the encoding phase (fMRI experiment), and in a separate behavioural follow-up experiment 24-hours post encoding. Consistent with Kang et al's. (2009) study, the immediate and delayed memory tests revealed that participants displayed greater memory for answers to questions that elicited high curiosity. In addition to this, the fMRI findings revealed that when the trivia questions were presented to participants, the SN/VTA and NAcc were found to linearly increase with curiosity ratings. This finding indicates that these regions that were previously found to correlate with reward anticipation (Adcock et al., 2006) also correlate with curiosity. Furthermore, activity observed in the right hippocampus and bilateral NAcc when high- versus low-curiosity questions were presented, successfully predicted later memory benefits for subsequent answers (Gruber et al., 2014). Moreover, the activity evoked by the presentation of the trivia answers in the SN/VTA were found to predict subsequent memory performance, however, this was independent of curiosity. These findings suggest that the anticipatory activity during high states of curiosity facilitated the learning of upcoming answers rather than the activity elicited during answer onset. Gruber et al. (2014) also found that participants' recognition memory for faces was greater when they were encoded in a high- compared to a low-curiosity state. However, due to the large inter-subject variability in this effect, the authors were not able to find question-related activity (i.e. in the high curiosity trials) that predicted the memory advantage for incidental faces. Taking into account these individual variations, Gruber et al. (2014) found a positive correlation between the curiosity-driven memory benefit and activity in both the hippocampus and SN/VTA. This finding indicated that those participants displaying the greatest activation in these regions during these high states of curiosity showed the largest memory advantage for incidental information. This finding also suggests that differences in SN/VTA and hippocampal activity during states of high curiosity might predict inter-individual variability in the memory effect for incidentally presented faces (Gruber et al., 2014). Further investigation is needed into the effects of these individual differences and preferably with a larger sample size.

1.4.2 Paradigms investigating the effects of state curiosity

The findings from Gruber et al. (2014) imply that states of intrinsic motivation (e.g., when our curiosity is piqued) are supported by similar mechanisms employed when a reward is extrinsically motivated, where anticipation for reward that is curiosity-related information facilitates learning. Similar to this idea, Mullaney, Carpenter, Grotenhuis, and Burianek (2014) postulated that brief delays of feedback with unpredictable anticipatory periods for upcoming information would facilitate participants' learning of new information. In this study, participants were presented with trivia questions to which they rated their curiosity in finding out the answer, where importantly the answers to trivia questions were displayed either immediately or after a short delay of 4 seconds. Mullaney et al. (2014) found that answers presented after a delay versus no-delay resulted in an increase in memory performance for high curiosity related answers. This study, as well as the reports by Gruber et al. (2014), imply that the anticipation of information harnesses states of high curiosity that subsequently enhances memory for curiosity-related information.

As well as investigating the effects of curiosity in the learning of interesting information, such as answers to trivia questions, recent studies have employed paradigms that examine the effects of curiosity in the learning of task-irrelevant information, comparable to that of Gruber et al. (2014). For example, Galli et al. (2018) examined whether elderly participants show curiosity-driven memory effects for trivia answers and incidental faces similar to young individuals. In a single trial, participants were presented with a trivia question followed by a face to which they had to judge whether the person depicted in the image knew the answer to the trivia question. Following this judgement, participants rated their curiosity in finding out the answer and were then presented with the correct answer (Galli et al., 2018). In a surprise memory test administered immediately after encoding, the authors found that questions that elicited high curiosity resulted in greater recall of trivia answers and better recognition of faces in both younger and older participants. This study highlights that the positive effect of curiosity on memory for interesting and incidental information that has previously been observed in younger samples also benefit elderly individuals (Galli et al. 2018). However, in a replication attempt, the authors found neither younger nor older participants displayed curiosity-driven face memory benefits (Galli et al. 2018). This suggests that there might be large individual differences underlying the incidental memory effect,

similar to that reported by Gruber et al. (2014). Extending beyond the effect of curiosity on immediate memory, Stare, Gruber, Nadel, Ranganath, and Gómez (2018) investigated whether the curiosity memory effect (i.e., high curiosity states result in better memory retention) is dependent on sleep-related consolidation. Similar to previous studies (Galli et al., 2018; Gruber et al., 2014), participants first rated their curiosity for a subset of trivia questions, viewed the answers to the questions along with faces that were presented prior to answer presentation. They later underwent a recall memory test for the answers to the trivia questions and a recognition memory task for the faces either immediately or after a delay of 12-hours that consisted of either sleep or wake. The authors found that the curiosity memory effect for answers and faces was present in both immediate and delayed tests, where there was no impact of the presence of sleep, suggesting that sleep does not benefit the effect of curiosity on learning.

Other research on the effects of curiosity have focussed on the effects of post answer interest on later memory. For example, Fastrich, Kerr, Castel, and Murayama (2018) investigated how interest in the question (i.e., pre-answer interest) and interest in the answer (i.e., post-answer interest) relates to later memory performance. The authors presented participants with trivia questions, to which participants first guessed the answer to the question, rated their confidence in their guess, and rated their curiosity in finding out the actual answer. After the correct answer was presented, participants provided their post-answer interest. A surprise memory test was administered approximately one week later, in which participants were presented with trivia questions from the initial session and asked to recall the correct answers. It was found that the positive relationship between pre-answer interest (i.e., curiosity) and memory performance was mediated by interest in the trivia answer. They also found that high errors in confidence (instances where participants gave high confidence ratings to the answers they provided, and later realising their answer was in fact incorrect) resulted in an increase in memory that was partially explained by increased post-answer interest (Fastrich et al., 2018). Similarly, McGillivray, Murayama, and Castel (2015) examined the effects of curiosity and post-answer interest on memory in older and younger adults where both samples were asked to read trivia questions, given the opportunity to guess the correct answer, asked to rate their curiosity in learning the answer to the trivia question, and provide a rating on their confidence in knowing the answer. Following these initial ratings for each question, the correct answer was presented immediately after to which participants rated their level of interest in the correct answer and the

likelihood that they would remember the answer. In an immediate memory test, participants were presented with half the trivia questions that were randomly selected from encoding, where participants were asked to recall the answer to each presented question. One-week later participants were tested on the remaining half of the trivia questions. The authors found that curiosity and confidence did not independently predict later memory, however, the effects of post-answer interest on memory in older but not younger adults increased from the short-delay to the long-delay memory test, supporting previous evidence that suggests memory benefits for information related to high levels of curiosity are preserved over a 12-hour delay (cf., Stare et al., 2018; Gruber et al., 2014).

An alternative approach in investigating states of curiosity involves using a more naturalistic task. One such study by Lydon-Staley, Zhou, Blevins, Zurn, and Bassett (2019a) required participants to browse Wikipedia and explore topics that interested them for a duration of 15 minutes per day over 21 days. In this study in comparison to traditional curiosity-trivia paradigms, the authors were able to measure how frequently participants exposed themselves to states of curiosity by quantifying participants qualitative Wikipedia browsing behaviours into tight and loose information seeking networks (i.e., states of curiosity). Here, different browsing behaviours that reflected different knowledge networks such as tight versus loose knowledge networks (browsing/sampling related versus diverse concepts) subsequently related to ‘hunter’ or ‘busybody’ styles of information seeking, respectively. Interestingly, Lydon-Staley et al. (2019a) found that participants scoring high in Deprivation Sensitivity (Kashdan et al., 2018) create tight knowledge networks and display hunter-like behaviours compared to participants scoring low in Deprivation Sensitivity who create loose knowledge networks and display busybody-like behaviours. Other studies investigating epistemic curiosity have employed eye-tracking methods, most of which examine the relationship between eye movements and curiosity (Daffner, Scinto, Weintraub, Guinessey, & Mesulam, 1994; Gottlieb, Oudeyer, Lopes, & Baranes, 2013; Risko, Anderson, Lanthier, & Kingstone, 2012; Voss, Bridge, Cohen, & Walker, 2017). For instance, Baranes et al. (2015) tracked participants’ eye movements while they read trivia questions and subsequently waited for the trivia answers to be presented. It was found that high curiosity trials were associated with participants directing their gaze towards the location of the answer (Baranes et al., 2015). Extending previous research that claim it is the state of being curious that facilitates learning, Wade and Kidd (2019) suggest that merely being on the

verge of knowing induces curiosity. The authors employed a modified version of the traditional curiosity-trivia paradigm where participants were asked to first guess the answers to trivia questions followed by an estimation of how close they thought their guess was to the correct answer, and their curiosity rating in finding out the answer. Wade and Kidd (2019) found that participants who believed their guess was close to the correct answer showed a greater level of curiosity in finding out the answer, and that learning is best predicted by not just curiosity but also prior knowledge. Stare et al. (2018) also found that answers to trivia questions that participants rated as them being highly confident in knowing the answer (i.e., having prior knowledge) were better remembered. However, when examining the extent to which prior knowledge influenced the effects of curiosity, the authors found that the effects of curiosity cannot just be explained by prior knowledge alone (Stare et al., 2018). Instead, it is likely that it is a range of factors that influence curiosity (Wade & Kidd, 2019).

So far, the evidence presented focusses on states of curiosity emerging in its epistemic form. In contrast to examining epistemic curiosity, Jepma, Verdonschot, van Steenbergen, Rombouts, and Nieuwenhuis (2012) used fMRI to investigate the neural mechanisms of the induction of perceptual curiosity and its subsequent relief. In the scanner, participants were presented with trials that consisted of an initial image followed by a second image. Employing combinations of blurred and clear images of objects, Jepma et al. (2012) were able to induce and reduce perceptual curiosity in certain trials. For example, trials that consisted of the presentation of a blurred object followed by a clear picture of the same object was believed to induce and then resolve perceptual curiosity, whilst a trial where a blurred picture of an object is followed by a clear picture of a different object would induce but not resolve perceptual curiosity. Similarly, a trial where a clear picture of an object is followed by a blurred picture of the same object would not induce or subsequently resolve perceptual curiosity, nor would a trial that consisted of a clear picture of an object followed by an identical clear picture. Based on participant self-report ratings, the blurred pictures had indeed elicited high curiosity. Focussing on the neural response elicited during the presentation of the first picture for each trial, the authors identified the anterior cingulate cortex (ACC) and anterior insular cortex to be more active when perceptual uncertainty was elicited (i.e., when the first picture of a trial was blurred compared to clear). To investigate the regions associated with the relief of perceptual curiosity, the authors identified regions of the brain where neural activity was larger in response to when the second image was a clear picture

corresponding to the blurred image initially presented, compared to when the second picture was clear and unrelated to the initially presented blurred image. Here, the hippocampus and striatum, encompassing regions of the NAcc, putamen and caudate, were associated with the reduction of perceptual uncertainty. This evidence suggests that reducing uncertainty/curiosity is rewarding and may subsequently facilitate learning and memory (Jepma et al., 2012).

Furthermore, the activation of the striatum may also reflect reward prediction errors that are associated with resolving perceptual curiosity (Jepma et al., 2012). Schultz (2017) defines a reward prediction error as the difference between the received reward and the reward that was expected to be given, signalled by dopamine neurons in the midbrain. In the context of curiosity, the information-gap theory proposed by Loewenstein (1994) indicates that curiosity is somewhat driven by predictions about the upcoming information's ability to resolve uncertainty. In addition to this idea, as well as studies that demonstrate valuable information results in memory enhancements (e.g. Adcock et al., 2006; Gruber et al., 2014; Kang et al., 2009; Mullaney et al., 2014), Marvin and Shohamy (2016) describe the 'information-as-reward hypothesis' that postulates curiosity follows the basic principles associated with reward motivated behaviour, in which information prediction errors play a role in learning and memory. In their study, participants were presented with a set of trivia questions where each question was followed by its corresponding answer. Participants were then asked to rate how curious they were to find out the answer, followed by a question asking how satisfied they were when they received the answer. Information prediction errors were calculated by taking the difference between the value of the received information (via satisfaction ratings) and the expected value of the information (via curiosity ratings), where Marvin and Shohamy (2016) found that participants were more likely to remember information that resulted in a more positive information prediction error, i.e., instances where satisfaction exceeded curiosity. This evidence is in line with previous research investigating the effects of post-answer interest on later memory (cf., McGillivray et al., 2015; Fastrich et al., 2018), and suggests that perhaps it is not just the state of curiosity one experiences that predicts memory, but also the value of information that is received and/or relief of uncertainty.

1.5 Relationship between state and trait curiosity

Within the research of curiosity, a few studies have investigated the relationship between state and trait curiosity. The former relating to experiencing curiosity in certain situations, whilst the latter relates to the propensity or capacity to experience curiosity (Loewenstein, 1994). Individuals high in trait curiosity will experience states of curiosity more frequently and intensely than individuals low in trait curiosity (Grossnickle, 2016; Kashdan & Roberts, 2004). Grossnickle (2016) also suggests that irrespective of whether a person is high or low in trait curiosity, they will encounter specific situations that facilitate a state of curiosity, where the frequency to which a curiosity state is experienced would vary, contingent on whether a person is high or low in trait curiosity (Kashdan et al., 2004; Naylor, 1981). This in turn would suggest there to be a positive association between state and trait curiosity. In line with this assumption, previous studies that have employed questionnaire measures of state and trait curiosity, such as the 20-Item State-Trait Curiosity Inventory (Spielberger et al., 1979), have found strong positive correlations between these two aspects of curiosity (Kashdan & Roberts, 2004; Reio & Callahan, 2004). In other instances in which state curiosity is measured through behavioural outcomes rather than questionnaires, also indicate that individual differences in trait curiosity are associated with individual differences in behaviours in a number of instances, such as in education and in work-related settings (Hassan et al., 2015; Mussel, 2013b; Kashdan & Yuen, 2007), as well as visual exploratory behaviours (Risko et al., 2012; Baranes et al., 2015). Tracking participants eye movements while they read trivia questions and waited for the trivia answers to be presented, Baranes et al. (2015) found that high curiosity trials were associated with participants directing their gaze towards the location of the answer (Baranes et al., 2015). In addition to this oculomotor effect observed during anticipation as a result of being in a state of curiosity, Baranes et al. (2015) also investigated the relationship between curiosity traits and eye movements. Interestingly, the authors found a negative correlation between eye distance to the answer and the aggregate trait curiosity score (i.e. measured via a Sensation Seeking Scale (Zuckerman, Kolin, Price, & Zoob, 1964), the Curiosity and Exploration Inventory II (Kashdan et al., 2009), and a Novelty Seeking Scale (Pearson, 1970)). This finding suggests that participants displaying higher curiosity traits have a stronger tendency to anticipate upcoming information and shift their gaze to the answer location in high- versus low-states of curiosity (Baranes et al., 2015). Furthermore, Lydon-Staley et al. (2019a) show, using the 5-Dimensional Curiosity scale as a measure of trait

curiosity, that participants scoring high in Deprivation Sensitivity create tight knowledge networks and display hunter-like behaviours compared to participants scoring low in Deprivation Sensitivity who instead create loose knowledge networks (i.e., display busybody-like behaviours). In contrast, participants scoring high in Joyous Exploration create loose knowledge networks, whilst participants scoring low in Joyous Exploration create tight knowledge networks. Given that state and trait curiosity are believed to be positively associated, whether these two dimensions of curiosity employ the same neural mechanisms is currently unknown.

1.6 Magnetic resonance imaging methods

Despite the growing and promising research into the concept of curiosity, the majority of this research has focussed on curiosity as a state and the neural mechanisms that underlies this dimension of curiosity. On the other hand, the neuroanatomical substrates underpinning individual differences in trait levels of curiosity are unknown. Given curiosity itself is a multifaceted construct, and thus may be supported by multiple neural systems, non-invasive imaging methods such as diffusion-weighted imaging (DWI) and resting-state fMRI can be used to investigate personality traits and their neuroanatomical correlates. DWI is an imaging method that enables researchers to examine the microarchitecture of the brain and explore structural connections, whilst resting-state fMRI measures intrinsic activity within the brain at rest (in the absence of an explicit task), exploring functional connectivity between brain regions and functional networks in the brain.

1.6.1 Diffusion-weighted magnetic resonance imaging

DWI is a variant method of Magnetic Resonance Imaging (MRI) that measures the random thermal motion of molecules, known as Brownian motion, within brain tissue (Le Bihan et al., 2001). This method specifically measures the diffusion of water molecules through structures in the brain where typically diffusion is more restricted in grey and white matter, compared to the cerebrospinal fluid (CSF) where there is free movement of water (Huisman, 2010). Further to this, given the influence of certain properties such as microstructural architecture (i.e., axon diameter, myelin thickness,

crossing/bending fibres) of cellular membranes on the diffusion of water within the brain, we can also determine the direction of diffusion (Alexander, Lee, Lazar, & Field, 2007; Groeschel et al., 2016; Huisman, 2010). For example, in white matter tracts the net movement of water molecules is forced to move in a particular direction, primarily along the direction that is parallel to the long axis of the tract and is restricted in the direction that is perpendicular to the tract. This type of diffusion is known as anisotropic diffusion and can be illustrated as an ellipsoid; whilst diffusion in CSF reflects isotropic diffusion and can be illustrated by a sphere, where the degree of diffusion is spread equally in all directions in space (**Figure 1.3**).

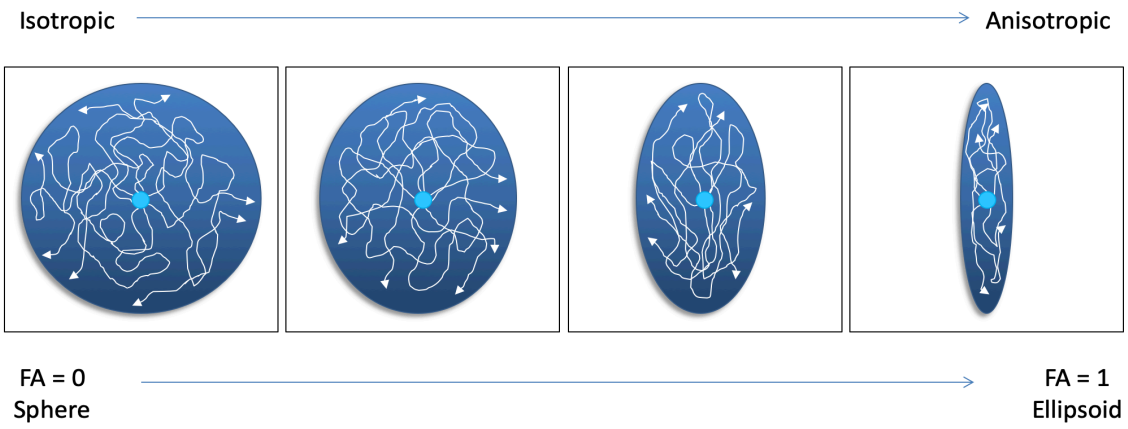


Figure 1.3: A graphical illustration of isotropic to anisotropic diffusion. Complete isotropic diffusion is represented as a perfect sphere with equal diffusion observed in all directions and a fractional anisotropy (FA) value of 0, whilst complete anisotropic diffusion with a FA value of 1 is represented as a narrow ellipsoid with predominant diffusion along the direction parallel to the long axis of the ellipsoid and restricted diffusion in the direction perpendicular to the ellipsoid. Lines and arrows represent the path of the random motion of water molecules. *(Huisman, 2010).*

In neuroscience research, the diffusion of water molecules measured using DWI is often characterised using the diffusion tensor model – also known as diffusion tensor imaging (DTI; Basser, Mattiello, & LeBihan, 1994), that analyses the three-dimensional shape of diffusion in each voxel within the brain (Le Bihan et al., 2001; Mori & Zhang, 2006). In order to obtain this three-dimensional representation, diffusion weighted images are acquired in three mutually perpendicular orientations called eigenvectors. The diffusion along these eigenvectors are quantified mathematically and referred to as

eigenvalues, where λ1 refers to the extent of diffusion along the principle diffusion direction (i.e., longitudinal axis), and λ2 and λ3 refers to the extent of diffusion along the two orientations orthogonal to the principle diffusion direction (i.e., radial axis) (**Figure 1.4**).

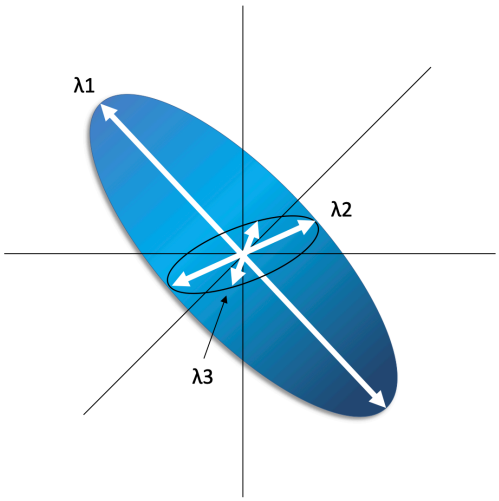


Figure 1.4: Diffusion ellipsoid. Eigenvalue λ1 refers to the extent of diffusion along the principle diffusion direction (i.e., longitudinal axis, eigenvector 1), and eigenvalues λ2 and λ3 refers to the extent of diffusion along the two orientations orthogonal to the principle diffusion direction (i.e., radial axis, eigenvectors 2 and 3).

The use of DWI allows for a variety of metrics that can be calculated. These metrics can be used to characterise the nature of diffusion within a voxel to then infer something about the underlying microstructural properties of white matter (Jones, 2008; Mori & Zhang, 2006). For instance, the anisotropic nature of diffusion of water at a voxel (of a tissue with the brain) is measured by the degree of fractional anisotropy (FA) where a value close to 1 indicates restricted diffusion, greater myelination and axonal coherence, whilst a value close to 0 indicates isotropic diffusion (**Figure 1.3**) (Beaulieu, 2002; Le Bihan, 2003; O'Donnell & Westin, 2011; Soares, Marques, Alves & Sousa, 2013; Seehaus et al., 2015). Another measure used in DWI is mean diffusivity (MD), which is the average of the tensor's eigenvalues ***λ1, λ2*** and ***λ3***. In other words, MD is the mean diffusion along the three axes of the diffusion ellipsoid (i.e., mean diffusion within a given voxel), where typically a greater MD value reflecting

increased diffusion along all directions may be related to reduced conduction velocity along axonal fibres (Hodgetts et al., 2015, 2017; Lewis et al., 2016). Typically, there appears to be an inverse relationship between FA and MD (Vettel, Cooper, Garcia, Yeh, & Verstynen, 2017), where it can be argued that examining one diffusion measure over the other may not be sufficient to characterise tissue change (Alexander et al., 2007). Instead, examining both FA and MD diffusion measures would aid in understanding the underlying microstructural properties of white matter and in what way the diffusion tensor is changing (Alexander et al., 2007).

1.6.1.1 Tractography

To study and visualise white matter in the brain, DTI allows for the three-dimensional reconstruction of such white matter pathways using tractography (Wakana et al., 2007). Tractography refers to the method of estimating the trajectories of fibre pathways that make up white matter tracts in the brain (Basser, Pajevic, Pierpaoli, Duda, & Aldroubi, 2000; Catani, Howard, Pajevic, & Jones, 2002; Jones, Horsfield, & Simmons, 1999; O'Donnell & Westin, 2011), and can be carried out using either deterministic or probabilistic methods. Tractography can be thought of consisting of three steps: seeding, propagation and termination (Soares et al., 2013). The former step typically involves defining regions of interest (ROIs) from which tracking is initiated at the seeds placed within each voxel of the ROI (Soares et al., 2013). Next, during propagation, streamlines are generated using either deterministic or probabilistic algorithms. Deterministic tractography is implemented by taking the principle eigenvector of the diffusion tensor for each imaging voxel and tracking these orientations throughout the brain, essentially tracing a single streamline across multiple voxels to establish whether two different points of the brain can be reached (Jones, 2010). In contrast to generating a single streamline at a given point in space, probabilistic tractography generates multiple streamlines passing through a seed. This latter approach considers a distribution of fibre orientation estimates at each voxel from which to select the next propagation direction (Jones, 2010). As such, probability maps are compiled which represent the likelihood of a voxel being part of a given fibre tract and also provides the multiple possible fibre directions that can be derived from each seed (Soares et al., 2013; Jones, 2010). The final step of tractography consists of termination of the tracking procedure using a well-

defined termination criterion that typically consists of a turning angle threshold and minimum FA threshold (Soares et al., 2013).

One of the limitations of streamline tractography approaches based on the tensor model is that they fail to take into account possible systematic errors when predicting fibre orientation. For example, in instances where there is a structure that consists of fibres that deviate from the uniform orientation (i.e., crossing, bending, splaying, or twisting fibres), the tensor model fails to capture these different fibre orientations as only the principle diffusion direction is accounted for (Jones, 2010), where subsequently the underlying structure of the brain is under-represented. Although probabilistic tractography is better able to account for crossing fibres in comparison to deterministic tracking algorithms (Behrens, Berg, Jbabdi, Rushworth, & Woolrich, 2007), this method of tracking is computationally intensive as it involves a large number of iterations (Hagler et al., 2009). Alternatively, the use of high angular resolution diffusion imaging (HARDI) data and employing methods of spherical deconvolution can help compensate for the problem of crossing fibres. HARDI methods involve acquiring DWI data using more than 6 diffusion-weighted directions and tend to use a higher b-value than the typical 1000, and/or more than one b-value (i.e., multiple shells of data) (O'Donnell & Westin, 2011). The b-value refers to the timing and strength of diffusion-sensitising gradients that are used to create the diffusion-weighted images (Beaulieu, 2002), where higher b-values typically require sampling along a greater number of diffusion-weighted directions (Dell'Acqua & Tournier, 2018). Employing more diffusion directions when acquiring diffusion data means that more orientations are collected and thus a better representation of the diffusion within a voxel is obtained (Le Bihan et al., 2001). Therefore, using HARDI data and subsequently adopting methods such as spherical deconvolution as an approach to model multiple fibre orientations, can improve tractography (Dell'Acqua & Tournier, 2018; Tournier, Calamante, Gadian, & Connelly, 2004; Tournier et al., 2008).

This imaging method has proven to be successful in describing the anatomical connections underlying global personality traits such as Openness to Experience (Privado, Román, Saénz-Urturi, Burgaleta, & Colom, 2017; Xu & Potenza, 2012). However, to our knowledge the neuroanatomical substrates underpinning individual differences in trait levels of curiosity has not been investigated. Fortunately, diffusion-

weighted MRI offers a chance to examine the anatomical connections that might be related to curiosity and its related behaviours.

1.6.2 Resting-state functional magnetic resonance imaging

Similar to diffusion MRI, investigating functional connectivity between brain regions provides new insights into the organisation of the human brain and its role in complex cognitive processes (Van den Heuvel & Pol, 2010). The brain consists of a complex network of functionally interconnected regions (Van den Heuvel & Pol, 2010), to which resting-state fMRI examines the intrinsic activity between such interconnected regions when at rest. In other words, this imaging method determines the level of co-activation or functional connectivity between brain regions in the absence of any cognitive and sensory stimuli (Smitha et al., 2017). Despite the evidence in favour of regional activity in reward-memory related areas (including the VTA, NAcc and hippocampus) when in a state of curiosity (Gruber et al., 2014; Kang et al., 2009), whether this network of regions is related to trait curiosity has not been investigated. Resting-state fMRI provides the necessary platform to investigate how functional connectivity and the continuous integration of information relates to human behaviour, where such organisation in the brain may help detect and explain individual differences observed in curiosity (Van den Heuvel & Pol, 2010; Dubois et al., 2018). This method of neuroimaging is used to measure functional connectivity (i.e., the co-activation between the fMRI BOLD time-series of different brain regions), ultimately indicating the functional communication between anatomically separated areas of the brain (Biswal, Zerrin Yetkin, Haughton & Hyde, 1995; Damoiseaux et al., 2006; Greicius, Krasnow, Reiss, & Menon, 2003; Salvador et al., 2005; Van den Heuvel & Pol, 2010). Resting-state fMRI specifically measures spontaneous low frequency fluctuations (<0.1 Hz) from the BOLD signal fluctuation when the brain is at rest. Given that the BOLD contrast is completely dependent on blood oxygen levels, where we observe a paramagnetic effect of deoxyhaemoglobin and the diamagnetic effect of oxyhaemoglobin, voxels that have a low concentration of deoxyhaemoglobin results in an increase in the BOLD signal whilst a high concentration results in a BOLD signal decrease (Heeger & Ress, 2002; Kim & Uğurbil, 1997; Ogawa, Menon, Kim, & Ugurbil, 1998; Smitha et al., 2017). Typically, in resting-state fMRI experiments participants are asked to relax, clear their minds, and to not think of anything in particular during which spontaneous brain activity is measured.

One of the first studies to show that functional networks at rest were not idle was conducted by Biswall and colleagues. Instead, they found that different regions in the brain showed a high correlation in their fMRI BOLD time-series (Biswal et al., 1995; Biswal, Kylen, & Hyde, 1997). This observed level of co-activation suggests that during rest anatomically separated brain areas show ongoing functional connectivity and information processing (Biswal et al., 1997; Cordes et al., 2000; Greicius et al., 2003; Lowe et al., 2000).

Over the years, resting-state fMRI methods have revealed various networks including the attention network, default mode network and salience network, where a failure in the functioning of such networks can result in the development of neuropsychiatric disorders (cf., Alonazi et al., 2019; Hoekzema et al., 2014; Tomiyama et al., 2019). There are many approaches to analyse resting-state fMRI data, such as independent component analysis (ICA) and ROI/seed-based functional connectivity analysis (Lv et al., 2018). Unlike ICA, a blind source separation approach that probes multiple simultaneous voxel-to-voxel interactions of distinct functional components (or networks) in the brain, ROI/seed-based approaches are more straightforward in that they examine the correlation between a selected *a priori* seed or ROI and all the other voxels in the brain (or second ROI), subsequently yielding a functional connectivity map that describes the functional connections of pre-defined brain regions (Smitha et al., 2017; Van den Heuvel & Pol, 2010). From here, a specific functional connection can be interrogated with regards to whether it relates to behaviour.

This section has attempted to provide a brief summary of two key imaging techniques that allow researchers to examine connectivity within the brain. DWI offers insights into the microstructure of the brain and how different brain regions are structurally connected. In contrast, resting-state fMRI informs us on the level of ‘communication’ or co-activation between brain regions, reflecting functional connectivity. The investigation of individual differences has also received great interest in the literature, given its utility in linking cognition and human behaviour to the brain (Kanai & Rees, 2011). In particular, non-invasive neuroimaging methods including DTI and resting-state fMRI enable researchers to examine inter-individual variability in a range of human behaviours such as perception, attention, intelligence and personality (Dubois & Adolphs, 2016; Forkel, Friedrich, Thiebaut de Schotten & Howells, 2020; Kanai & Rees, 2011). Despite the advantage of these methods as measures of individual

differences, DWI and resting-state methods have been questioned with regards to their value and interpretability (see Jones, 2010; Morcom & Fletcher, 2007). However, DWI and resting-state fMRI overall appear to offer invaluable insights into the brain network and have the potential to investigate how individual differences in structural and/or functional connectivity in the brain relates to certain types of behaviours and characteristics, such as trait and state curiosity.

1.7 Aims of the thesis and overview of the experimental chapters

This thesis consists of four experimental chapters that aim to explore the underlying mechanisms of state and trait curiosity using DWI and resting-state fMRI methods. Chapter 2 and 3 investigate the neural mechanisms underlying trait curiosity. In Chapter 2, two experiments were conducted to examine the neuroanatomical connections underpinning individual variation in trait curiosity. Participants in both sets of experiments completed a short series of questionnaires measuring different dimensions of EC and PC, and underwent a multi-shell DWI sequence in which tractography was employed to extract white matter pathways including the fornix and inferior longitudinal fasciculus. Experiment 2 tested whether the findings from Experiment 1 could be replicated and also utilised the 5-Dimensional Curiosity scale. The results of Experiment 1 are available as a pre-print and submitted for publication (Valji et al., 2019). In Chapter 3, the participants described in Chapter 2 (Experiment 1 and Experiment 2) also underwent a resting-state fMRI scan, where regional based functional connectivity analysis was used to investigate the BOLD functional connectivity between structures that support motivation-based memory including the VTA, NAcc and hippocampus. Subsequently, in two separate experiments, functional connectivity between these structures were correlated with curiosity trait questionnaires to investigate whether individual variability in the functional connectivity between regions involved in the hippocampal-VTA loop may also be associated with individual differences in trait curiosity. In Chapter 4, participants completed a curiosity-trivia paradigm to which the effects of state curiosity and curiosity-related information prediction errors on subsequent memory was tested after a 24-hour delay. The two experiments in this chapter attempt to extend earlier effects of curiosity-based memory for incidental information by providing a more incidental encoding situation. In the second behavioural experiment, participants

also completed a series of curiosity-related questionnaires that were subsequently correlated with memory performance for trivia answers, as a means to examine the theorised positive relationship between state and trait curiosity, where it was hypothesised that participants who score higher in trait curiosity would benefit more from being in a high curiosity state. In Chapter 5, the three-way relationship between structure, functional connectivity and curiosity-related memory was investigated. Here, the participants that completed the curiosity-trivia paradigm in Chapter 4 (Experiment 2), also completed the DWI scan sequence described in Chapter 2 (Experiment 2), and the resting-state fMRI scan sequence described in Chapter 3 (Experiment 2). Using a mediation analysis, the final experimental chapter examined the three-way relationship between fornix white matter microstructure, ROI-to-ROI RSFC and curiosity-related answer memory benefit.

Chapter 2: Neuroanatomical substrates of trait curiosity

2.1 Introduction

In contrast to the nascent experimental field of state curiosity, individual differences in trait curiosity have been investigated over the last decades. Perhaps as one of the most influential ideas, Berlyne (1954) considered curiosity as emerging as a desire for knowledge, known as Epistemic Curiosity (EC), or as an exploratory behaviour resulting in greater perception of the environment, defined as Perceptual Curiosity (PC). These two types of curiosity can be further separated into Specific and Diversive-based Curiosity subsets where the former refers to the desire to reduce uncertainty by searching for the particular information that somebody is lacking, whilst Diversive-based Curiosity refers to the general seeking of novel, complex or surprising information as a means to reduce feelings of boredom and increase arousal (Berlyne, 1960, 1966; Litman & Spielberger, 2003). It was later proposed that curiosity could be evoked by both positive feelings of interest and aversive feelings of deprivation and uncertainty which subsequently led to the development of the EC scale (Litman & Jimerson, 2004; Litman, 2008), where Deprivation- and Interest-type curiosity reflect the concepts of Specific and Diversive Curiosity, respectively (Litman, 2008).

Interestingly, such trait curiosity has been found to be positively associated with learning. For example, Hassan et al. (2015) found EC mediated the relationship between each of the Big Five personality traits, Conscientiousness and Openness to Experience, and learning, whilst Mussel (2013b) demonstrated that curiosity positively correlated with performance in work settings. Similarly, curiosity measures have also been shown to influence learning in educational settings (Grossnickle, 2016; Hidi, 2016). For instance, (Kashdan & Yuen, 2007) examined whether trait curiosity was related to school grades and perceived school quality in a group of high school students, and found that when students believed their academic environment provided novel and challenging experiences to learn from, those students who scored high in trait curiosity outperformed

their peers scoring low in trait curiosity. This evidence indicates that the degree to which these different types of curiosity traits emerge is highly variable between individuals.

Importantly, the neuroanatomical substrates underpinning these individual differences in trait levels of curiosity are unknown. However, some studies using DWI methods describe anatomical connections underlying global personality traits, including Openness to Experience. This trait reflects an individuals' propensity to seek, detect, comprehend and utilise a breadth of original and complex patterns of information – characteristics similar to traits in curiosity (DeYoung, 2014; John et al., 2008; Woo et al., 2014); John & Srivastava, 1999). Early studies have utilised the revised NEO Five Factor Inventory (Costa & McCrae, 1992) when examining the neural correlates of global personality traits. For example, Xu and Potenza (2012) aimed to investigate the relationship between white matter tracts and 5 psychological traits (Extraversion, Agreeableness, Conscientiousness, Neuroticism and Openness to Experience) in a sample of 51 healthy participants. Here, the authors found that Openness to Experience and Agreeableness, but not Neuroticism, negatively correlated with MD of the superior longitudinal fasciculus and corona radiata. Furthermore, Openness was found to negatively correlate with MD of white matter interconnecting regions of the PFC. This evidence suggests that individuals scoring high in Openness show greater white matter integrity (low MD values) in tracts that connect cortical and subcortical regions. Following the findings from Xu and Potenza's (2012) study, Privado et al. (2017) also using the NEO Five Factor Inventory (Costa & McCrae, 1992) examined the relationship between global personality traits and FA of white matter tracts. In their sample of 46 healthy women, Privado et al. (2017) found a significant positive correlation between Openness to Experience and white matter tracts connecting anterior with posterior regions, including the inferior longitudinal fasciculus (ILF), a structure that consists of short and long fibres where the long-distance structures originate at the extrastriate cortex and terminate in the region of the parahippocampal gyrus and amygdala (Catani, Jones, Donato, & Ffytche, 2003). This evidence suggests that long-distance structural fibres are perhaps associated with higher level cognitive processes (Privado et al., 2017) such as searching for information that subsequently guides future behaviours.

Individual differences in other personality traits, such as novelty seeking (i.e., the excitability, impulsivity and exploratory drive thought to be driven by individual differences in the dopamine system) and reward dependence have also been found to relate with specific white matter circuits. For example, Cohen, Schoene-Bake, Elger, and

Weber (2009) had 20 participants undergo a DWI sequence and complete personality questionnaires measuring reward dependence and novelty seeking. Here, novelty seeking was found to positively relate to fiber tracts that connected the amygdala and hippocampus with the ventral striatum, whilst reward dependence positively related to fiber tracts connecting the PFC and striatum (Cohen et al., 2009). One structure known to connect the hippocampus with areas including the mamillary bodies, PFC and the ventral striatum is the fornix (Catani & Thiebaut de Schotten, 2008; Christiansen et al., 2016; Poletti & Creswell, 1977). In particular, the lateral fornix has been found to connect to the anterior hippocampus, which supplies the most numerous inputs to areas involved in reward anticipation, including the NAcc. Whilst the medial fornix has been found to connect to the posterior hippocampus, involved in spatial navigation and detailed memories (Christiansen et al., 2017; Hartley, Maguire, Spiers, & Burgess, 2003; Saunders & Aggleton, 2007). Christiansen et al. (2017) using deterministic tractography on HARDI data in 40 participants, were able to divide the fornix into these lateral and medial segments that have previously been found in rats and non-human primates. Using a novel tractography protocol the authors found that in the human brain, the anterior hippocampal fibers (fornix fibers that connect to the anterior hippocampus) encompassed the lateral body of the fornix, and the posterior hippocampal fibers (fornix fibers that connect to the posterior hippocampus) predominantly encompassed the medial body of the fornix (Christiansen et al., 2017). Notably, it has been suggested that there is no precise anatomical boundary that reflects distinct anterior and posterior hippocampal functions, but that there is an anatomical gradient between anterior and posterior functions (Aggleton, 2012; Strange, Witter, Lein & Moser, 2014). This idea suggests there being a posterior-anterior long axis gradient of representational specialisation from fine detail to gist memory with a graded nature of connectivity (Aggleton, 2012).

With regards to the differences in function of the ILF and fornix, Hodgetts et al. (2017) found that inter-individual variation in ILF microstructure related to semantic autobiographical memories whilst variability in microstructure of the fornix correlated with episodic autobiographical memories. In this study participants completed the modified version of the Galton-Crovitz cue word paradigm (Crovitz & Schiffman, 1974), where for each word presented participants were given 1-minute to produce a detailed and specific autobiographical memory. These accounts were then coded into episodic or external categories where the former described events, time/place, emotion/thought and perceptual details, whilst the latter focussed on semantic details that described general

and self-related knowledge facts and opinions (Hodgetts et al., 2017). These semantic and episodic details that were recalled during cued autobiographical retrieval were subsequently correlated with fractional anisotropy (FA) and mean diffusivity (MD) measures of the ILF and fornix. Here, Hodgetts et al. (2017) found that the number of sematic details recalled negatively correlated with ILF MD and showed a moderate (though non-significant) positive correlation with ILF FA. In contrast the number of episodic details recalled did not significantly correlate with either ILF FA or MD. Instead, the number of episodic details recalled significantly correlated with fornix microstructure (positive correlation with fornix FA and negative correlation with fornix MD). To complete this double dissociation, no significant correlation was observed between the number of semantic details recalled and fornix FA/MD. This evidence suggests that the fornix, the main input/output of the hippocampus, relates to episodic memory; whilst the ILF connecting the occipital lobe with the anterior temporal lobe (ATL), is implicated in semantic memory (Hodgetts et al., 2017; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017).

With regards to the dissociation of different sub-types of curiosity, it is possible that epistemic and perceptual trait curiosity both map onto the fornix, a structure shown to relate to episodic details. In contrast the ILF, shown to relate to semantic details, is perhaps associated with aspects of Epistemic rather than Perceptual Curiosity. Therefore, this experiment examined whether different sub-types of curiosity map onto specific anatomical connections. In this chapter, diffusion-weighted imaging was employed to investigate how specific white matter pathways including the fornix and ILF relate to individual differences in Epistemic Curiosity (i.e., the desire to acquire new knowledge) and Perceptual Curiosity (i.e., curiosity in an environment rich with novel stimuli). Given the evidence that the ILF is a critical part of a network supporting semantic processing and semantic cognition (Jouen et al., 2015; Chen et al., 2017a; Hodgetts et al., 2017; Ripolles et al., 2017; Herbet, Zemmoura, & Duffau, 2018) this chapter examined whether ILF microstructure (FA and MD) would show a significant correlation (positive and negative, respectively) with Interest and Deprivation subscales of EC, compared to Diversive and Specific subscales of PC that are less likely to involve semantic processing and/or cognition. Next, I examined whether significant trait curiosity correlations with bilateral ILF microstructure were driven specifically by the left as opposed to the right ILF, based on evidence that suggests semantic knowledge may show subtle interhemispheric (left>right) gradations for verbal stimuli (Rice, Hoffman, Ralph, & Matthew, 2015; Hoffman & Lambon Ralph, 2018). For instance, if a significant

correlation was observed between ILF microstructure (e.g., ILF MD) and trait curiosity (e.g., Deprivation EC), I then investigated the relationship between this trait measure and microstructure of the left and right ILF (e.g., the negative relationship Deprivation EC and MD of the left and right ILF).

In contrast to the ILF, given that the fornix supports episodic memory, exploratory behaviour and information seeking via hippocampal-striatal connections (Aggleton & Brown, 1999; Goto & Grace, 2008; Hodgetts et al., 2015, 2017; Metzler-Baddeley, Jones, Belaroussi, Aggleton, & O'Sullivan, 2011) this chapter examined the relationship between fornix microstructure and Interest/Deprivation subscales of EC and Diversive/Specific subscales of perceptual trait curiosity. Specifically, I expected trait curiosity measures to show positive correlations with fornix FA and negative correlations with fornix MD. From here, trait measures that showed an association with the whole fornix (e.g., positive correlation between Interest EC and fornix FA), were subsequently correlated with segments of the fornix. Specifically, given evidence of a posterior (fine-grained) to anterior (gist-based) gradient of representational specialisation along the long-axis of the hippocampus (Ranganath & Ritchey, 2012; Poppenk, Evensmoen, Moscovitch, & Nadel 2013; Strange et al., 2014; Murray, Wise & Graham, 2017), it was expected that fornical fibres associated with posterior and anterior hippocampus (Christiansen et al., 2017; Saunders & Aggleton, 2007) would be more strongly associated with subscales that tap into PC and EC, respectively. Fifty-one female participants underwent a two-shell DWI sequence and completed questionnaires measuring subsets of EC and PC (Collins et al., 2004; Litman, 2008). Whole brain deterministic constrained spherical deconvolution (CSD) tractography was performed, where FA and MD for the fornix and ILF were extracted for each participant and correlated with the curiosity self-report measures.

2.2 Experiment 1

2.2.1 Materials and Methods

2.2.1.1 Participants

Fifty-one healthy female adult undergraduate students, with a mean age of 20 years (standard deviation (SD) ± 1, range = 19-24) were recruited from Cardiff University and were scanned at the Cardiff University Brain Research Imaging Centre (CUBRIC). They provided written consent prior to participating in the study, which was approved by the Cardiff University Research Ethics Committee, and received a remuneration of approximately £25 for their participation.

2.2.1.2 Trait curiosity measures

Participants completed the Epistemic Curiosity Scale (EC) (Litman, 2008; Appendix 1) and the Perceptual Curiosity Scale (PC) (Collins et al., 2004; Appendix 2). The EC scale consists of five Interest EC items and five Deprivation EC items with participants answering on a scale ranging from 1 (almost never) to 4 (almost always). The Interest EC items are associated with behaviours that stimulate positive affect and/or involve learning something completely new (e.g. “I enjoy learning about subjects that are unfamiliar to me”). In contrast, Deprivation EC items describe behaviours that reduce negative feelings of information deprivation and uncertainty (e.g. “I can spend hours on a single problem because I just can’t rest without knowing the answer”). The PC scale (Collins et al., 2004) comprised of twelve items (6 Diversive PC items and 6 Specific PC items) and again participants respond on a scale that ranged from 1 (almost never) to 4 (almost always). The Diversive PC items describe exploratory behaviours in which one seeks out new places and a broad range of sensory stimulation (e.g. “I like to discover new places to go”), whereas Specific PC describes exploration of novel, specific and sensorially stimulating stimuli (e.g. “When I hear a strange sound, I usually try to find out what caused it”). Cronbach’s alpha was calculated for each self-report measure using

SPSS (version 23) where Cronbach's alpha coefficients for all curiosity subsets of interest were ≥0.70 and <0.90 suggesting good internal consistency (Tavakol & Dennick, 2011) (Appendix 7). These measures were selected as they enabled us to measure the dimensions of curiosity proposed by Berlyne (1954, 1960, 1966): dimension 1 defining Epistemic and Perceptual Curiosity, and dimension 2 describing Interest/Diversive and Deprivation/Specific Curiosity. Specifically, these questionnaires enabled the measurement of Interest and Deprivation-based EC, and Diversive and Specific-based PC.

2.2.1.3 Imaging acquisition

Imaging data were obtained at CUBRIC, Cardiff University on a 3 Tesla MRI scanner (Siemens Magnetom Prisma) with a 32-channel head coil. T1-weighted structural 3D images were acquired using an MPRAGE sequence (orientation = sagittal; repetition time (TR) = 2250ms; echo time (TE) = 3.06ms; inversion time (TI) = 900ms; flip angle = 9°; field of view (FOV) = 256mm²; slice thickness = 1mm; voxel size = 1mm³; number of slices = 224; bandwidth = 230Hz/pixel; total acquisition time = 7 minutes 36 seconds).

Diffusion weighted images were acquired using a multi-shell sequence (orientation = transversal/axial; TR = 9400ms; TE = 67.0ms; FOV = 256mm²; slice thickness = 2mm; voxel size = 2mm³; number of slices = 80). Diffusion gradients were applied in (i) 30 isotropic directions by using a diffusion-weighted factor b=1200sec/mm², (ii) in 60 isotropic directions by using a diffusion-weighted factor b=2400sec/mm², and (iii) a volume without diffusion gradients (b=0sec/mm²) (bandwidth = 1954Hz/pixel; total acquisition time = 15 minutes 51 seconds).

2.2.1.4 Experimental procedure

Participants changed into MRI scrubs and lay in the MRI scanner where they were asked to keep as still as possible for the duration of the scanning session. During the T1 structural scan and multi-shell diffusion sequence, participants watched an animated DVD to help reduce movement, boredom and nervousness. Other sequences were acquired during the scanning session (e.g., resting-state fMRI and MR spectroscopy),

however are not relevant to the present experiment. After the scanning session participants completed the EC and PC scales followed by a series of other self-report measures and tasks not relevant to this experiment. Finally, participants were debriefed and compensated for their participation in the study.

2.2.1.5 Diffusion MRI pre-processing

T1-weighted structural images were subjected to a 'brain-tissue only' mask using FSL's Brain Extraction Tool (Smith, 2002). Using ExploreDTI (v4.8.3; Leemans, Jeurissen, Sijbers, & Jones, 2009) each b-value image was then co-registered to the T1 structural image. Subsequently, all b-value images were corrected for head motion and eddy currents within ExploreDTI. Tensor fitting was conducted on the b-1200 data given the tensor model assumes hindered (Gaussian) diffusion, and at lower b-values more of the signal is due to hindered rather than restricted diffusion (Jones, Knösche, & Turner, 2013). To correct for voxel-wise partial volume artefacts arising from free water contamination, the two-compartment 'Free Water Elimination' (FWE) procedure was applied to the current b-1200 data – this improves reconstruction of white matter tracts near the ventricles such as the fornix (Pasternak, Sochen, Gur, Intrator, & Assaf, 2009; Pasternak et al., 2014), yielding whole brain voxel-wise free-water corrected FA and MD tissue maps. Following FWE, corrected diffusion tensor-derived structural metrics were computed. FA reflects the extent to which diffusion within biological tissue is anisotropic (constrained along a single axis). MD (10^{-3} mm^2 s^{-1}) reflects overall degree of diffusivity (Vettel et al., 2017). The resulting free water corrected FA and MD maps were inputs for the tractography analysis.

2.2.1.6 Tractography

As higher b-values allow for better fibre orientation estimations (Vettel et al., 2017), tractography was performed on the b-2400 data using the damped Richardson-Lucy spherical deconvolution (dRL-SD) algorithm. Spherical deconvolution provides a direct estimate of the underlying distribution of fibre orientations in the brain and when applied to tractography leads to accurate reconstructions of the major white matter pathway, and an improved ability to describe complex white matter anatomy (Dell'Acqua & Tournier,

2018). The algorithm extracted peaks in the fibre orientation density function (fODF) at the centre of each voxel, where streamlines along the orientation of the fODF peaks were reconstructed using a step size of 0.5mm. Streamline tracts were terminated if the direction of the pathway changed through an angle greater than 45° or if the fODF threshold fell below 0.05. These parameters are the default deterministic dRL streamline tractography parameters optimised for standard tractography used by CUBRIC.

In ExploreDTI, manual tractography was carried out using AND, NOT, and SEED ROI gates on colour-coded FA maps to extract specific white matter tracts. AND gates (**Figure 2.1** - green) were used to extract fibres that passed through the gate, NOT gates (**Figure 2.1** - red) were used to exclude any fibres that passed through the gate, and finally SEED gates (**Figure 2.1** - blue) were used as a starting point to extract fibres that passed through this gate and then to include only those fibres that then passed through any added AND gates. Manual tractography was carried out on a minimum of 15 subjects in order to calculate a tract model to perform automated tractography on all 51 data sets (Explore DTI; Parker et al., 2013). This procedure enables the construction of white matter tracts in space in which streamlines belonging to particular anatomical features of interest consistently project to distinct sub-regions, allowing the reconstruction of streamline data by observing their projected positions (Parker et al., 2013). After running the automated tractography software each tract pathway in each subject was visually inspected, and any erroneous fibres were pruned using additional NOT gates. These tract masks from the b=2400 data were then intersected with the b=1200 free-water corrected FA and MD maps to then derive free-water corrected tract-specific measures of mean MD and mean FA values (i.e., calculated by averaging the individual values at each 0.5mm step along the selected tract) for statistical analysis.

2.2.1.6.1 Inferior longitudinal fasciculus tractography

The ILF (**Figure 2.1B**) was reconstructed using a two-ROI approach in each hemisphere (Wakana et al., 2007). In the mid-saggital slice of the brain, the coronal crosshair was placed posterior to the corpus callosum. In the coronal plane a SEED gate was drawn around the entire cortex of interest. Next in the coronal view, the last slice where the temporal lobe was separate from the frontal lobe was identified and one AND gate was drawn around the temporal lobe. Any stray fibres not consistent with the ILF

pathway were removed with NOT gates. FA and MD of the right and left ILF were averaged to provide a bilateral measure for the main analyses.

2.2.1.6.2 Fornix tractography

The fornix (**Figure 2.1A**) was traced in line with the landmarks described in Catani and Thiebaut de Schotten (2008). In the mid saggital slice of the brain, the coronal crosshair was placed at the anterior commissure and moved approximately 6 voxels posterior in the brain. In the coronal plane, one AND gate was drawn around the fornix bundle where the anterior pillars enter the body of the fornix. Finally, NOT gates were drawn around any protruding areas that were not part of the fornix.

2.2.1.6.3 Anterior and posterior hippocampal fornix tractography

A method adapted from prior work was employed to reconstruct the anterior and posterior hippocampal fornix fibres (Christiansen et al., 2017). Both anterior and posterior hippocampal fornix reconstructions required the AND and NOT gates that were applied during whole fornix tractography. Some NOT gates were augmented to enable better extraction of the anterior and posterior hippocampal streamlines of the fornix. A standard landmark for the anterior-posterior hippocampal boundary was proposed to be a small bundle of grey matter that outlines the most anterior extent of the parahippocampal gyrus that is called the uncal apex (Poppenk et al., 2013). This landmark was identified for each hemisphere separately when carrying out manual tractography of the anterior and posterior hippocampal fornix. In order to perform this, the uncal apex was first localised at its anterior part and traced to its posterior boundary. The first coronal slice, in which the uncal apex was not visible anymore, was used as the landmark in order distinguish between fibres that project into anterior (head of the hippocampus) and posterior hippocampus (body and tail of the hippocampus) (**Figure 2.1C**).

After the left and right hemispheric landmarks were identified, one NOT gate on each hemisphere was drawn around the hippocampus to set boundaries for posterior hippocampal fornix tracts, removing fibres that pass through these NOT gates (**Figure 2.1D**). After the posterior hippocampal fornix was identified, the same coordinates of the

anterior-posterior hippocampal boundary landmark for each hemisphere were used to replace the NOT gates with AND gates for the left and right anterior hippocampal fornix reconstruction (**Figure 2.1E**). The posterior, left, and right anterior hippocampal fornix were saved as separate tracts to aid subsequent automated tractography (**Figure 2.2**). Note that diffusion tensor metrics of the whole fornix and those averaged across anterior and posterior hippocampal fornix segments were highly correlated (FA, $r(49) = 0.940$, $p < 0.001$; MD, $r(49) = 0.942$, $p < 0.001$) indicating that the anterior and posterior hippocampal fornix reconstructions matched the whole fornix reconstructions.

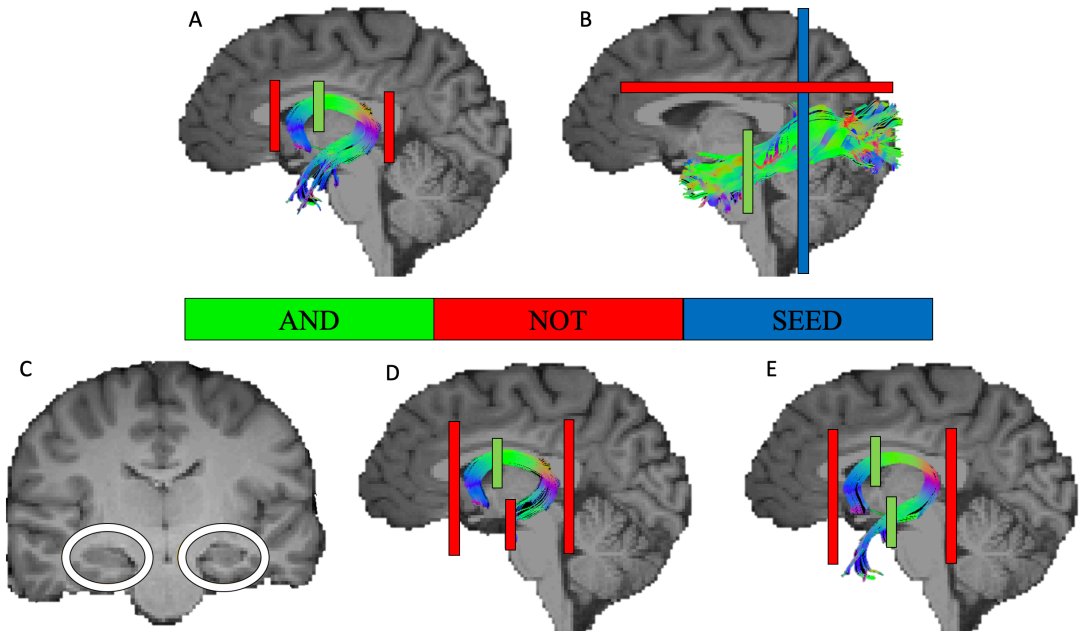


Figure 2.1: Automated tractography reconstructions of the fornix, its anterior and posterior hippocampal fornix fibres and the inferior longitudinal fasciculus (ILF). AND (green), NOT (red), and SEED (blue) ROI gates for each of the tracts are displayed on the sagittal midline plane. **(A)** Fornix tractography using AND and NOT gates. **(B)** Left ILF tractography using SEED, AND and NOT gates. **(C)** Location of AND and NOT gates for tractography of the anterior and posterior hippocampal fornix, respectively. **(D)** Posterior hippocampal fornix tractography using one additional NOT gate placed between the head and the body of the hippocampus to only include fornical fibres that connect with posterior hippocampus (i.e., hippocampal body and tail). **(E)** Anterior hippocampal fornix tractography using one additional AND gate placed between the head and body of the hippocampus (i.e., identical location as NOT gate in **(D)**) to include fibres that pass through this ROI gate to the anterior hippocampus.

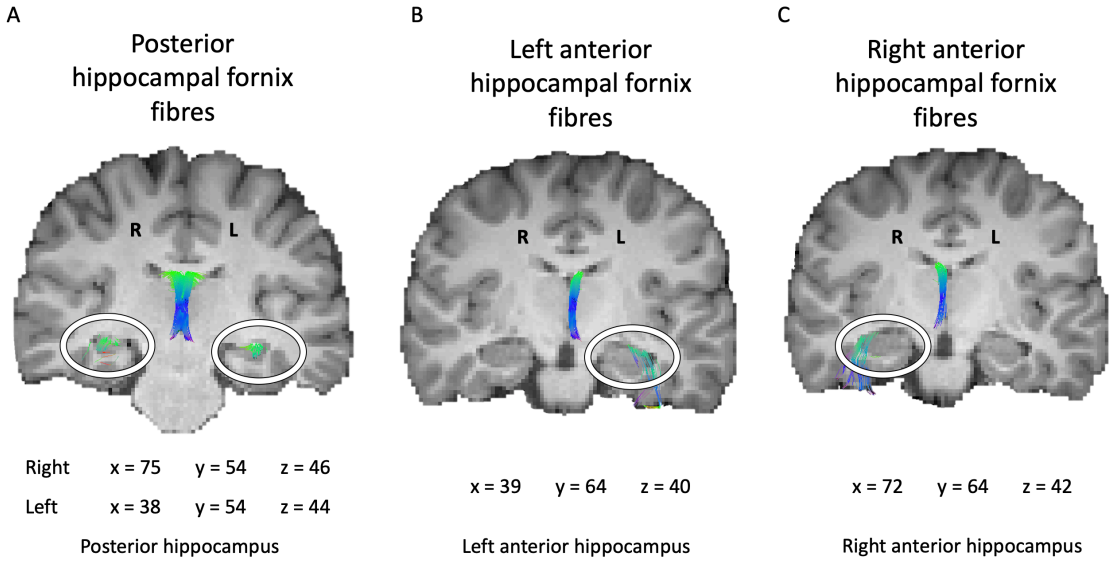


Figure 2.2: Automated tractography reconstructions of anterior and posterior hippocampal fornix fibres on coronal slices. (**A**) Tractography of the fornix fibres projecting to the posterior hippocampus. (**B**) Tractography of fornix fibres projecting to the left anterior hippocampus. (**C**) Tractography of the fornix fibres projecting to the right anterior hippocampus.

2.2.1.7 Statistical analysis

For the questionnaire data, in the event of missing responses (2 participants failed to give a response to one PC item), the mean value of the remaining items that were answered in the full scale was calculated which then replaced the missing item score. For each curiosity subscale (i.e., the two subscales of PC and EC), the total score for each participant was calculated. Participants' data with diffusion tensor metrics +/– 3 SD beyond the group mean were considered as outliers and removed from respective analyses. This resulted in one participant's data being removed from all analyses involving ILF MD and a different participant's data being removed from analyses including bilaterally averaged ILF FA.

To test for associations between curiosity trait scores and microstructure of the selected anatomical tracts, directional Pearson's correlations were conducted using MATLAB. Previous studies utilising white matter MD and FA measures have observed that performance negatively correlates with fornix/ILF MD and positively correlates with

fornix/ILF FA (c.f., Hodgetts et al., 2015, 2017; Postans et al., 2014). Furthermore, since higher FA and lower MD is typically associated with microstructural properties that support efficient information transfer along a white matter tract, and thus portray 'stronger' white matter connectivity (Beaulieu, 2002; Vettel et al., 2017), it was predicted there would be a positive correlation between levels of trait curiosity and FA measures, and a negative correlation with MD.

To determine whether the Pearson's correlation coefficient *r* was statistically significant, non-parametric permutation tests that randomly permute the real data between participants were performed. An advantage of using non-parametric tests was that it makes no assumption about the distribution of the data being examined. First, permutation tests were conducted separately for the two microstructure metrics of the ILF (i.e., FA and MD) and for the EC and PC subscales, so that the correction method used in the present experiment corrected for multiple comparisons across the subscales within a curiosity scale (e.g., Diversive and Specific PC) for a single DTI measure (e.g. ILF FA). Therefore, I ran 4 separate permutation tests when examining the relationship between trait curiosity and ILF microstructure. In the follow-up analyses for Specific Curiosity subscales that correlated with bilateral ILF microstructure, follow-up permutation tests that corrected for multiple comparisons across both hemispheres (e.g., left and right ILF MD) were conducted. In this instance, 2 separate permutation tests were conducted, one with Interest EC (and ILF MD) and the other with Deprivation EC (and ILF MD). For the fornix, similar to the bilateral ILF, I ran 4 separate permutation tests when examining the relationship between trait curiosity and fornix microstructure. Finally, in the follow-up analyses for Specific Curiosity subscales that correlated with whole fornix microstructure, follow-up permutation tests that corrected for multiple comparisons across the three individual fornix segmentations (e.g., left anterior, right anterior, bilateral posterior hippocampal fornix) were conducted. In this instance, 2 separate permutation tests were conducted, one with Interest EC (and fornix FA segmentations) and the other with Specific PC (and fornix MD segmentations).

The steps taken for a single permutation test were as follows: First, Pearson's correlations were performed on the real data (i.e., correlations between the scores of the two curiosity subscales and the microstructure measure (e.g., Diversive PC with ILF MD and Specific PC with ILF MD)). Thereby, the empirical correlation coefficients reflecting the relationship between the two curiosity subscales and a specific microstructure measure were obtained. Second, within each curiosity subscale, I shuffled the curiosity

scores across participants, which resulted in pairs containing a curiosity score and a microstructure value that is randomly assigned across participants. On these shuffled data, I then calculated surrogate Pearson's coefficients for the two curiosity subscale scores and the microstructure metric, and saved the maximum surrogate Pearson's *r* across the two correlations (i.e., subscale-microstructure$_{max}$) (Groppe, Urbach, & Kutas, 2011). Third, the second step was repeated 5000 times. Based on the 5000 permutations, I created a null distribution of all surrogate subscale-microstructure$_{max}$ coefficient values and determined the alpha cut-off point ($p < 0.05$; one-sided; i.e., 4750th data point of the surrogate null distribution) in order to test the statistical significance of the real Pearson's coefficients reflecting the relationship between the two subscales and the microstructure measure. This approach allowed us to correct for multiple comparisons across the two subscales within each curiosity scale. The 95% confidence intervals (CI) for each correlation was derived using a bootstrapping method based on 1000 iterations.

2.2.2 Results

2.2.2.1 Trait curiosity

The mean and standard deviation of each subset of curiosity along with directional Pearson's correlations between subscales of EC and PC is summarised in **Table 2.1**. where a Bonferroni correction by dividing the 0.05 alpha by the number of comparisons (i.e., 0.05/6 = 0.0083) was applied. Significant positive correlations were observed between Interest EC and the other three subscales of curiosity. Specific PC was also found to significantly correlate with Deprivation EC and Diversive PC.

Table 2.1: Mean and standard deviation of each subscale of curiosity, and their respective correlations with other subscales of curiosity.

Self-report measure	Mean (SD)		ECI	ECD	PCD	PCS
ECI	15.18 (2.40)	Pearson's *r*(49)	-	-	-	-
ECD	11.92 (3.52)	Pearson's *r*(49)	**0.607*** **	-	-	-
PCD	18.90 (3.16)	Pearson's *r*(49)	**0.549*** **	0.205	-	-
PCS	15.86 (3.50)	Pearson's *r*(49)	**0.503*** **	**0.371****	**0.586*** **	-

**** p < 0.01, *** p < 0.001, one-tailed Bonferroni corrected**
ECI, *Interest Epistemic Curiosity*; ECD, *Deprivation Epistemic Curiosity*; PCD, *Diversive Perceptual Curiosity*; PCS, *Specific Perceptual Curiosity*; C*orrelations are based on 51 participants.*

2.2.2.2 Epistemic Curiosity – but not Perceptual Curiosity – correlates with ILF microstructure

ILF FA.

A series of permutation tests (one-tailed) that investigated the relationships between trait curiosity scores and microstructure in *a-priori* selected anatomical tracts were conducted. Each permutation test corrected for multiple comparisons for the two subscales separately within the EC and PC scale. The first permutation test targeted ILF FA and EC, where bilaterally averaged ILF FA did not significantly correlate with either subscale of EC (Deprivation EC, $r(48) = 0.143$, $p_{corr} = 0.243$, 95% CI [-0.11, 0.36]; Interest EC, $r(48) = 0.191$, $p_{corr} = 0.151$, 95% CI [-0.07, 0.44]). A further permutation test was conducted on bilaterally averaged ILF FA with the two subscales of PC, where again neither subscale significantly correlated with bilateral ILF FA (Specific PC, $r(48) = 0.109$, $p_{corr} = 0.329$, 95% CI [-0.23, 0.43]; Diversive PC, $r(48) = 0.207$; $p_{corr} = 0.122$, 95% CI [-0.11, 0.45]).

ILF MD.

Targeting ILF MD, a permutation test (one-tailed) revealed a significant negative correlation between ILF MD and Interest EC ($r(48) = -0.289$, $p_{corr} = 0.038$, 95% CI [-0.51, -0.06], **Figure 2.3A**) and a significant negative correlation between ILF MD and Deprivation EC ($r(48) = -0.388$, $p_{corr} = 0.004$, 95% CI [-0.57, -0.12], **Figure 2.3B**). In

contrast, bilateral ILF MD did not significantly correlate with any subscale of PC (Diversive PC, $r(48) = 0.020$, $p_{corr} = 0.710$, 95% CI [-0.26, 0.27], **Figure 2.3C**); Specific PC, $r(48) = -0.134$, $p_{corr} = 0.267$, 95% CI [-0.39, 0.16], **Figure 2.3D**).

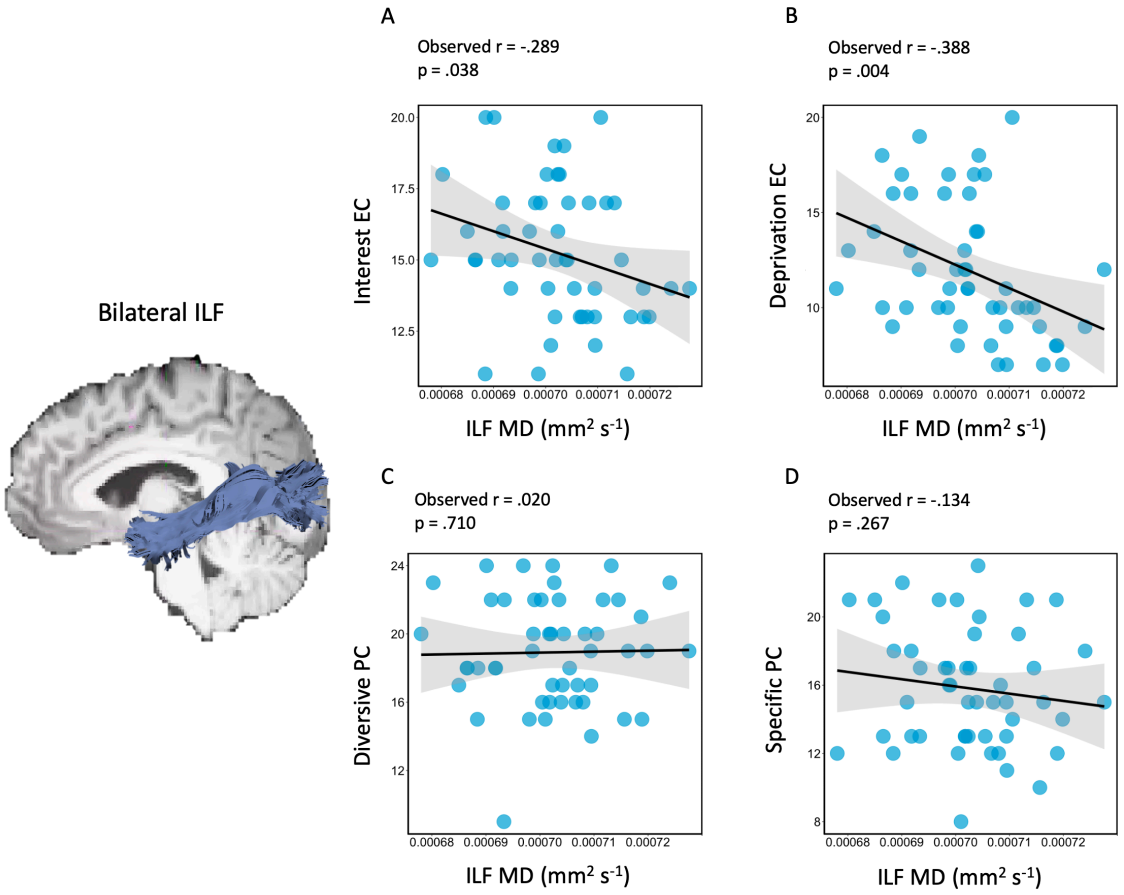


Figure 2.3: Bilateral inferior longitudinal fasciculus (ILF) microstructure only shows relationship with Epistemic Curiosity. These results were obtained from non-parametric permutation tests that corrected for multiple comparisons across the two subscales within the Epistemic Curiosity scale (EC) and Perceptual Curiosity scale (PC). A significant negative correlation was found between MD ($mm^2\ s^{-1}$) of the ILF with Interest- and Deprivation EC (**A**, **B**, respectively). No significant correlations were found between ILF MD ($mm^2\ s^{-1}$) with Diversive and Specific PC (**C**, **D**, respectively). The line of best fit and 95% confidence interval are shown on each scatter plot with 50 data points.

Neuropsychological and imaging evidence suggests that semantic knowledge is represented bilaterally in the ATL but may show subtle inter-hemispheric (left > right) gradations for verbal stimuli (Rice et al., 2015; Hoffman & Lambon Ralph, 2018). Therefore, whether the significant correlation between bilateral ILF MD and both EC subscales were driven specifically by the left as opposed to the right ILF was examined. Separate permutation tests (one-tailed) were conducted for each subscale of EC with left ILF MD and right ILF MD as the two variables of interest (i.e., correcting for multiple comparisons across the two hemispheres). The first permutation test on Deprivation EC found that both left and right ILF MD significantly correlated with Deprivation EC (left ILF: $r(48) = -0.341$, $p_{corr} = 0.016$, 95% CI [-0.57, -0.08]; right ILF: $r(48) = -0.358$, $p_{corr} = 0.012$, 95% CI [-0.56, -0.11]). The second permutation test investigating whether Interest EC correlates with left and right ILF MD indicated a negative relationship for both tracts, but neither reached significance with the adopted multiple comparisons correction (left ILF: $r(48) = -0.254$, $p_{corr} = 0.066$, 95% CI [-0.49, 0.09]); right ILF: $r(48) = -0.267$, $p_{corr} = 0.051$, 95% CI [-0.47, -0.06]).

In order to assess whether bilateral ILF MD correlations with subsets of EC were significantly different from each other as well as the subsets of PC, Olkin's Z-tests (two-tailed; Cocor R package; Diedenhofen & Musch, 2015) were conducted. For EC, the correlation between ILF MD and Deprivation EC was not significantly different to the correlation between ILF MD and Interest EC ($z(50) = -0.849$, $p = 0.396$). Comparing EC and PC subscales, it was found that the correlation between ILF MD and Deprivation EC was not significantly different than the correlation between ILF MD and Specific PC ($z(50) = -1.721$, $p = 0.085$), however it was significantly stronger than the correlation between ILF MD and Diversive PC ($z(50) = -2.212$, $p = 0.027$). Furthermore, the correlation between ILF MD and Interest EC was found to be significantly stronger than the correlation between ILF MD and Diversive PC ($z(50) = -2.407$, $p = 0.016$), however, the correlation between ILF MD and Interest EC was not significantly different than the correlation between ILF MD and Specific PC ($z(50) = -1.172$, $p = 0.241$).

2.2.2.3 Interest Epistemic Curiosity correlates with fornix microstructure

Whole fornix FA.

Regarding fornix FA, permutation tests (one-tailed) revealed a significant positive correlation between Interest EC and fornix FA ($r(49) = 0.281$, $p_{corr} = 0.039$, 95% CI [0.004, 0.51], **Figure 2.4A**). In contrast, Deprivation EC showed no significant correlation with fornix FA ($r(49) = 0.155$, $p_{corr} = 0.214$, 95% CI [-0.12, 0.42], **Figure 2.4B**). A second permutation test (one-tailed) was conducted on fornix FA with the two subscales of PC, Diversive and Specific, but neither subscale significantly correlated with fornix FA (Specific PC, $r(49) = 0.111$, $p_{corr} = 0.328$, 95% CI [-0.27, 0.43]; Diversive PC, $r(49) = 0.064$, $p_{corr} = 0.466$, 95% CI [-0.20, 0.35]).

Whole fornix MD.

Permutation tests (one-tailed) revealed no significant negative correlation between fornix MD and Interest EC ($r(49) = -0.110$, $p_{corr} = 0.332$, 95% CI [-0.37, 0.17]) or Deprivation EC ($r(49) = -0.029$, $p_{corr} = 0.574$, 95% CI [-0.31, 0.30]). The second permutation test (one-tailed), investigating the association between fornix MD and the two subscales of PC, indicated that Diversive PC did not significantly correlate with fornix MD ($r(49) = -0.159$; $p_{corr} = 0.214$, 95% CI [-0.40, 0.11]), whilst Specific PC not quite reaching statistical significance showed a negative correlation with fornix MD ($r(49) = -0.250$, $p_{corr} = 0.070$, 95% CI [-0.50, 0.05]).

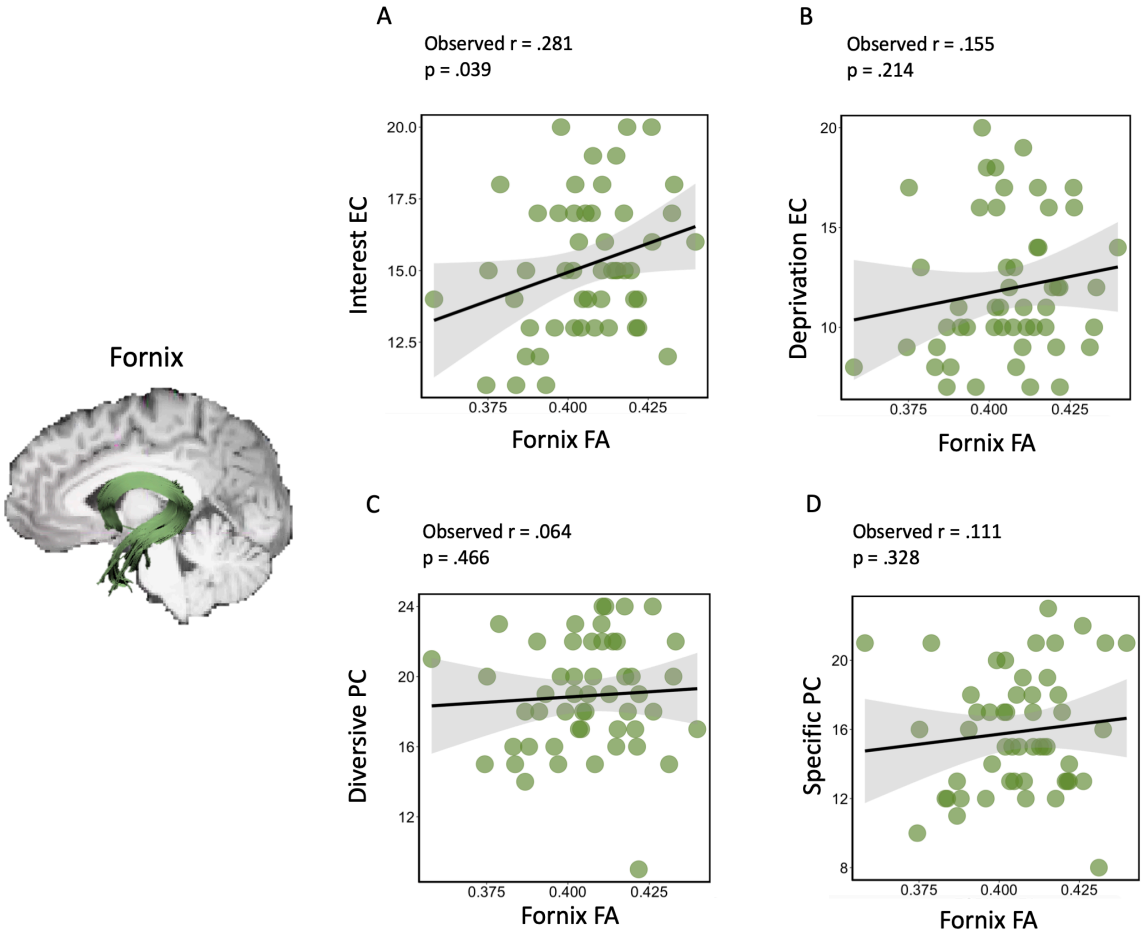


Figure 2.4: Fornix microstructure shows a relationship with aspects of Epistemic Curiosity. These results were obtained from non-parametric permutation tests correcting for multiple comparisons across subscales within the Epistemic Curiosity scale (EC) and across subscales within the Perceptual Curiosity scale (PC). A significant positive correlation was found between fractional anisotropy (FA) of the whole fornix and Interest EC **(A)** but not with Deprivation EC **(B),** nor subscales within the PC scale (**C-D**). The line of best fit and 95% confidence interval are shown on each scatter plot with 51 data points.

2.2.2.4 Specific Perceptual Curiosity shows an association with posterior hippocampal fornix microstructure

Recent accounts postulate a posterior-anterior gradient of representational granularity along the long axis of the hippocampus, linked to a gradient in anatomical

connectivity (Aggleton, 2012; Strange et al., 2014), from 'fine' perceptual detail to gist-like representations, respectively (Poppenk et al., 2013; Robin & Moscovitch, 2017; Sheldon, Fenerci, & Gurguryan, 2019). This account suggests that a stronger correlation might be evident between posterior hippocampal fornix and aspects of PC, and anterior hippocampal fornix and aspects of EC, respectively. To examine this possible dissociation, I chose to correlate the Specific PC subset of the PC scale (i.e., associated with detailed perceptual information seeking) with anterior/posterior hippocampal fornix MD, as this subset compared to Diversive PC approached significance when correlated with fornix microstructure (i.e., fornix MD). Conversely, I chose to correlate the Interest EC subset of the EC scale (i.e., associated with behaviours that stimulate positive affect and/or involve schematic or gist-based representations) with anterior/posterior hippocampal fornix FA, as this subset significantly correlated with fornix microstructure (fornix FA).

A first permutation test (one-tailed; corrected for multiple comparisons) targeted MD of the three individual fornix segmentations (i.e., left anterior, right anterior, bilateral posterior hippocampal fornix). (Note that posterior hippocampal fornical fibres form the medial fornix cannot easily be separated into separate hemispheres). It was found that Specific PC significantly correlated with posterior hippocampal fornix MD ($r(49) = -0.277$, $p_{corr} = 0.047$, 95% CI [-0.55, -0.002], **Figure 2.5B**), but it did not correlate significantly with left or right anterior hippocampal fornix MD (left: $r(49) = -0.189$, $p_{corr} = 0.176$, 95% CI [-0.45, 0.06], **Figure 2.5A**; right: $r(49) = -0.028$, $p_{corr} = 0.610$, 95% CI [-0.29, 0.26], **Figure 2.5C**). This finding suggests that Specific PC might mainly be supported by fornical fibres that have connections to the posterior hippocampus. Olkin's z-tests (two-tailed) were employed to test whether the correlation between Specific PC and posterior hippocampal fornix MD was significantly different than the correlation between Specific PC and left/right anterior hippocampal fornix MD. The correlation between posterior hippocampal fornix MD and Specific PC was not significantly different than the correlation between *left* anterior hippocampal fornix MD and Specific PC ($z(51) = -0.934$, $p = 0.351$), however, it was significantly stronger than the correlation between *right* anterior hippocampal fornix MD and Specific PC ($z(51) = -2.268$, $p = 0.023$).

In contrast, although Interest EC was found to significantly correlate with *whole* fornix FA, the three distinct fornix segmentations did not reveal significant correlations with Interest EC after correcting for multiple comparisons (left anterior hippocampal fornix FA, $r(49) = 0.269$, $p_{corr} = 0.065$, 95% CI [-0.03, 0.52], **Figure 2.5D**; right anterior

hippocampal fornix FA ($r(49) = 0.080$, $p_{corr} = 0.479$, 95% CI [-0.16, 0.31], **Figure 2.5F**; posterior hippocampal fornix FA, $r(49) = 0.272$, $p_{corr} = 0.062$, 95% CI [-0.01, 0.48], **Figure 2.5E**). Olkin's z-test indicated that the correlation between left anterior hippocampal fornix FA and Interest EC was not significantly different than the correlation between posterior hippocampal fornix FA and Interest EC ($z(51) = -0.031$, $p = 0.975$). In addition, Olkin's z-test indicated that the correlation between right anterior hippocampal fornix FA and Interest EC was not significantly different than the correlation between posterior hippocampal fornix FA and Interest EC ($z(51) = -1.443$, $p = 0.149$).

In summary, this experiment found that two individual subscales that tap into Epistemic and Perceptual Curiosity showed significant correlations with fornix microstructure. In particular, the whole fornix FA was found to significantly correlate with Interest EC, whilst Specific PC significantly correlated with posterior hippocampal fornix microstructure, which was significantly stronger compared to the relationship with right anterior hippocampal fornix microstructure. With regards to microstructure of the ILF, both subsets of EC showed a significant negative correlation with MD, where Deprivation but not Interest EC showed significant negative correlations with both left and right ILF MD. **Table 2.2** summarises the correlations conducted in this experiment between curiosity subscales and DTI measures.

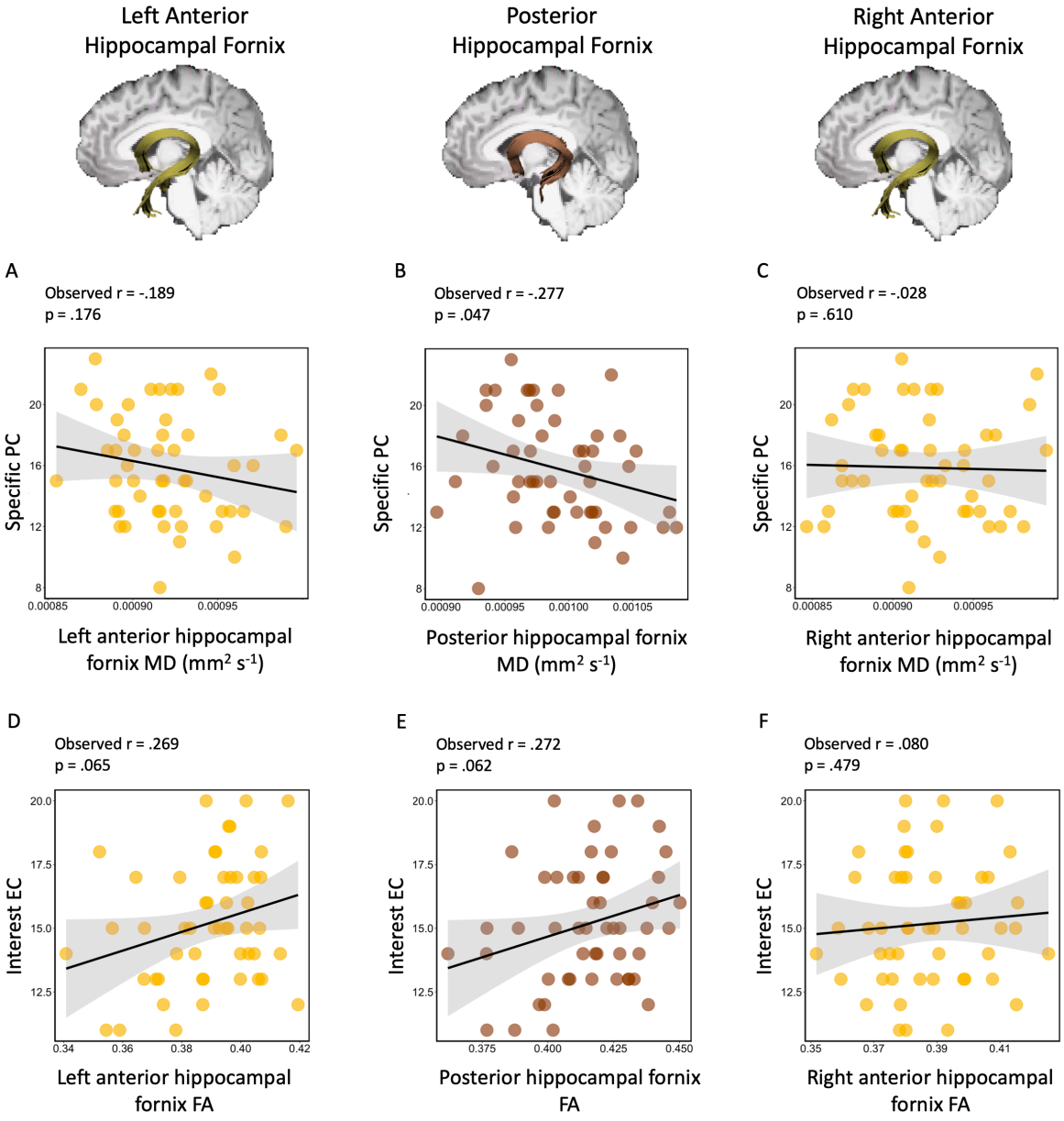


Figure 2.5: Specific Perceptual Curiosity, but not Interest Epistemic Curiosity, shows a significant difference between correlations with anterior and posterior hippocampal fornix microstructure. These results were obtained from non-parametric permutation tests correcting for multiple comparisons across the three individual fornix segmentations. Specific PC did not significantly correlate with MD (mm^2 s^{-1}) of the left anterior hippocampal fornix **(A)** or right anterior hippocampal fornix **(C)** (i.e., fornix fibres that project specifically into anterior hippocampus), but was found to negatively correlate with MD (mm^2 s^{-1}) of the posterior hippocampal fornix **(B)**. Interest EC did not significantly correlate with FA of the left anterior hippocampal fornix **(D)**, nor with FA of the posterior hippocampal fornix **(E)** or FA of the right anterior hippocampal fornix **(F)**. The line of best fit and 95% confidence interval are shown on each scatter plot with 51 data points.

Table 2.2. Summary of directional correlations conducted in the present experiment, between trait curiosity measures and DTI measures.

DTI Measures	Curiosity subscales			
	Interest EC	Deprivation EC	Diversive PC	Specific PC
Bilateral ILF FA				
Pearson's *r*(48)	0.191	0.143	0.207	0.109
p_{corr}	0.151	0.243	0.122	0.329
Bilateral ILF MD				
Pearson's *r*(48)	**-0.289****	**-0.388*****	0.020	-0.134
p_{corr}	**0.038**	**0.004**	0.710	0.267
Left ILF MD				
Pearson's *r*(48)	**-0.254***	**-0.341****	-	-
p_{corr}	**0.066**	**0.016**	-	-
Right ILF MD				
Pearson's *r*(48)	**-0.267***	**-0.358****	-	-
p_{corr}	**0.051**	**0.012**	-	-
Fornix FA				
Pearson's *r*(49)	**0.281****	0.155	0.064	0.111
p_{corr}	**0.039**	0.214	0.466	0.328
Left anterior hippocampal fornix FA				
Pearson's *r*(49)	**0.269***	-	-	-
p_{corr}	**0.065**	-	-	-
Medial hippocampal fornix FA				
Pearson's *r*(49)	**0.272***	-	-	-
p_{corr}	**0.062**	-	-	-
Right anterior hippocampal fornix FA				
Pearson's *r*(49)	0.080	-	-	-
p_{corr}	0.479	-	-	-
Fornix MD				
Pearson's *r*(49)	-0.110	-0.029	-0.159	**-0.250***
p_{corr}	0.332	0.574	0.214	**0.070**
Left anterior hippocampal fornix MD				
Pearson's *r*(49)	-	-	-	-0.189
p_{corr}	-	-	-	0.176
Medial hippocampal fornix MD				
Pearson's *r*(49)	-	-	-	**-0.277****
p_{corr}	-	-	-	**0.047**
Right anterior hippocampal fornix MD				
Pearson's *r*(49)	-	-	-	-0.028
p_{corr}	-	-	-	0.610

***p < 0.1, ** p < 0.05, *** p < 0.005**; EC, *Epistemic Curiosity*; PC, *Perceptual Curiosity*; MD, *mean diffusivity;* FA *fractional anisotropy;* MD *mean diffusivity*

2.3 Experiment 2

Experiment 1 suggested that ILF microstructure (MD) related to both subscales of EC traits, but not with PC traits. Furthermore, fornix microstructure (FA) was found to correlate with Interest EC and the posterior hippocampal fornix microstructure (MD) correlated with Specific PC. Given Psychology's "crisis of confidence", there has been an increase in the attempts to replicate studies. One such study conducted by Boekel et al. (2015) aimed to replicate 5 structural brain-behaviour correlation studies, in which only one correlation was successfully replicated. This study highlights the importance of replication of structure brain-behaviour correlations; thus, Experiment 2 of this chapter examined whether the significant findings from Experiment 1 could be replicated. Based on a priori-power analysis this experiment aimed to collect 64 participants, however this desired sample size was not met, and the final sample consisted of 55 participants. In contrast to Experiment 1, Experiment 2 employed a sample that consisted of male and female participants. Furthermore, the procedure involved the inclusion of reward-based experiments (not discussed in the present thesis), a curiosity-trivia paradigm (discussed in Chapter 4 and 5) and a bank of questionnaires administered after being in a state of curiosity. One limitation of DTI is that its indices (FA and MD) may not always relay the same information. For instance, in Experiment 1 whilst Interest EC showed a positive association with fornix FA, no significant negative association was observed with fornix MD. It is likely that these DTI FA and MD measures are sensitive, but non-specific, to different microstructural properties (Alexander et al., 2011; Winston, 2012). Nonetheless, these measures are still informative with regards to overall microstructural integrity of white matter tracts, where the use of one diffusion measure over the other may not be sufficient to characterise tissue change (Alexander et al., 2007). Therefore, in the present experiment I decided to run identical correlations to Experiment 1, examining the relationship between trait curiosity and both white matter FA and MD, where I expected positive and negative relationships, respectively. To investigate the relationship between microstructure (FA and MD) and EC/PC subscales, permutation tests similar to that in Experiment 1 were employed. Following these permutation tests, a replication Bayes factor analysis (Verhagen & Wagenmakers, 2014; Wagenmakers, Verhagen & Ly, 2016) was conducted to assess the replicability of the structural brain-behaviour correlations initially found in Experiment 1. Finally, in addition to the Epistemic and Perceptual Curiosity scales employed in Experiment 1, Experiment 2 also examined the relationship between white matter microstructure and the 5-Dimensional Curiosity scale (Kashdan et

al., 2018). This scale was included as an additional measure of trait curiosity as it examined other dimensions of curiosity not included in the EC and PC scales. Therefore, this scale allowed me to examine the bandwidth of curiosity rather than solely focussing on the aspects of curiosity proposed by Berlyne (1954, 1960, 1966). The 5-Dimensional Curiosity scale consisted of subscales including Joyous Exploration, Deprivation Sensitivity, Stress Tolerance, Social Curiosity and Thrill Seeking. The latter 3 dimensions are not addressed in the EC and PC scales, whilst Joyous Exploration and Deprivation Sensitivity were thought to reflect dimensions of Interest/Diversive Curiosity and Deprivation/Specific Curiosity, respectively. First, I correlated the 5-Dimensional Curiosity subscales with subscale of EC and PC, where Joyous Exploration was expected to positively correlate with Interest EC and Diversive PC, and Deprivation Sensitivity was expected to positively correlate with Deprivation EC and Specific PC. I then ran permutation tests to investigate the relationship between the 5 subscales of the 5-Dimensional Curiosity scale and microstructure (FA and MD) of the fornix and ILF.

2.3.1 Materials and Methods

2.3.1.1 Participants

Fifty-five healthy adults (47 females) with a mean age of 19 years (SD ± 1.75, range = 18-25) were recruited from Cardiff University and were scanned at the Cardiff University Brain Research Imaging Centre (CUBRIC). Participants signed a written consent form before participating in the study that had been approved by the Cardiff University Ethics Committee. Participants were compensated with either course credits or payment for their participation.

2.3.1.2 Trait curiosity measures

Participants completed a variety of sub-scales from questionnaires that measured types of curiosity and information seeking. Participants completed the Epistemic Curiosity Scale (EC) (Litman, 2008; Appendix 1) and the Perceptual Curiosity Scale (PC) (Collins et al., 2004; Appendix 2), identical to that in Experiment 1. In addition to these

scales, the 5-Dimensional Curiosity scale (Kashdan et al., 2018; Appendix 3) was also administered. This scale consisted of 5 subscales (Joyous Exploration, Deprivation Sensitivity, Stress Tolerance, Social Curiosity, and Thrill Seeking) each comprising of 5 items. The Joyous Exploration items describe curiosity behaviours that are pleasurable (e.g. “I view challenging situations as an opportunity to grow and learn”), whilst Deprivation Sensitivity describe aspects of curiosity that work tension (e.g. “I like to try to solve problems that puzzle me”). The Stress Tolerance items describe a person’s ability for coping with complex, new and uncertain stimuli (e.g. “It is difficult to concentrate when there is a possibility that I will be taken by surprise”), Social Curiosity items describe behaviours that help navigate the interpersonal world (e.g. “I like to learn about the habits of others”). Finally, Thrill Seeking items describe when a person endures dangerous or risky situations to obtain pleasurable experiences (e.g. “I would like to explore a strange city or section of town, even if it means getting lost”). Participants were asked to rate each statement on a scale from 1 (does not describe me at all) to 4 (completely describes me). Items 11-15 (Stress Tolerance items) were reverse scored. Cronbach’s alpha was calculated for each self-report measure using SPSS (version 23) where Cronbach’s alpha coefficients for all curiosity subsets of interest were >0.70 and <0.90 suggesting good internal consistency (Tavakol & Dennick, 2011) (Appendix 8). Similar to Experiment 1, the EC and PC subscales were selected as they enabled us to measure the dimensions of curiosity proposed by Berlyne (1954, 1960, 1966): dimension 1 defining Epistemic and Perceptual Curiosity, and dimension 2 describing Interest/Diversive and Deprivation/Specific Curiosity. Specifically, these questionnaires enabled the measurement of Interest and Deprivation-based EC, and Diversive and Specific-based PC. In contrast, the 5-Dimensional Curiosity scale was added as this scale measured other dimensions of curiosity that the EC and PC scales did not account for (i.e., Stress Tolerance, Social Curiosity and Thrill Seeking). This scale also included items for the Joyous Exploration and Deprivation Sensitivity dimensions of curiosity that had better wording, reading level, and specificity in comparison to other measures used in the literature (c.f., Kashdan et al., 2018).

2.3.1.3 Imaging acquisition

Imaging data were obtained at CUBRIC, Cardiff University on a 3 Tesla MR scanner (Siemens Magnetom Prisma) with a 32-channel head coil. The MRI sequences

and acquisition of MRI data were matched as closely as possible to Experiment 1. T1-weighted 3D images were acquired using an MPRAGE sequence (orientation = sagittal; TR = 2250ms; TE = 3.06ms; TI = 900ms; flip angle = 9°; FOV = 256mm²; slice thickness = 1mm; voxel size = 1mm³; number of slices = 224; bandwidth = 230Hz/pixel; total acquisition time = 7 minutes 36 seconds.

Diffusion weighted images were acquired using a multi-shell sequence (orientation = transversal/axial; TR = 9400ms; TE = 70.0ms[1]; FOV = 256mm²; slice thickness = 2mm; voxel size = 2mm³; number of slices = 80). Diffusion gradients were applied in (i) 30 isotropic directions by using a diffusion-weighted factor b=1200sec/mm², (ii) in 60 isotropic directions by using a diffusion-weighted factor b=2400sec/mm², and (iii) a volume without diffusion gradients (b=0sec/mm²) (bandwidth = 1954Hz/pixel; total acquisition time =15 minutes 51 seconds).

2.3.1.4 Experimental procedure

Participants changed into MRI scrubs and lay in the MRI scanner where they were asked to keep as still as possible for the duration of the scanning session. During the T1 structural scan and multi-shell diffusion sequence, participants watched an animated DVD to help reduce movement, boredom and nervousness. Other sequences were acquired during the scanning session (e.g., resting-state fMRI (Chapter 3) and MR spectroscopy), however are not relevant to the present experiment. Participants returned for a duration of two consecutive days and completed a series of behavioural tasks (e.g., two reward-related memory paradigms (not relevant to the current experiment) and a curiosity-trivia paradigm), followed by a series of self-report measures (some of which are not relevant to the current experiment). The questionnaires were administered back-to-back in a randomised order. The trait curiosity scales of interest to this experiment were completed after the curiosity-trivia paradigm (See Chapter 4, Experiment 2) on day 2. Participants were debriefed and compensated for their participation in the study.

[1] TE is different to the TE employed in Chapter 2, Experiment 1 due to software changes with the Siemens VE11C upgrade.

2.3.1.5 Diffusion MRI pre-processing and tractography

The diffusion MRI pre-processing and tractography of the ILF, fornix, anterior and posterior hippocampal fornix was identical to that in Experiment 1. Note that the diffusion tensor metrics of the whole fornix and those averaged across anterior and posterior hippocampal fornix segments were highly correlated (FA, $r(45) = 0.924$, $p < 0.001$; MD, $r(45) = 0.965$, $p < 0.001$) indicating that the anterior and posterior hippocampal fornix reconstructions matched the whole fornix reconstruction.

2.3.1.6 Statistical analysis

As in Experiment 1, for each curiosity self-report measure the total score for each participant was calculated. Participants' data with trait curiosity scores +/– 3SD beyond the group mean were considered as outliers and removed from respective analyses. This resulted in one participant's data being removed from analyses involving the Joyous Exploration subscale and a different participant being removed from analyses involving the Social Curiosity subscale. Additionally, participants' data with diffusion tensor metrics +/– 3SD beyond the group mean were considered as outliers and removed from respective analyses. This resulted in one participant's data being removed from the analyses involving bilateral ILF MD and left ILF MD. Furthermore, following automated tractography the data from 8 participants were removed from all analyses of interest due to poor white matter reconstructions (<10 reconstructed fibre strands), where for the bilateral ILF and right ILF analyses an additional 2 participants were excluded. A possible reason for poor white matter reconstructions in some participants but not others could be due to differences/problems with how the DTI data was acquired during the MRI sequence, which could have resulted in a poorer signal in areas of interest to be used in extracting white matter tracts.

Identical to the analysis steps employed in Experiment 1, to test for the associations between curiosity trait scores (EC and PC subscales) and microstructure (FA and MD) of the selected anatomical tracts (ILF and fornix), directional Pearson's correlations were conducted using MATLAB, where a positive correlation was predicted between levels of trait curiosity and FA and a negative correlation was predicted with

MD. To determine whether the Pearson's correlation coefficient *r* was statistically significant, non-parametric permutation tests identical to Experiment 1 were performed.

To assess the replication of Experiment 1 with Experiment 2, I employed Bayesian hypothesis testing and computed the replication Bayes factor for subscale-microstructure correlations that reached significance in Experiment 1. The replication Bayes factor compares the null hypothesis to an alternative hypothesis that is specified to the direction of the relationship that was found in the original study *and* its effect size (Verhagen & Wagenmakers, 2014). The replication Bayes factor is defined as follows:

The 1st hypothesis is that of the skeptic and holds that the effect is spurious; this is the null hypothesis that postulates a zero effect size, H_0: $\delta = 0$. The 2nd hypothesis is that of the proponent and holds that the effect is consistent with the one found in the original study, an effect that can be quantified by a posterior distribution. Hence, the 2nd hypothesis—the replication hypothesis—is given by H_r: $\delta \sim$ "posterior distribution from original study." The weighted-likelihood ratio between H0 and Hr quantifies the evidence that the data provide for replication success and failure.
(Verhagen & Wagenmakers, 2014, p.1457).

Therefore, the replication Bayes factor test answers the question "Is the effect from the replication attempt comparable to what was found before, or is it absent?" (Verhagen & Wagenmakers, 2014, p.1458).

The posterior distribution is generated by combining the correlation observed in the present data with the information about a correlation that is available from a previous experiment (i.e., the prior distribution). In a scenario where we have no beliefs and know nothing about the correlation, an uninformative uniform prior distribution is employed, where every correlation between -1 and 1 has equal probability. Next, once a correlation is established, the posterior distribution (of Experiment 1) will have less probability at values further away from the observed correlation and a higher probability around the observed correlation. After observing the data in Experiment 1, the posterior distribution generated represents the beliefs we now have about the correlation of interest. When we want to update this belief with Experiment 2, the posterior distribution from Experiment 1 is taken as the prior for Experiment 2.

To calculate the replication Bayes factor, first the posterior distribution of Experiment 1 was obtained where a uniform prior on the correlation was assumed. Next, the Bayes factor was computed by integrating over this posterior distribution as opposed to a uniform distribution (Boekel et al., 2015; Verhagen & Wagenmakers, 2014). The data for the replication Bayes factor correlation test were imported into R software, where the R code used to calculate the replication Bayes factor was taken from the following link: *http://www.josineverhagen.com/?page_id=76* (Wagenmakers et al., 2016).

The Bayes factor expressed as BF_{01} quantifies on a continuous scale the intensity that the observed data occurred under the null versus the alternative hypothesis ($BF_{0+/-}$). For example, a BF_{01} of 2.5 denotes that the observed data is 2.5 times as likely to occur under the null than under the alternative hypothesis. **Table 2.3** displays the different categories of evidence for BF_{01} (Wetzels & Wagenmakers, 2012, p.1060). In summary, a BF_{01} greater than 1 denotes the data is more likely to occur under the null hypothesis H0 than under the alternative hypothesis H1, whilst a BF_{01} less than 1 denotes the data is more likely to occur under the alternative hypothesis H1 than under the null hypothesis H0. Analogously, a BF_{01} of 0.1 is the same as a BF_{10} of 10 (i.e., $1/BF_{01} = BF_{10}$), where a BF_{10} ($BF_{+/-0}$) value between 10 and 30 affords strong evidence for the alternative hypothesis H1, whilst a BF_{10} value between 1/10 and 1/30 affords strong evidence for the null hypothesis H0 (Jeffreys, 1961; Wetzels & Wagenmakers, 2012).

Table 2.3: Labels of categorisation for Bayes factor BF_0-/BF_0+ evidence for the null hypothesis (Jeffreys, 1961; Wetzels & Wagenmakers, 2012).

Bayes factor BF0(+/-)	Interpretation
>100	Decisive evidence for H0
30 – 100	Very strong evidence for H0
10 – 30	Strong evidence for H0
3 – 10	Substantial evidence for H0
1 – 3	Anecdotal evidence for H0
1	No evidence
1/3 – 1	Anecdotal evidence for H1
1/10 – 1/3	Substantial evidence for H1
1/30 – 1/10	Strong evidence for H1
1/100 – 1/30	Very strong evidence for H1
< 1/100	Decisive evidence for H1

Finally, to test the association between the 5 subscales of the 5-Dimensional Curiosity scale and microstructure (FA and MD) of the fornix and ILF, directional Pearson's correlations were conducted using MATLAB, where a positive correlation was predicted between levels of trait curiosity and FA and a negative correlation was predicted with MD. To determine whether the Pearson's correlation coefficient *r* was statistically significant, non-parametric permutation tests were performed. Permutation tests were conducted separately for the two microstructure metrics of the ILF (i.e., FA and MD) with the 5 subscales of the 5-Dimensional Curiosity scale, so that the permutation test corrected for multiple comparisons across the subscales within the 5-Dimensional Curiosity scale (e.g., Joyous Exploration, Deprivation Sensitivity, Stress Tolerance, Social Curiosity and Thrill Seeking) for a single DTI measure (e.g., ILF FA). The same approach was adopted for the fornix. Therefore, I ran 4 separate permutation tests when examining the relationship between the 5-Dimensional Curiosity subscales and white matter microstructure.

2.3.2 Results

2.3.2.1 Trait curiosity

The mean and standard deviation of each subset of curiosity along with directional Pearson's correlations between subscales of EC and PC is summarised in **Table 2.4**, where a Bonferroni correction by dividing the 0.05 alpha by the number of comparisons (i.e., 0.05/6 = 0.0083) was applied. Significant positive correlations were observed between Interest EC and the other three subscales of curiosity. Specific PC was also found to significantly correlate with and Diversive PC.

Table 2.4: Mean and standard deviation of each subscale of curiosity, and their respective correlations with other subscales of curiosity.

Self-report measure	Mean (SD)		ECI	ECD	PCD	PCS
ECI	13.96 (2.64)	Pearson's *r*(53)	-	-	-	-
ECD	10.24 (2.76)	Pearson's *r*(53)	**0.447*** **	-	-	-
PCD	18.09 (3.37)	Pearson's *r*(53)	**0.506*** **	0.245	-	-
PCS	14.44 (3.71)	Pearson's *r*(53)	**0.376** **	0.280	**0.590*** **	-

**** p < 0.01, *** p < 0.001, one-tailed, Bonferroni corrected**
ECI, *Interest Epistemic Curiosity*; ECD, *Deprivation Epistemic Curiosity*; PCD, *Diversive Perceptual Curiosity*; PCS, *Specific Perceptual Curiosity*. C*orrelations are based on 55 participants.*

2.3.2.2 Epistemic Curiosity shows a relationship towards ILF FA but not ILF MD

Similar to Experiment 1, a series of permutation tests (one-tailed) that investigated the relationships between trait curiosity scores and microstructure in *a-priori* selected anatomical tracts were conducted. Each permutation test corrected for multiple comparisons for the two subscales separately within the EC and PC scale. The first permutation test targeted ILF FA and subscales of EC. This test found that bilaterally

averaged ILF FA showed a positive relationship with both subscales of EC, not quite reaching statistical significance (Interest EC, $r(43) = 0.249$, $p_{corr} = 0.084$, 95% CI [-0.02, 0.50], **Figure 2.6A**; Deprivation EC, $r(43) = 0.280$, $p_{corr} = 0.056$, 95% CI [-0.02, 0.54], **Figure 2.6B**). A further permutation test was conducted on bilaterally averaged ILF FA with the two subscales of PC, where neither subscale significantly correlated with bilateral ILF FA (Diversive PC, $r(43) = 0.020$; $p_{corr} = 0.595$, 95% CI [-0.27, 0.30], **Figure 2.6C**; Specific PC, $r(43) = 0.056$, $p_{corr} = 0.497$, 95% CI [-0.20, 0.31], **Figure 2.6D**).

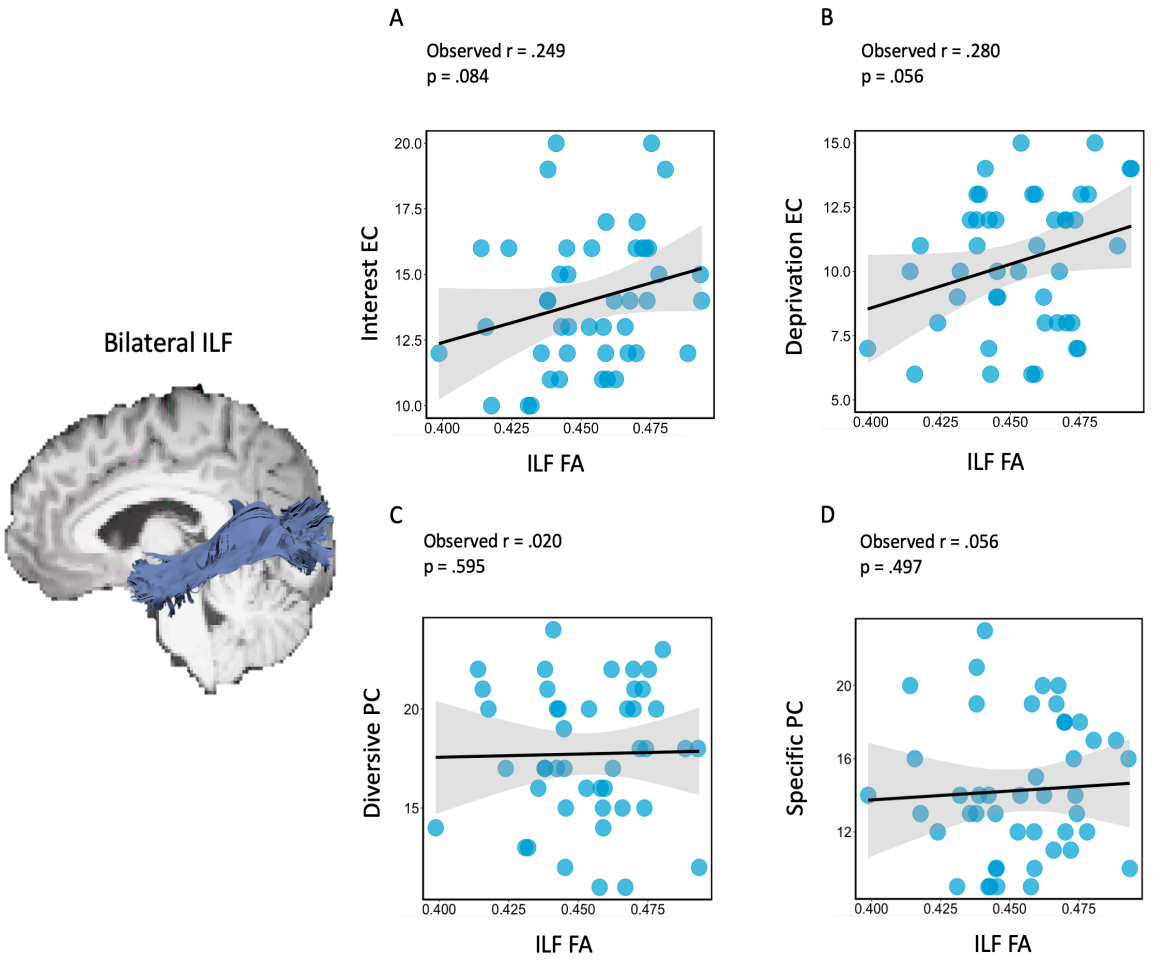


Figure 2.6: Bilateral inferior longitudinal fasciculus (ILF) microstructure shows a positive relationship (though not statistically significant at p<0.05) with aspects of Epistemic Curiosity. These results were obtained from non-parametric permutation tests correcting for multiple comparisons across subscales within the Epistemic Curiosity scale (EC) and across subscales within the Perceptual Curiosity scale (PC). A positive relationship was found between fractional anisotropy (FA) of the bilateral ILF and Interest EC **(A)** and Deprivation EC **(B)**, but not with subscales within the PC scale **(C-D)**. The line of best fit and 95% confidence interval are shown on each scatter plot with 45 data points.

Next, targeting ILF MD, a permutation test (one-tailed) revealed no significant negative correlations between ILF MD and Interest EC ($r(42) = 0.208$, $p_{corr} = 0.980$, 95% CI [-0.10, 0.50]) nor with Deprivation EC ($r(42) = 0.120$, $p_{corr} = 0.914$, 95% CI [-0.24, 0.43]). Furthermore, bilateral ILF MD did not significantly correlate with any subscale of PC (Diversive PC, $r(42) = -0.016$, $p_{corr} = 0.627$, 95% CI [-0.29, 0.25]); Specific PC, $r(42) = 0.115$, $p_{corr} = 0.894$, 95% CI [-0.15, 0.39]). Given no significant relationship was found between bilateral ILF and trait curiosity, this study did not further investigate the left and right lateralisation effects.

2.3.2.3 No significant correlations between trait curiosity and fornix microstructure

Regarding fornix FA, permutation tests (one-tailed) revealed no significant positive correlation between Interest EC and fornix FA ($r(45) = 0.118$, $p_{corr} = 0.343$, 95% CI [-0.19, 0.41]). Similarly, Deprivation EC showed no significant correlation with fornix FA ($r(45) = -0.074$, $p_{corr} = 0.849$, 95% CI [-0.39, 0.24]). A second permutation test (one-tailed) was conducted on fornix FA with the two subscales of PC, but neither subscale significantly correlated with fornix FA (Specific PC, $r(45) = 0.030$, $p_{corr} = 0.575$, 95% CI [-0.25, 0.32]); Diversive PC, $r(45) = -0.080$, $p_{corr} = 0.845$, 95% CI [-0.38, 0.26]).

Permutation tests (one-tailed) revealed no significant negative correlation between fornix MD and Interest EC ($r(45) = -0.114$, $p_{corr} = 0.352$, 95% CI [-0.40, 0.20]) or Deprivation EC ($r(45) = -0.054$, $p_{corr} = 0.521$, 95% CI [-0.31, 0.22]). The second permutation test (one-tailed), investigating the association between fornix MD and the two subscales of PC, also showed that neither Specific nor Diversive PC significantly correlated with fornix MD (Specific PC, $r(45) = 0.091$, $p_{corr} = 0.855$, 95% CI [-0.22, 0.39]); Diversive PC, ($r(45) = -0.066$; $p_{corr} = 0.468$, 95% CI [-0.41, 0.29]).

Given no significant relationships nor any relationships that approached significance were found between fornix microstructure and trait curiosity, segments of the fornix were not expected to correlate with trait curiosity. Separate permutation tests ran for each subset of curiosity when correlated with the three individual fornix FA segmentations revealed no significant positive correlations (ps ≥ 0.276) (Appendix 9).

Similarly, separate permutation tests ran for each subset of curiosity when correlated with the three individual fornix MD segmentations revealed no significant negative correlations (*p*s ≥ 0.254) (Appendix 10).

2.3.2.4 Replication Bayes Factor

Replication Bayes Factor analyses were employed to test whether the 4 significant findings found in Experiment 1 were replicated in Experiment 2. Experiment 1 reported that individual differences in bilateral ILF MD was negatively associated with Interest and Deprivation EC. The replication Bayes Factor analysis (BF_{0r}) with informative priors (Verhagen & Wagenmakers, 2014) indicated that for these effects there is evidence in favour of the null hypothesis compared to the alternative hypothesis (**Table 2.5**).

Table 2.5: Results of one-sided Bayesian hypothesis tests for negative correlations between ILF MD and subsets of EC.

Data pair					Replication	
ROI	n(orig)	n(rep)	*r*(orig)	*r*(rep)	BF0r	Category (H0)
Bilateral ILF MD and ECI	50	44	-0.289	0.208	8.134	Substantial
Bilateral ILF MD and ECD	50	44	-0.388	0.120	18.089	Strong

ECI, *Interest Epistemic Curiosity*; ECD, *Deprivation Epistemic Curiosity*; ILF, *inferior longitudinal fasciculus;* MD, *mean diffusivity*; orig, *original study*; rep, *replication study.*

Experiment 1 reported that individual differences in fornix FA was positively associated with Interest EC. The replication Bayes Factor analysis (BF_{0r}) with informative priors (Verhagen & Wagenmakers, 2014) indicated that for this effect there is evidence in favour of the null hypothesis compared to the alternative hypothesis **(Table 2.6).**

Table 2.6: Results of the one-sided Bayesian hypothesis test for a positive correlation between Interest EC and fornix FA.

Data pair					Replication	
ROI	n(orig)	n(rep)	*r*(orig)	*r*(rep)	BF0r	Category (H0)
Fornix FA and ECI	51	47	0.281	0.118	1.356	Anecdotal

ECI, *Interest Epistemic Curiosity*; FA, *fractional anisotropy*; orig, *original study*; rep, *replication study.*

Experiment 1 reported that individual differences in posterior hippocampal fornix MD was negatively associated with Specific PC. The replication Bayes Factor analysis (BF_{0r}) with informative priors (Verhagen & Wagenmakers, 2014) indicates that for this effect there is evidence in favour of the null hypothesis compared to the alternative hypothesis (**Table 2.7**).

Table 2.7: Results of the one-sided Bayesian hypothesis test for a negative correlation between Specific PC and posterior hippocampal fornix MD.

Data pair					Replication	
ROI	n(orig)	n(rep)	*r*(orig)	*r*(rep)	BF0r	Category (H0)
Posterior hippocampal fornix MD and PCS	51	47	-0.277	0.120	5.962	Substantial

PCS, *Specific Perceptual Curiosity*; MD, *mean diffusivity*; orig, *original study*; rep, *replication study.*

The replication Bayes Factor analysis indicated that Experiment 2 was unable to successfully replicate the 4 correlations found in Experiment 1. The potential reasons for not replicating the findings from Experiment 1 will be discussed.

2.3.2.5 Relationship between subsets of the 5-Dimensional Curiosity scale and white matter microstructure

In addition to the EC and PC scales the relationship between white matter microstructure and Kashdan's 5-Dimensional Curiosity scale was also examined. This scale included subsets that tapped into the bandwidth of curiosity and did not solely focus on the epistemic and perceptual aspects of curiosity. I first explored the relationship between each subset of the 5-Dimensional Curiosity scale with subscales of EC and PC where I expected Joyous Exploration to positively correlate with Interest EC and Diversive PC, whilst Deprivation Sensitivity was expected to positively correlate with Deprivation EC and Specific PC. **Table 2.8** illustrates directional Pearson's correlations between these selected trait curiosity self-report measures. Applying a Bonferroni correction by dividing the 0.05 alpha by the number of comparisons (i.e., 0.05/20 = 0.0025), this analysis indicated that Interest EC positively correlated with Joyous Exploration, whilst Deprivation EC positively correlated with Deprivation Sensitivity. With regards to Perceptual Curiosity, Diversive PC positively correlated with Joyous Exploration, Stress Tolerance and Thrill Seeking. In contrast, Specific PC did not correlate with any subsets of the 5-Dimensional curiosity scale.

Table 2.8: One-tailed Pearson's correlations between each subscale of the 5-Dimensional Curiosity scale and each subset of Epistemic Curiosity and Perceptual Curiosity.

Self-report measure	Mean (SD)		ECI	ECD	PCD	PCS
Joyous Exploration	25.31(4.00)	Pearson's *r*(52)	**0.676*** **	0.299	**0.443*** **	0.179
Deprivation Sensitivity	21.44(5.61)	Pearson's *r*(53)	0.240	**0.665*** **	0.060	0.089
Stress Tolerance	22.25(6.52)	Pearson's *r*(53)	0.318	-0.052	**0.382** **	0.183
Social Curiosity	27.61(4.22)	Pearson's *r*(52)	0.053	0.063	-0.040	0.172
Thrill Seeking	22.62(5.71)	Pearson's *r*(53)	0.354	0.184	**0.596*** **	0.214

**** p < 0.01, *** p < 0.001, one-tailed, Bonferroni corrected.**

ECI, *Interest Epistemic Curiosity*; ECD, *Deprivation Epistemic Curiosity*; PCD, *Diversive Perceptual Curiosity*; PCS, *Specific Perceptual Curiosity; Joyous Exploration and Social Curiosity correlations are based on 54 participants; Deprivation Sensitivity, Stress Tolerance and Thrill Seeking correlations are based on 55 participants.*

A series of permutation tests (one-tailed) that investigated the relationship between the 5-Dimensional Curiosity subsets and microstructure in *a-priori* selected anatomical tracts were conducted. Each permutation test corrected for multiple comparisons for the 5 subsets within the 5-Dimensional Curiosity scale. The 2 permutation tests targeting the ILF FA and ILF MD showed no significant correlations with any of the subsets from the 5-Dimensional Curiosity scale (**Table 2.9**). The permutation test that targeted fornix FA showed a positive relationship with Joyous Exploration that approached significance ($r(43) = 0.312$, $p_{corr} = 0.084$, 95% CI [0.07, 0.54]). The remaining subscales showed no significant correlations with fornix FA (**Table 2.9**). The final permutation test targeting the fornix MD showed no significant correlations with any of the subsets from the 5-Dimensional Curiosity scale (**Table 2.9**).

Table 2.9: Separate non-parametric permutation tests were carried out for each white matter DTI metric correlated with the 5 subsets from the 5-Dimensional Curiosity scale. One-tailed Pearson correlation coefficients, p-values and 95% confidence intervals are reported for each diffusion metric (i.e., FA and MD) for the ILF and fornix when correlated with the 5-Dimensional Curiosity subscales.

Permutation test	5-Dimensional Curiosity subscales				
	Joyous Exploration	Deprivation Sensitivity	Stress Tolerance	Social Curiosity	Thrill Seeking
ILF FA					
Pearson's *r*(41)	0.098	0.213	-0.358	0.203	-0.201
p_{corr}	0.740	0.330	0.999	0.363	0.999
CI [LL, UL]	[-0.24, 0.43]	[-0.13, 0.49]	[-0.62,-0.07]	[-0.08, 0.49]	[-0.49, 0.12]
ILF MD					
Pearson's *r*(40)	0.110	-0.051	0.029	-0.029	-0.038
p_{corr}	0.998	0.861	0.971	0.902	0.886
CI [LL, UL]	[-0.25, 0.38]	[-0.37, 0.26]	[-0.33, 0.34]	[-0.38, 0.34]	[-0.37, 0.27]
Fornix FA					
Pearson's *r*(43)	0.312	-0.060	0.080	0.082	0.015
p_{corr}	**0.084***	0.988	0.778	0.772	0.925
CI [LL, UL]	[0.07, 0.54]	[-0.35, 0.27]	[-0.21, 0.40]	[-0.22, 0.40]	[-0.25, 0.26]
Fornix MD					
Pearson's *r*(43)	-0.230	-0.091	-0.058	0.115	-0.164
p_{corr}	0.254	0.752	0.846	0.998	0.478
CI [LL, UL]	[-0.49, 0.06]	[-0.30, 0.12]	[-0.31, 0.20]	[-0.26, 0.50]	[-0.46, 0.18]

***p < 0.1**; FA, *fractional anisotropy*; MD, *mean diffusivity*; ILF, *inferior longitudinal fasciculus;* CI, *confidence interval*; LL, *lower limit*; UL, *upper limit; Fornix FA and MD correlations are based on 45 participants; ILF FA correlations are based on 43 participants; ILF MD correlations are based on 42 participants.*

2.4 Discussion

Curiosity motivates us to seek out information and it facilitates knowledge acquisition (Loewenstein, 1994; Litman, 2005; Silvia & Kashdan, 2009; Gottlieb & Oudeyer, 2018). While a fledgling line of research has shown that curiosity states - the momentary experience of curiosity - enhance hippocampus-dependent memory (for a review, see Gruber et al., 2019), there is also a broad spectrum of variation in stable tendencies to experience or express curiosity – trait curiosity. Importantly, trait curiosity has been shown to predict real-world outcomes, such as academic achievement and job performance (Kashdan & Yuen, 2007; Mussel, 2013b).

In line with the prediction that ILF microstructure is associated with aspects of epistemic rather than perceptual trait curiosity, Experiment 1 found that bilateral ILF MD negatively correlated with both Interest and Deprivation EC traits, but not with the two subscales of PC. However, no significant positive correlations were observed between bilateral ILF FA and subscales of EC (or PC). With regards to whether the significant correlation between bilateral ILF MD and both EC subscales were driven by the left as opposed to the right ILF, I found that both left and right ILF MD negatively correlated with Deprivation EC. In contrast, Interest EC when correlated with the left and right ILF MD showed negative correlations that did not quite reach statistical significance. Somewhat in line with the prediction that subscales of EC and PC would both map onto fornix microstructure, fornix FA (but not MD) significantly correlated with Interest EC (but not Deprivation EC or the PC subscales) and fornix MD (but not FA) showed a correlation that approached significance with Specific PC (but not Diversive PC or the EC subscales). Consequently, it was found that correlations between Interest EC and FA fornix segmentations that make up the whole fornix (specifically, the left anterior hippocampal fornix and posterior hippocampal fornix) approached significance, whilst Specific PC significantly correlated with MD of only the posterior hippocampal fornix. These findings appear to support the notion that curiosity is a multifaceted motivational construct and that distinct aspects of curiosity map onto specific white matter tracts underlying well-characterised brain networks that support distinct representational systems (Murray et al., 2017). However, in Experiment 2, the two subscales of EC showed positive but non-significant associations with ILF FA, and no significant relationships were observed between fornix microstructure and the EC and PC subscale trait measures. Furthermore, using Bayesian hypothesis tests, evidence was found in

support of the null hypothesis for the 4 significant correlations that were found in Experiment 1. The extent of this support for the null hypothesis ranged from anecdotal to strong (Bayes factor < 3 to Bayes factor > 10). In other words, no evidence was found for the presence of such correlations between microstructure and trait curiosity, and thus were unable to successfully replicate the findings from Experiment 1. Potential reasons for the lack of replication will be discussed below. Finally, exploratory analyses were conducted to examine the relationship between subscales of the 5-Dimensional Curiosity scale and white matter microstructure where Joyous Exploration (found to correlate with Interest EC and Diversive PC) showed a positive relationship with fornix FA that approached significance.

2.4.1 Epistemic Curiosity and ILF microstructure

The ILF, which connects ventral aspects of ATL, occipito-temporal, and occipital cortex (Herbet et al., 2018; Panesar, Yeh, Jacquesson, Hula, & Fernandez-Miranda, 2018), appears critical for bidirectional interactions between an ATL-based bilateral semantic 'hub' and representations supported by occipital and middle/posterior temporal regions (Patterson, Nestor, & Rogers, 2007; Lambon Ralph et al., 2017; Chen et al., 2017b). In addition to demonstrations of altered ILF microstructure in semantic dementia (Agosta et al., 2010), recent studies report associations between bilateral ILF microstructure and individual differences in semantic learning (Ripollés et al., 2017) and memory (Horowitz-Kraus, Wang, Plante, Holland, 2014; Hodgetts et al., 2017). In Experiment 1, it was found that participants with reduced diffusivity (i.e., lower MD values) in the ILF showed higher trait scores in both dimensions of EC. Critically, this experiment found evidence to suggest that the ILF supported both the general exploration of semantic information motivated by positive affect (EC as a feeling-of-interest) but also the search for specific information in order to close a knowledge gap (EC as an aversive feeling-of-deprivation) (Litman, 2005, 2008; Loewenstein, 1994; Lauriola et al., 2015). One explanation for this may be that perhaps the more that we learn, the more we are attuned to the gaps in our conceptual knowledge and attending to these gaps is tension-producing and enjoyable at the same time (Loewenstein, 1994). In addition, the association between EC and ILF microstructure is in line with the literature on the higher-order personality trait Openness to Experience, of which curiosity is a facet (Woo et al., 2014). For example, Privado et al. (2017) demonstrated that ILF

microstructure was associated with levels of trait Openness. The present findings extend this work by pinpointing that the exploration and specific search for semantic information might be one critical factor that carries the association between Openness and ILF microstructure. However, in Experiment 2 the two subscales of EC showed positive, but non-significant associations with ILF microstructure, specifically ILF FA. Additionally, Experiment 2 also employed a replication Bayes factor analysis (Verhagen & Wagenmakers, 2014) that focussed on the relationship between ILF MD and the subsets of EC, evidence from which supported the null hypothesis that stipulated the effect in Experiment 2 was not equal to the effect found in Experiment 1, indicating a failed replication. Possible reasons for the lack of replication are discussed below.

2.4.2 Curiosity and fornix microstructure

Given that the hippocampus has been implicated in a number of processes critical to curiosity, including exploration, reward seeking and novelty detection (O'Keefe & Nadel, 1978; Otmakhova et al., 2013; Murray et al., 2017; Kumaran & Maguire, 2009; Voss et al 2017), Experiment 1 investigated the relationship between curiosity and microstructure of the fornix - the principal tract linking the hippocampus with sites beyond the temporal lobe (Saunders & Aggleton, 2007; Aggleton, Wright, Rosene, & Saunders, 2015). Regarding the relationship between curiosity and fornix microstructure, analyses targeted the microstructure of the whole fornix but also the anterior and posterior hippocampal fornix segments that correspond to the functional subdivisions of the anterior and posterior hippocampus, respectively (Christiansen et al., 2017; Saunders & Aggleton, 2007). Given current theoretical ideas, the anterior and posterior hippocampal fornix fibres may reflect functional subdivisions of the anterior and posterior hippocampus reflecting gist-based (schematic) and perceptually detailed (episodic) information, respectively (Poppenk et al., 2013; Robin & Moscovitch, 2017; Ranganath & Ritchey, 2012; Sheldon et al., 2019). Therefore, the present study investigated whether the functional subdivisions of the fornix, connecting to the anterior and posterior hippocampus, may potentially map onto EC and PC, respectively.

Partially consistent with this hypothesis, Experiment 1 found that posterior hippocampal fornix (but not the anterior hippocampal fornix) microstructure (MD) showed an association with Specific PC, which is described as the desire to reduce uncertainty

by searching for specific novel perceptual information. Of note, recent work has highlighted a role for (posterior) HC circuitry in detailed visual exploration (Liu, Shen, Olsen, & Ryan, 2017; Voss et al., 2017) and Risko et al. (2012) used a scene-viewing task to demonstrate that participants' PC trait score predicted the degree to which they explored visual scenes. These studies using eye-movements to investigate hippocampal-based and curiosity-based visual exploration and the posterior hippocampal fornix findings from Experiment 1, highlight how individual differences in curiosity may play a critical part in the degree of exploration of one's perceptual environment. This could serve to accumulate information from the visual world, contributing to the formation of detailed memory representations mediated by posterior hippocampal circuitry.

In contrast, in Experiment 1 it was found that Interest EC positively correlated with microstructure of the whole fornix, rather than anterior hippocampal fornix specifically. Interest EC is described as the desire for diversive exploration and information seeking which is accompanied by positive affect (Litman, 2008). Although Interest EC reflects the reward-driven explorative search for new knowledge, presumably involving interactions between anterior hippocampal schematic or gist-based representations and reward/value representations mediated by nucleus accumbens and ventromedial PFC (Poppenk et al., 2013; Aggleton et al., 2015), Interest EC also triggers search for detailed information rather than gist-based information, presumably involving more fine-grained posterior hippocampal representations. Interest EC may therefore involve coordination along the entire hippocampal longitudinal axis, in line with the graded and overlapping nature of long axis connectivity (Aggleton, 2012; Strange et al., 2014).

In the replication attempt no significant correlations were found between fornix microstructure and trait curiosity. Furthermore, employing replication Bayes factor analysis (Verhagen & Wagenmakers, 2014) that focussed on the relationship between posterior hippocampal fornix MD and Specific PC, the evidence supported the null hypothesis that stipulated the effect in Experiment 2 was not equal to the effect found in Experiment 1. Additionally, replication Bayes factor analysis (Verhagen & Wagenmakers, 2014) focussing on the relationship between whole fornix FA and Interest EC, indicated there to be anecdotal evidence in support for the null hypothesis that stipulated the effect in Experiment 2 was not equal to the effect found in Experiment 1. Experiment 2 also investigated the relationship between white matter microstructure and

subscales of the 5-Dimensional Curiosity scale where it was found that Joyous Exploration positively correlated with Interest EC, and also showed a positive association with fornix FA that approached significance. The present replication attempt suggests that perhaps fornix FA may be the most 'robust' tract measure across the two experiments as 'only' anecdotal evidence was found for not replicating the Interest EC-fornix FA relationship in Experiment 1, and Joyous Exploration that positively correlated with Interest EC was the only subset of the 5-Dimensional Curiosity scale that showed a positive (though not statistically significant) relationship with fornix white matter microstructure.

2.4.3 Possible explanations for the lack of replication

A lack of replication raises the question as to whether the results from Experiment 1 are in fact false positives and Experiment 2 instead correctly reveals there is no true effect or relationship (Maxwell, Lau, & Howard, 2015). Based on Experiment 2, that was unable to replicate the findings from Experiment 1, one might thus conclude that the correlations between trait curiosity and white matter connectivity of the fornix and ILF tested in this chapter simply may not exist. However, Boekel et al. (2015) attempted to replicate 5 structural brain-behaviour correlation studies, in which only one correlation was successfully replicated, and advise that a single attempt at replication cannot be conclusive in confirming or refuting of a finding. Furthermore, Maxwell et al. (2015) argues that a failure to replicate may not necessarily be a failure but rather the replication study having low statistical power.

Although the replication attempt was kept as close as possible to Experiment 1, there were a few procedural differences which may explain why a successful replication did not occur. First, the final sample size of Experiment 2 had fewer participants than Experiment 1, though this is not considerably less, it is encouraged that replication attempts use larger sample sizes as a means to further decrease the uncertainty held for the replicability of these effects/relationships (Boekel et al., 2015; Masouleh, Eickhoff, Hoffstaedter, Genon, & Alzheimer's Disease Neuroimaging Initiative, 2019). Another possible reason that may account for the failure to replicate could be explained through additional systematic differences between Experiment 1 and 2 other than sample size. For instance, Experiment 1 included only female participants for reasons not specific to

curiosity but due to the aims of another experiment involving genotyping, whilst Experiment 2 included both male and female participants. In the present chapter, when conducting correlations between curiosity self-report measures and white matter DTI metrics for only the female participants of Experiment 2, it appears that the correlation between fornix FA and Interest EC increased from $r(45) = 0.118$, $p = 0.215$ (uncorrected; male and female participants) to $r(38) = 0.186$, $p = 0.125$ (uncorrected; female participants only). Similarly, fornix MD when correlated with Interest EC decreased from $r(45) = -0.114$, $p = 0.223$ (uncorrected; male and female participants) to $r(38) = -0.219$, $p = 0.087$ (uncorrected; female participants only) where FA and MD measures for all fornix segments also indicated more positive and more negative associations, respectively, with Interest EC than when males are also included in the sample (Appendix 4A). Furthermore, the correlation between fornix FA and Specific PC increased from $r(45) = 0.030$, $p = 0.421$ (uncorrected; male and female participants) to $r(38) = 0.162$, $p = 0.159$ (uncorrected; female participants only), where the correlation between Specific PC and posterior hippocampal fornix FA also increased from $r(45) = 0.065$, $p = 0.332$ (uncorrected; male and female participants) to $r(38) = 0.180$, $p = 0.133$ (uncorrected; female participants only). Although these correlations are not significantly different from each other, they indicate an increase in the hypothesised direction, similar to the findings from Experiment 1. It is possible that gender may play a role in the relationship between trait curiosity and white matter microstructure. For instance, one study that examined gender differences in the Big Five found that whilst no gender differences were observed on the global level of the Big Five, women appeared to score higher than men in the Openness aspect of the Openness trait, whilst men scored higher than women in the intellect aspect of the Openness trait (Weisberg, DeYoung, & Hirsh, 2011). Furthermore, other research suggests there being gender differences in white matter structures, including the ILF and the fornix, where some differences in tract microstructure offer an explanation as to why gender differences are observed in certain types of tasks (Kanaan et al., 2014). As a result, further investigation is warranted into whether gender differences in trait curiosity exist and whether this difference can perhaps explain individual differences in white matter connectivity, or vice versa.

Another likely reason for a failed replication could be due to differences across the two experiments in when the curiosity measures were administered. In Experiment 1, after the scanning session participants first completed the EC and PC curiosity scales followed by other self-report measures and behavioural tasks. These behavioural tasks

held no curiosity/reward/salience component and the other questionnaires administered were not related to curiosity, whilst in Experiment 2 participants first completed the curiosity-trivia paradigm (See Chapter 4, Experiment 2) and reward/salience based behavioural tasks followed by the series of self-report measures. Given recent evidence showing trait curiosity levels fluctuate across time even within-individuals (Lydon-Staley et al., 2019a; Lydon-Staley, Zurn & Bassett, 2019b), it is possible that trait measures of curiosity administered after a behavioural task, especially one that elicits different levels of curiosity, could result in dissimilar self-reports to when administering curiosity trait measures prior to reward/salience based behavioural tasks such as in Experiment 1. As such, it was found that trait scores were significantly lower in Experiment 2 than in Experiment 1 for all subsets of curiosity except Diversive PC (Appendix 4B). Therefore, it is possible that the state a person is in could influence the self-report ratings they subsequently make (Lydon-Staley et al., 2019a). It is also considered that perhaps the large number of questionnaires that were administered in Experiment 2 compared to Experiment 1 may have caused participants to become fatigued resulting in less reliable curiosity trait scores. In particular, in Experiment 1 the EC and PC scales were administered separately to other questionnaires not relevant to the thesis, whilst in Experiment 2 these scales were part of a bank of questionnaires that were administered back-to-back in a randomised order. It is possible that in Experiment 2 where a larger number of questionnaires were administered back-to-back may have resulted in respondent fatigue in which participants become tired and provide perfunctory responses (Ben-Nun, 2008; Porter, Whitcomb & Weitzer, 2004). Given the number of differences between the two experiments in this chapter, a future experiment that aims to examine whether the findings from Experiment 1 withstand, should consider the effects of fatigue and impact of exposure to salient states when administering trait questionnaires as possible factors that could influence participants' self-reports. For example, first administering EC and PC subscales separately to other questionnaire measures and also before or without a cognitive task may result in similar findings to Experiment 1.

2.4.4 Limitations and future directions

First, correlational analyses cannot establish causality in brain-behaviour relationships. Longitudinal studies would be needed to determine whether trait curiosity shapes white matter connections, vice versa, or whether both reinforce each other in a

bidirectional manner. For instance, recent work on adaptive myelination suggests that change in myelination through activity-dependent adaptation of an initially hard-wired process occurs in response to experiences and contributes to learning (Bechler, Swire, & ffrench-Constant, 2018). Second, interpreting the biological relevance of tensor metrics from white matter tracts, such as the scalar measures that are FA and MD, can be challenging. Whilst FA and MD are typically inversely related, where a high FA and low MD suggest 'stronger' white matter connectivity (Vettel et al., 2017), Experiment 1 found that for the majority of microstructure-curiosity correlations that only one of the two diffusion metrics significantly correlated with curiosity. Dissociations between FA and MD measures could be due to a number of biological properties such as axon diameter and density, myelination and the arrangement of fibres in a given voxel (Beaulieu, 2002). For instance, high FA has been found to reflect high myelin density and structured histological orientation whereas high values of MD are more likely to reflect low myelin density and diffuse histological orientation (Seehaus et al., 2015). However, in the replication experiment MD subscale-microstructure relationships exhibited positive relationships – refuting the predictions and findings from Experiment 1 of a negative relationship between MD and behaviour. Given such inconsistencies in the diffusion metrics of connectivity, future work on the microstructural correlates of trait curiosity could employ more sensitive measures of white matter change such as the hindrance modulated orientational anisotropy (HMOA) index (Dell'Acqua, Simmons, Williams, & Catani, 2013), or apply advanced modelling techniques, such as the "Neurite Orientation Dispersion and Density Imaging" model (NODDI (Zhang, Schneider, Wheeler-Kingshott, & Alexander, 2012)) for estimating biologically specific properties of the white matter.

2.5 Chapter Summary

The aim of this chapter was to investigate the relationship between white matter structural connectivity and self-report measures of trait curiosity. Specifically, this research examined the relationship between EC and PC traits with fornix and ILF microstructure. Experiment 1 found inter-individual variation in the microstructure of the fornix related to Interest EC, and inter-individual variation in the microstructure of the ILF related to both interest and Deprivation EC. Furthermore, posterior hippocampal fornix microstructure was associated with Specific PC. In Experiment 2, the aim was to replicate the findings from Experiment 1, however this study was unsuccessful in these

attempts perhaps due to reasons such as differences in the sample recruited and when/how the questionnaire measures were administered. In conclusion, the present findings on the relationship between curiosity traits and anatomical connections underlying well characterised brain networks are unclear, however, they do provide a foundation for future studies to further examine the relationship between curiosity traits and neuroanatomical substrates.

Chapter 3: Resting-state functional connectivity within the hippocampal-VTA loop underlying trait curiosity

3.1 Introduction

State and trait curiosity are believed to be positively related, whereby those high in trait curiosity experience states of curiosity – engaging in information seeking and exploratory behaviours – more frequently and intensely than those low in trait curiosity (Grossnickle, 2016; Litman, 2005; Litman et al., 2005; Kashdan & Steger, 2007). For example, inter-individual differences observed in trait curiosity have been found to affect curiosity-based behaviours (Lydon-Staley et al., 2019a). Although there is a growing body of evidence investigating the neural mechanisms of state curiosity (Gruber et al., 2014; Kang et al., 2009; Jepma et al., 2012), to our knowledge there is little or no evidence on the functional neural mechanisms underlying trait curiosity. Studies that have investigated motivation-based behaviours have found that such behaviours rely on the hippocampus and structures involved in reward processing and motivation – the VTA and NAcc. These structures have been found to show high intrinsic connectivity, forming a functional loop that subsequently regulates learning (Kahn & Shohamy, 2013; Lisman & Grace, 2005; Shohamy & Adcock, 2010). Anatomical evidence indicate that dopamine neurons located in the VTA directly project to both the hippocampus and the NAcc. In turn the hippocampus and NAcc indirectly project back to the VTA closing the anatomical loop. Furthermore, the hippocampus also has strong anatomical connections to the NAcc (Groenwegen, Vermeulen-Van Der Zee, Kortschot, & Wittex, 1987; Lisman, Grace, & Duzel, 2011). Importantly, motivation-based behaviours that rely on this hippocampal-VTA loop have shown to vary considerably across individuals (e.g. Adcock et al., 2006; Gruber et al., 2014). For example, Kahn and Shohamy (2013) demonstrate inter-individual variability in functional connectivity between the regions in this network, which offer an explanation to the individual differences observed in studies where curiosity-related neural activity and its associated memory benefits have been found to greatly

vary between individuals (cf., Gruber et al., 2014). Consistent with the findings on states of curiosity, it has been suggested that trait curiosity is also positively associated with learning (Grossnickle, 2016; Hassan et al., 2015; Hidi, 2016; Kashdan & Yuen, 2007; Mussel, 2013a, 2013b). Therefore, similar to states of curiosity in which neuroimaging evidence suggests that state curiosity affects hippocampus-dependent learning via increased activation in the mesolimbic circuit (Gruber et al., 2014; Kang et al., 2009; Chiew & Adcock (2019); **Figure 3.1**), it is possible that trait curiosity could be related to functional connections related to memory, information-seeking, exploration, and novelty.

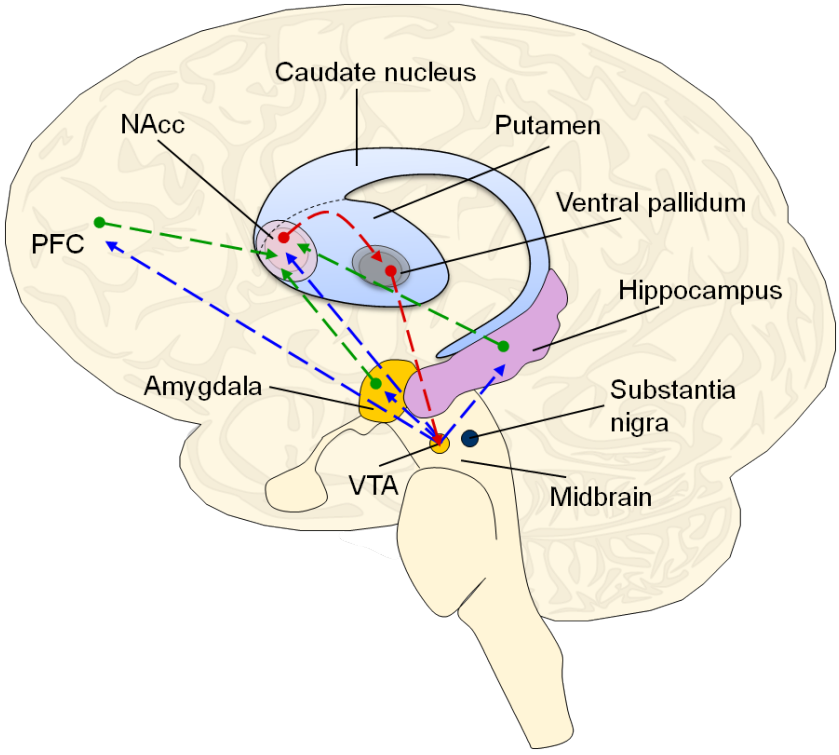


Figure 3.1: Mesolimbic pathway. Blue lines indicate dopaminergic input from the ventral tegmental area (VTA) to the hippocampus, amygdala, prefrontal cortex (PFC) and nucleus accumbens (NAcc). Green lines indicate excitatory glutamatergic input from the hippocampus, amygdala and PFC to the NAcc. Red lines indicate inhibitory GABAergic inputs from the NAcc to the ventral pallidum, that in turn reduces GABAergic inhibition from the ventral pallidum to the VTA, subsequently stimulating dopaminergic neurons in the midbrain (VTA). (*See Lisman & Grace, 2005; Shohamy & Adcock, 2010; Figure taken from Gruber et al., 2019, reproduced with permission*).

Despite a lack of evidence capturing the neural mechanisms of trait curiosity, there is evidence indicating that functional brain connectivity using resting-state fMRI best predicts personality traits including Openness to Experience (Dubois, Galdi, Han, Paul, & Adolphs, 2018); a construct described as a hierarchically organized and multifaceted concept reflecting cognitive exploration and ability to deal with novel information (DeYoung, 2014; Woo et al., 2014). Resting-state fMRI measures changes in blood oxygenation and blood flow in response to neural activity whilst the participant is at rest (i.e., not relying on any specific cognitive task) and can be used to examine correlated self-generated activity between brain regions and their subsequent relationship with personality traits (Dubois et al., 2018). For example, Beaty et al. (2016) using resting-state fMRI methods investigated whether individual differences in Openness to Experience could explain variability in global efficiency of the brains default mode network. Specifically, they found that participants scoring high in trait Openness to Experience displayed more efficient information processing within the default mode network (Beaty et al., 2016). Alternatively, other studies have examined the relationship between Openness and the dopaminergic circuit. Passamonti et al. (2015) recruited 46 participants to undergo one resting-state fMRI sequence followed by two task-based fMRI experiments. Using the revised NEO Five Factor Inventory (Costa & McCrae, 1992) to assess individual differences in Openness, Passamonti et al. (2015) consistently found across the task-dependent and resting-state sessions that individual differences in functional connectivity between the SN/VTA and the dorsolateral PFC predicted trait Openness, such that those scoring high in Openness showed greater functional connectivity between these regions. Openness to Experience is a personality trait that mirrors a person's cognitive exploration and their ability to deal with novel information (DeYoung, 2014; John et al., 2008; Woo et al., 2014), to which curiosity is believed to mirror qualities of this global trait. Given the similarities between curiosity and Openness to Experience, as well as the use of resting-state fMRI in investigating inter-individual differences in functional connectivity and trait Openness, this neuroimaging method may therefore be useful for unpacking how individual differences in RSFC within the mesolimbic circuit predicts trait curiosity.

Curiosity can be described as an attraction to novel intellectual concepts (Woo et al., 2014). Seeking out novel and ambiguous stimuli can be better defined as Perceptual Curiosity (PC; Berlyne, 1954). One study found that striatal and hippocampal regions showed greater activation when perceptual uncertainty was reduced (Jepma et al.,

2012). This finding supports classic drive theories of curiosity that postulate curiosity is an aversive state of arousal, where its reduction is in itself rewarding and can subsequently motivate future exploratory behaviours (Jepma et al., 2012; Loewenstein, 1994). Thus, perhaps those with high trait PC possess the desire to reduce uncertainty where the reduction of such uncertainty is in itself rewarding and subsequently motivates them to continue to explore their environment (Jepma et al., 2012; Loewenstein, 1994). Using fMRI methods, Krebs, Heipertz, Schuetze, and Düzel (2011) found novelty increased neural activity within the SN/VTA (c.f., Bunzeck & Düzel, 2006) and the functional connectivity between the medial SN/VTA and mesolimbic regions, including the hippocampus and NAcc. These structures show high intrinsic connectivity and have been found to be functionally involved during states of curiosity (Kahn & Shohamy, 2013; Kang et al., 2009), where Gruber et al., (2014) further found that individual differences in task-based functional connectivity between SN/VTA and the hippocampus predicted the curiosity-related face memory benefit. It is therefore possible that individual variability in the functional connectivity between these structures is perhaps also related to variability in sub-types of trait curiosity. Schuler et al. (2019), using resting-state fMRI examined the relationship between measures linked to creativity and subcortical networks of the dopaminergic system. The authors found that the SN/VTA resting-state network, that comprised of regions including the SN/VTA, hippocampus, and caudate, positively correlated with emotional stability and ideational behaviour suggesting that variability in the dopaminergic network is reflective of individual differences in trait creativity. With regards to motivational processing in the hippocampus, evidence suggests that the anterior hippocampus (i.e., hippocampal head) supplies the most numerous inputs to areas including the NAcc involved in reward anticipation, whilst the posterior hippocampus (i.e., hippocampal body and tail) is involved in spatial navigation and detailed memories (Aggleton et al., 2015; Christiansen et al., 2016; Christiansen et al., 2017; Hartley et al., 2003; Saunders & Aggleton, 2007). It has been suggested that there is no precise anatomical boundary that reflects distinct anterior and posterior hippocampal functions, but instead there is an anatomical gradient between anterior and posterior functions (Aggleton, 2012; Strange et al., 2014). Furthermore, Poppenk et al. (2013) suggest there being a functional specialisation along the long axis of the hippocampus where the anterior and posterior hippocampus contribute to specialised functions such as gist-like representations and ‘fine’ perceptual detail, respectively (Aggleton, 2012). Although there is little or no evidence on the functional neural mechanisms underlying trait curiosity, or as to whether trait curiosity employs the same

neural mechanism as state curiosity, it may be possible that individual variability in the functional connectivity between regions involved in the dopaminergic system, specifically the hippocampal-VTA loop, may also be associated with individual differences in trait curiosity.

Although the findings from Chapter 2 indicate the need for additional research in investigating the relationship between brain structure and curiosity traits, based on fMRI evidence that show the functional organisation of the brain is related to individual differences in personality traits (Adelstein et al., 2011), it is possible that individual variability in sub-types of trait curiosity are associated with specific functional connections. The use of resting state fMRI may further enable us to predict trait curiosity as resting-state fMRI data "is a predictor that could have better mechanistic interpretation than structural MRI measures (since ultimately it is brain function, not structure, that generates the behavior on the basis of which we can infer personality)" (Dubois et al., 2018, p.6). Therefore, using resting-state fMRI the present chapter examined whether the functional connectivity between specific regions involved in the mesolimbic pathway (including the VTA, NAcc, & hippocampus) with the hippocampus being defined into its anterior and posterior segments, is associated with subscales of EC (i.e., the desire to acquire new knowledge) and subscales of PC (i.e., curiosity in an environment rich with novel stimuli). In Experiment 1, fifty-one female participants completed questionnaires measuring EC and PC (Collins, Litman, & Spielberger, 2004; Litman, 2008) and underwent resting-state fMRI where a ROI-to-ROI functional connectivity analysis was utilised to examine the RSFC between structures involved in reward processing, learning, and memory. Given the evidence for high intrinsic connectivity between the VTA, NAcc, and hippocampus and their integrative role in regulating memory for items associated with reward (Gruber et al., 2014; Kahn & Shohamy, 2013; Lisman & Grace, 2005; Shohamy & Adcock, 2010), and evidence for possible cross-hemispheric projections between these regions (Floresco, Seamans & Phillips, 1997; Fox et al., 2016; Molochnikov & Cohen, 2014; Jurkowlaniec, Tokarski & Trojniar, 2003), left and right hemispheric ROIs were employed to investigate RSFC within the hippocampal-VTA loop. Therefore, I predicted there to be increased functional connectivity (i.e., positive associations; similar to other fMRI studies that usually test for single-sided tests, e.g., Gruber et al., 2014) between the VTA, NAcc, and anterior, posterior hippocampal ROIs (left and right ROIs). Furthermore, with regards to their subsequent relationship with curiosity traits, positive associations were expected. Taking into account the posterior-

anterior gradient of representational granularity along the long axis of the hippocampus, linked to a gradient in anatomical connectivity from 'fine' perceptual detail to gist-like representations, respectively (Aggleton, 2012; Poppenk et al., 2013; Robin & Moscovitch, 2017; Sheldon et al., 2019), it was likely that Interest/Diversive aspects of curiosity (i.e., general information-seeking/exploratory behaviours employed to increase arousal by seeking uncertainty to reduce boredom) would show stronger positive correlations with inter-individual differences in functional connectivity of the anterior hippocampus (left/right) with the NAcc (left/right) and VTA (left/right) versus functional connectivity measures involving the posterior hippocampus (left/right). Similarly, it was likely that Deprivation/Specific aspects of curiosity (i.e., information-seeking/exploratory behaviours that reduce uncertainty) would show stronger positive correlations with inter-individual differences in functional connectivity of the posterior hippocampus (left/right) with the NAcc (left/right) and VTA (left/right) versus functional connectivity measures involving the anterior hippocampus (left/right). Finally, based on previous evidence highlighting the relationship between the SN/VTA, NAcc and reward/novelty (e.g. Krebs et al., 2011; Schott et al., 2008; Wittmann et al., 2005) it was hypothesised that functional connectivity between the NAcc (left/right) and the VTA (left/right) would show significant positive correlations with all subscales of curiosity.

3.2 Experiment 1

3.2.1 Materials and Methods

3.2.1.1 Participants

Fifty-one healthy female adult undergraduate students, with a mean age of 20 years (SD ± 1, range = 19-24) were recruited from Cardiff University and were scanned at the Cardiff University Brain Research Imaging Centre (CUBRIC). This sample was identical to the sample reported in Chapter 2, Experiment 1. All participants signed a written consent form before participating in the study, which was approved by the Cardiff University Research Ethics Committee. Participants received a remuneration of

approximately £25 for their participation. Resting state data for two participants were excluded due to failure in completing the resting-state fMRI scan and/or missing functional data.

3.2.1.2 Trait curiosity measures

Participants completed the Epistemic Curiosity Scale (EC) (Litman, 2008; Appendix 1) and the Perceptual Curiosity Scale (PC) (Collins et al., 2004; Appendix 2), identical to that in Chapter 2, Experiment 1. Cronbach's alpha was calculated for each self-report measure using SPSS (version 23) which indicated good internal consistency for all curiosity subsets (Tavakol & Dennick, 2011) (Appendix 7).

3.2.1.3 Imaging acquisition

Imaging data were obtained at CUBRIC, Cardiff University on a 3 Tesla MR scanner (Siemens Magnetom Prisma) with a 32-channel head coil. T1-weighted 3D images were acquired using an MPRAGE sequence (orientation = sagittal; TR = 2250ms; TE = 3.06ms; TI = 900ms; flip angle = 9°; FOV = 256mm²; slice thickness = 1mm; voxel size = 1mm³; number of slices = 224; bandwidth = 230Hz/pixel; total acquisition time = 7 minutes 36 seconds).

Resting-state fMRI images were acquired using an echo planar imaging sequence (orientation = transversal/axial; TR = 3000ms; TE = 30.0ms; flip angle = 89°; FOV = 192mm²; slice thickness = 2mm; voxel size = 2mm³; number of slices = 50, bandwidth = 2170Hz/pixel; total acquisition time = 10 minutes 11 seconds).

3.2.1.4 Experimental procedure

Participants were asked to change into MRI scrubs and placed in the scanner where they were asked to keep as still as possible during the duration of the scanning session. During the T1 structural scan participants watched a DVD to help reduce movement, boredom, and nervousness. During the resting-state fMRI scan participants

were asked to clear their mind and think of nothing in particular while fixating their gaze on a fixation cross. Other sequences were acquired during the scanning session (e.g., multi-shell diffusion sequence & MR spectroscopy), however are not relevant to the present experiment. After the scanning session participants completed the EC and PC scales described above, followed by a series of other self-report measures and tasks not relevant to this experiment. Finally, participants were debriefed and compensated for their participation in the study.

3.2.1.5 Resting-state functional connectivity pre-processing

Resting-state data was pre-processed using CONN toolbox (version 18b; Whitfield-Gabrieli & Nieto-Castanon, 2012; www.nitrc.org/projects/conn) in conjunction with the Statistical Parametric Mapping (SPM) 12 modules (Wellcome Trust Centre for Neuroimaging, London) executed using MATLAB (version 2015). Using standard parameters in CONN, imaging data were subjected to slice-time correction (Interleaved Siemens) in order to correct for different acquisition times for the different slices in the functional data; realignment and unwarp correcting for head movement; functional outlier detection using Artifact Detection Tool (ART) to identify potential outlier scans due to abrupt movements; segmentation and normalisation to MNI (Montreal Neurological Institute) space; and spatial smoothing with a 6mm full-width-half-maximum (FWHM) Gaussian kernel. In order to remove unwanted motion, physiological, and other artefacts from the BOLD signal before computing functional connectivity, the following were applied to the data: denoising, specific to functional connectivity analyses, was applied to implement band-pass filtering (0.01-0.1Hz), a linear detrending term, an anatomical component based noise correction method (aCompCor) that removed 10 noise components of the signal from white matter and CSF (Behzadi, Restom, Liau & Liu, 2007), and motion regression with 12 regressors (6 motion parameters and 6 first-order temporal derivatives that were estimated during realignment). Data for two participants were not pre-processed due to failure in completing the resting-state fMRI scan and/or missing functional data. Therefore, the final sample for analysis of the resting-state data consisted of 49 participants.

3.2.1.6 Statistical analysis

3.2.1.6.1 Regions of interest

For the ROI-to-ROI based functional connectivity analyses, the functional connectivity between two ROIs during rest was examined. Based on evidence for possible cross-hemispheric projections between the VTA, hippocampus and NAcc (Floresco, Seamans & Phillips, 1997; Fox et al., 2016; Molochnikov & Cohen, 2014; Jurkowlaniec, Tokarski & Trojniar, 2003), left and right hemispheric ROIs were employed to investigate RSFC within the hippocampal-VTA loop. The following ROIs were selected for the current analyses: the left and right VTA (Murty et al., 2014), the left and right NAcc (Harvard-Oxford atlas), and the left and right hippocampal head, body, and tail (these ROIs were derived from tracing the hippocampus based on the average participant brain (using DARTEL) from the Gruber et al. (2016) dataset). Source and target areas represented ROIs included in the ROI-to-ROI functional connectivity analysis. When conducting functional connectivity analysis between two ROIs, one ROI is typically treated as the source area and the other is treated as the target area in CONN **(Figure 3.2)**.

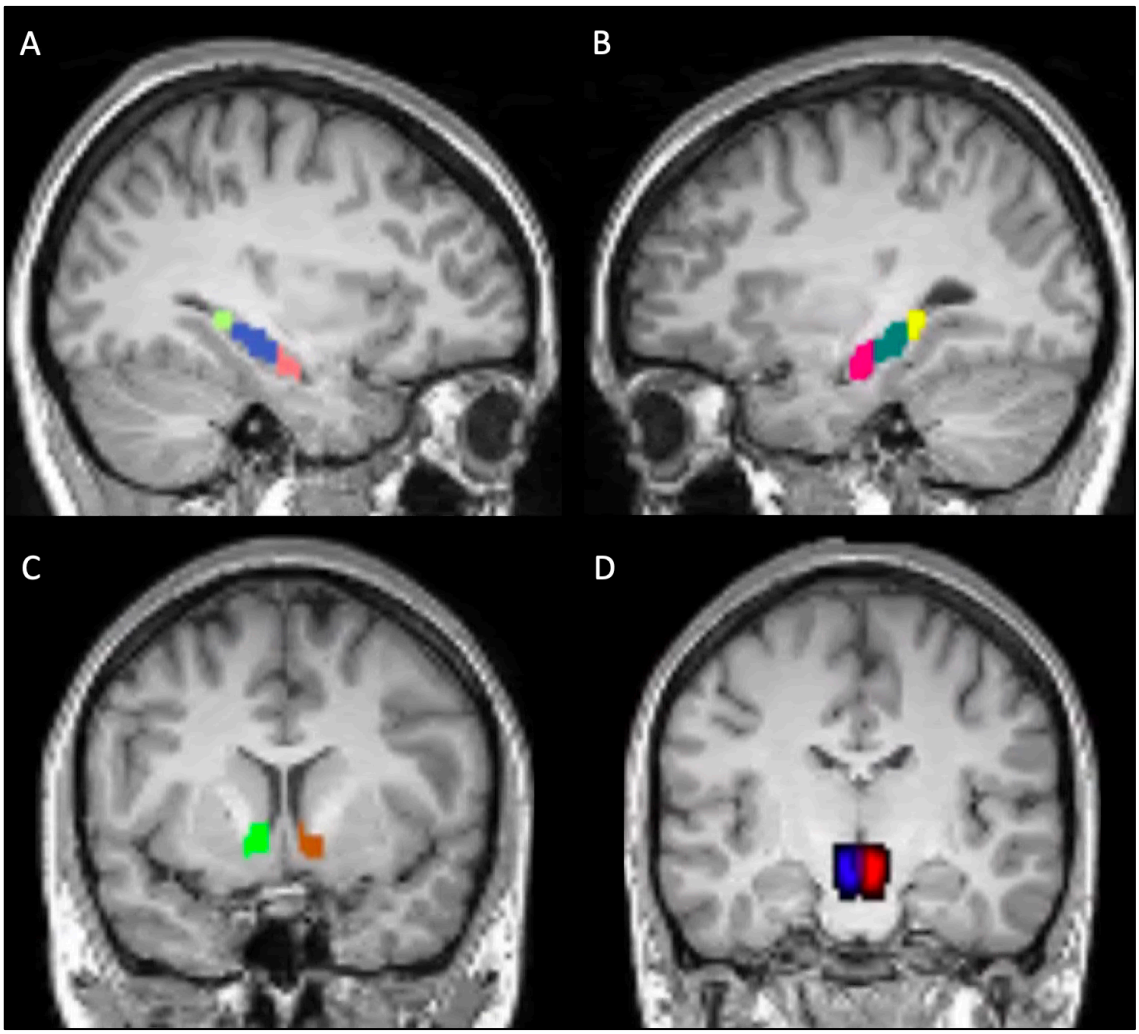


Figure 3.2: Regions of interest (ROI) included in the RSFC analyses. **(A)** left anterior hippocampus (pink (left hippocampal head), x = -26, y = -15, z = -20), left posterior hippocampus (blue (left hippocampal body), x = -28, y = -27, z = -12; and green (left hippocampal tail), x = -24, y = -38, z = -2); **(B)** right anterior hippocampus (magenta (right hippocampal head), x = 27, y = -14, z = -20), right posterior hippocampus (teal (right hippocampal body), x = 30, y = -25, z = -12; and yellow (right hippocampal tail), x = 27, y = -35, z = -3); **(C)** Left nucleus accumbens (bright green, x = -9, y = 11, z = -7) and right nucleus accumbens (brown, x = 9, y = 12, z = -7); **(D)** left ventral tegmental area (navy blue, x = -3, y = -15, z = -15) and right ventral tegmental area (red, x = 4, y = -16, z = -14). *Note.* The hippocampal head represented the anterior hippocampus, whilst the masks of the hippocampal body and tail together represented the posterior hippocampus (the average connectivity values across the hippocampal body and tail were taken as the source ROI when carrying out correlations with a target ROI).

3.2.1.6.2 Functional connectivity analysis

ROI based functional connectivity analysis was carried out using CONN on the 49 datasets, where for each pre-defined ROI mask the BOLD time series was computed by averaging the voxel time series across all voxels within the ROI. Fisher-transformed bivariate correlation coefficients were computed between source and target ROI BOLD time series as a measure of functional connectivity. The hippocampal head represented the anterior hippocampus, whilst the masks of the hippocampal body and tail together represented the posterior hippocampus (the average connectivity values across the hippocampal body and tail were taken as the source ROI when carrying out correlations with a target ROI). For each ROI-to-ROI analysis a one sample t-test was performed to test whether the means of connections were greater than zero. To correct for multiple tests a false discovery rate (FDR; Benjamini & Hochberg, 1995) correction was applied over the set of target ROIs. Results were thresholded at $p<0.001$, one tailed, as it was believed that positive functional connectivity between the selected ROIs were modulating trait curiosity. With regards to voxelwise correction methods, this is the threshold that is suggested in the fMRI literature when wanting to avoid inflated false positives (Carter et al., 2016; Eklund et al., 2016; Yeung, 2018). Finally, the fisher-transformed ROI-to-ROI connectivity values for each subject were extracted and subsequently correlated with trait curiosity self-report measures.

For the questionnaire data, in the event of missing responses (2 participants failed to give a response to one PC item), the mean value of the remaining items that were answered in the full scale was calculated which then replaced the missing item score. For each curiosity subscale (i.e., the two subscales of PC and EC), the total score for each participant was calculated. To test whether the Pearson's correlation coefficient *r,* reflecting the positive association between RSFC between ROIs and each of the trait measures of curiosity, was statistically significant, non-parametric permutation tests (one-tailed) that randomly permuted the real data between participants were performed. Permutation tests control the family-wise-error rate and were conducted separately for the four trait measures of curiosity (i.e., ECI, ECD, PCD and PCS) where each test corrected for multiple comparisons across the selected ROI-to-ROI RSFC measures. Employing a correction method that accounts for all possible correlations (i.e., 80 correlations) was considered too conservative. Therefore, in this chapter the 'family of tests' was defined as a set of paired variables that resulted in the highest number of

comparisons when keeping one variable constant (i.e., keeping curiosity subscale constant versus ROI-to-ROI RSFC). Therefore, when correlating curiosity trait measures and functional connectivity measures, I ran 4 separate permutation tests (one for each curiosity subscale) that corrected for functional connectivity measures (20 ROI-to-ROI measures). The methodological steps taken to carry out these non-parametric permutation tests are described in Chapter 2. The 95% confidence intervals (CI) for each correlation was derived using a bootstrapping method based on 1000 iterations.

3.2.2 Results

3.2.2.1 Trait curiosity

The mean and standard deviation of each subset of curiosity along with directional Pearson's correlations between subscales of EC and PC is summarised in **Table 2.1** (Chapter 2, section 2.2.2.1).

3.2.2.2 Resting-state functional connectivity results

Average fisher-transformed bivariate correlation coefficients were calculated between source and target ROI BOLD time series. All source ROIs positively correlated with respective target ROIs, indicating positive functional connectivity at a FDR-corrected threshold of $p<0.001$ (Appendix 11).

3.2.2.3 Resting-state functional connectivity and trait curiosity

Here, left and right ROIs of the VTA, NAcc, anterior, and posterior hippocampus were defined, where a series of permutation tests (one-tailed) were conducted correcting for multiple comparisons across the 20 pairs of ROIs when correlated with each subscale of curiosity. The first permutation test indicated that out of the 20 correlations conducted[1] between ROI-to-ROI functional connectivity coefficients and Interest EC, no significant positive correlations were observed ($ps \geq 0.127$) (Appendix 12A). Similarly, no significant

correlations were observed in the second permutation test that corrected for multiple comparisons across the 20 pairs of ROIs when correlated with Deprivation EC (*p*s ≥ 0.819) (Appendix 12B). In the third permutation test correcting for multiple comparisons across the 20 pairs of ROIs, Diversive PC showed a positive relationship with RSFC between left anterior hippocampus and left NAcc that approached significance ($r(47)$ = 0.361, p_{corr} = 0.083, 95% CI [0.08, 0.59], **Figure 3.3**, **Table 3.1**). The final permutation test indicated that the positive correlations expected between ROI-to-ROI functional connectivity coefficients and Specific PC did not reach significance (*p*s ≥ 0.124) (Appendix 12C).

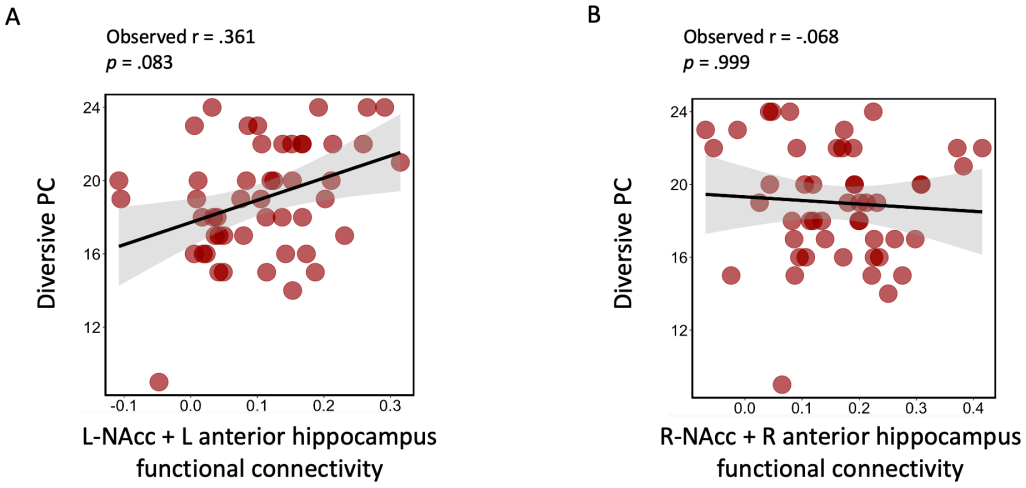


Figure 3.3: (A) Positive relationship between left nucleus accumbens (NAcc) and left anterior hippocampus resting-state functional connectivity and Diversive PC that approached significance. **(B)** No significant relationship between right NAcc and right anterior hippocampus resting-state functional connectivity and Diversive PC. The line of best fit and 95% confidence intervals are shown on each scatter plot with 49 data points.

[1]Twenty comparisons that include the left and right posterior hippocampus each being correlated with each left and right NAcc and VTA, left and right anterior hippocampus each being correlated with each left and right NAcc and VTA, left and right NAcc each being correlated with each left and right VTA.

Table 3.1: RSFC-behaviour correlations are based on 49 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Diversive PC.

ROI-to-ROI functional connectivity	Diversive PC		
	r(47)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	-0.030	0.999	[-0.33, 0.30]
L-pos. HC + R-NAcc	0.023	0.995	[-0.26, 0.29]
L-pos. HC + L-VTA	-0.026	0.999	[-0.30, 0.23]
L-pos. HC + R-VTA	-0.030	0.999	[-0.28, 0.20]
R-pos. HC + L-NAcc	-0.122	0.999	[-0.41, 0.21]
R-pos. HC + R-NAcc	-0.042	0.999	[-0.33, 0.22]
R-pos. HC + L-VTA	0.180	0.730	[-0.13, 0.43]
R-pos. HC + R-VTA	-0.034	0.999	[-0.30, 0.22]
L-ant. HC + L-NAcc	**0.361**	**0.083***	[0.08, 0.59]
L-ant. HC + R-NAcc	-0.009	0.998	[-0.24, 0.25]
L-ant. HC + L-VTA	-0.080	0.999	[-0.38, 0.16]
L-ant. HC + R-VTA	-0.103	0.999	[-0.33, 0.11]
R-ant. HC + L-NAcc	0.106	0.930	[-0.15, 0.40]
R-ant. HC + R-NAcc	-0.068	0.999	[-0.39, 0.24]
R-ant. HC + L-VTA	-0.169	0.999	[-0.40, 0.08]
R-ant. HC + R-VTA	-0.173	0.999	[-0.41, 0.09]
L-NAcc + L-VTA	0.300	0.226	[-0.01, 0.54]
L-NAcc + R-VTA	0.270	0.343	[-0.004, 0.54]
R-NAcc + L-VTA	-0.001	0.998	[-0.33, 0.32]
R-NAcc + R-VTA	0.123	0.899	[-0.16, 0.39]

***p < 0.1**; PC, *Perceptual Curiosity*; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

In this experiment a positive association was found between Diversive PC and RSFC between the left anterior hippocampus and left NAcc. No other correlations were observed between ROI-to-ROI RSFC measures and curiosity traits. A possible reason for this could be that the measures of EC and PC are perhaps too restrictive. For example, the subsets within each scale that reflect Interest/Diversive or Deprivation/Specific Curiosity are bound to either Epistemic or Perceptual Curiosity. This highlights the need for a robust questionnaire that reflects Diversive/Interest and Deprivation/Specific Curiosity regardless of PC and EC. The next experiment was intended to first replicate any findings from Experiment 1. It also utilized Kashdan's 5-Dimensional Curiosity scale that consisted of subsets that tapped into the bandwidth of curiosity rather than focussing on epistemic/perceptual dimensions of curiosity. For instance, the Joyous Exploration subset of the 5-Dimensional Curiosity scale describes the preference for novel experiences and information where feeling curious and subsequent exploratory behaviours are deemed pleasurable. This subset can be thought to reflect both aspects of Interest EC and Diversive PC. Similarly, the Deprivation Sensitivity subset of the 5-Dimensional Curiosity scale that describes the aversive aspect of curiosity, in which individuals seek out information as a means to escape the tension elicited from not knowing something, can be thought to reflect both Deprivation EC and Specific PC. Extending beyond these aspects of curiosity that have been previously captured in the literature (Litman, 2005; 2008), the 5-Dimensional Curiosity scale also includes subsets that capture the perceived ability in coping with anxiety involved in encountering the unknown, better described as Stress Tolerance, and also captures a person's tendency to seek out adventure and pleasure particularly when significant risks are present, categorised as Thrill Seeking. The final subset describes an individual's fascination and fixation in how other people think, act, and feel, also known as Social Curiosity. This scale, in contrast to the EC and PC scales, better portrays curiosity as multidimensional trait that varies between individuals.

3.3 Experiment 2

Experiment 1 indicated that the relationship between Diversive PC and RSFC between the left anterior hippocampus and left NAcc approached significance. However, no other relationships were observed between the remaining curiosity subsets and ROI-to-ROI RSFC measures. Despite several differences between Experiment 1 and 2,

including differences in sample demographics, trait questionnaire administration and its potential subsequent effect on participants' self-reports, Experiment 2 examined whether the same RSFC-trait relationship would be evident as in Experiment 1. This experiment also examined whether individual differences in other trait measures of curiosity, such as the 5-Dimensional Curiosity scale, also relates to individual variability in the functional connectivity between ROIs involved in the hippocampal-VTA loop. Furthermore, the procedure involved the inclusion of a reward-based experiments (not discussed in the present thesis), a curiosity-trivia paradigm (discussed in Chapter 4 and 5) and a bank of questionnaires administered after being in a state of curiosity. In addition to the Epistemic and Perceptual Curiosity scales employed in Experiment 1, the relationship between ROI-to-ROI RSFC and the subsets of the 5-Dimensional Curiosity scale (Kashdan et al., 2018) was also examined. The 5-Dimensional Curiosity scale consisted of subscales including Joyous Exploration, Deprivation Sensitivity, Stress Tolerance, Social Curiosity, and Thrill Seeking. The advantage of this scale over the EC/PC scales is that it explores the bandwidth of curiosity rather than focussing on specific aspects of a dimension of curiosity. Given that the sample reported in Experiment 2 of the present chapter is identical to that reported in Experiment 2 of Chapter 2, I was aware that Interest EC positively correlated with Joyous Exploration; Deprivation EC positively correlated with Deprivation Sensitivity; and Diversive PC positively correlated with Joyous Exploration, Stress Tolerance, and Thrill Seeking (p.70). Therefore, it was hypothesised that inter-individual differences in functional connectivity of the anterior hippocampus with the NAcc and VTA would each positively correlate with Joyous Exploration, Stress Tolerance, and Thrill Seeking. Similarly, I expected that inter-individual differences in functional connectivity between the posterior hippocampus with the NAcc and VTA would each positively correlate with Deprivation Sensitivity. Finally, it was hypothesised that functional connectivity between the NAcc and the VTA would positively correlate with all subscales of curiosity. The ROIs employed in this experiment and the hypothesised relationships between ROI-to-ROI RSFC and trait curiosity were motivated by the findings from Experiment 1 and the prior literature. To examine the relationship between RSFC and trait questionnaires, permutation tests that corrected for multiple comparisons (identical to Experiment 1) were employed.

3.3.1 Materials and Methods

3.3.1.1 Participants

Fifty-five healthy adults (47 females) with a mean age of 19 years (SD ± 1.75, range = 18-25) were recruited from Cardiff University and were scanned at the Cardiff University Brain Research Imaging Centre (CUBRIC). This sample was identical to the sample reported in Chapter 2, Experiment 2. Participants signed a written consent form before participating in the study that had been approved by the Cardiff University Ethics Committee. Participants were compensated with either course credits or payment for their participation.

3.3.1.2 Trait curiosity measures

Participants completed a variety of sub-scales from questionnaires that measured types of curiosity and information seeking. Identical to Chapter 2, Experiment 2, participants completed the Epistemic Curiosity Scale (EC) (Litman, 2008; Appendix 1), the Perceptual Curiosity Scale (PC) (Collins et al., 2004; Appendix 2), and the 5-Dimensional Curiosity scale (Kashdan et al., 2018; Appendix 3). Cronbach's alpha was calculated for each self-report measure using SPSS (version 23) which indicated good internal consistency for all curiosity subsets (Tavakol & Dennick, 2011) (Appendix 8).

3.3.1.3 Imaging acquisition

The MRI sequences and acquisition of MRI data were matched as closely as possible to Experiment 1. Imaging data was obtained at CUBRIC, Cardiff University on a 3 Tesla MR scanner (Siemens Magnetom Prisma) with a 32-channel head coil. T1-weighted 3D images were acquired using an MPRAGE sequence (orientation = sagittal; TR = 2250ms; TE = 3.06ms; TI = 900ms; flip angle = 9°; FOV = 256mm²; slice thickness = 1mm; voxel size = 1mm³; number of slices = 224; bandwidth = 230Hz/pixel; total acquisition time = 7 minutes 36 seconds).

Resting-state fMRI images were acquired using an echo planar imaging sequence (orientation = transversal/axial; TR = 3000ms; TE = 30.0ms; flip angle = 89°; FOV = 192mm²; slice thickness = 2mm; voxel size = 2mm³; number of slices = 50, bandwidth = 2170Hz/pixel; total acquisition time = 10 minutes 11 seconds).

3.3.1.4 Experimental Procedure

Participants changed into MRI scrubs and lay in the MRI scanner where they were asked to keep as still as possible for the duration of the scanning session. During the T1 structural scan participants watched an animated DVD to help reduce movement, boredom, and nervousness. Other sequences were acquired during the scanning session (e.g., multi-shell diffusion sequence and MR spectroscopy), however are not relevant to the present experiment. Participants returned for a duration of two consecutive days and completed a series of behavioural tasks (not relevant to the current experiment) and a series of self-report measures (some of which are not relevant to the current experiment). The trait curiosity scales of interest were completed after a curiosity-trivia paradigm (See Chapter 4, Experiment 2) on day 2. Participants were debriefed and compensated for their participation in the study.

3.3.1.5 Resting-state functional connectivity pre-processing

The RSFC pre-processing was identical to that in Experiment 1. Scans for two participants were removed due to excess motion artefacts identified by CONN. Therefore, the final sample for analysis of the resting-state data consisted of 53 participants.

3.3.1.6 Statistical analysis

3.3.1.6.1 Regions of interest and functional connectivity analysis

Identical to Experiment 1, the functional connectivity between two ROIs during rest was examined. Based on evidence for possible cross-hemispheric projections between the VTA, hippocampus and NAcc (Floresco, Seamans & Phillips, 1997; Fox et al., 2016; Molochnikov & Cohen, 2014; Jurkowlaniec, Tokarski & Trojniar, 2003), left and right hemispheric ROIs were employed to investigate RSFC within the hippocampal-VTA loop. The ROIs selected for the current analyses were identical to Experiment 1. These included the left and right VTA (Murty et al., 2014), the left and right NAcc (Harvard-Oxford atlas; and left and right hippocampal head, body and tail (these ROIs were derived from tracing the hippocampus based on the average participant brain (using DARTEL) from the Gruber et al. (2016) dataset). Source and target areas represented ROIs included in the ROI-to-ROI functional connectivity analysis. When conducting functional connectivity analysis between two ROIs, one ROI is typically treated as the source area and the other is treated as the target area in CONN **(Figure 3.2)**.

ROI based functional connectivity analysis was carried out using CONN on 53 datasets, where for each pre-defined ROI mask the BOLD time series was computed by averaging the voxel time series across all voxels within the ROI. Fisher-transformed bivariate correlation coefficients were computed between source and target ROI BOLD time series as a measure of functional connectivity. The hippocampal head represented the anterior hippocampus, whilst the masks of the hippocampal body and tail together represented the posterior hippocampus (the average connectivity values across the hippocampal body and tail were taken as the source ROI when carrying out correlations with a target ROI). For each ROI-to-ROI analysis a one sample t-test was performed to test whether the means of connections were greater than zero. To correct for multiple tests a FDR correction (Benjamini & Hochberg, 1995) was applied over the set of target ROIs. Results were thresholded at $p<0.001$, one tailed, as it was believed that positive functional connectivity between the selected ROIs were modulating trait curiosity. Finally, the fisher-transformed ROI-to-ROI connectivity values for each subject were extracted and subsequently correlated with trait curiosity self-report measures.

For each curiosity self-report measure the total score for each participant was calculated. Participants' data with trait curiosity scores +/– 3 SD beyond the group mean were considered as outliers and removed from respective analyses. This resulted in one participant's data being removed from analyses involving the Joyous Exploration subscale and a different participant being removed from analyses involving the Social Curiosity subscale. Identical to the analysis steps employed in Experiment 1, to test whether the Pearson's correlation coefficient *r,* reflecting the positive association between RSFC between ROIs and each of the trait measures of curiosity, was statistically significant, non-parametric permutation tests (one-tailed) that randomly permuted the real data between participants were performed. Permutation tests were conducted separately for each subset of EC, PC, and the 5-Dimensional Curiosity scale where each test corrected for multiple comparisons across the selected ROI-to-ROI RSFC measures. The methodological steps taken to carry out these non-parametric permutation tests are described in Chapter 2. The 95% confidence intervals (CI) for each correlation was derived using a bootstrapping method based on 1000 iterations.

3.3.2 Results

3.3.2.1 Trait curiosity

The mean and standard deviation of each subset of curiosity along with directional Pearson's correlations between subscales of EC and PC is summarised in **Table 2.4** (Chapter 2, section 2.3.2.1).

3.3.2.2 Resting-state functional connectivity results

Average fisher-transformed bivariate correlation coefficients were calculated between source and target ROI BOLD time series, where all source ROIs positively correlated with respective target ROIs, indicating positive functional connectivity at a FDR-corrected threshold of $p<0.001$ (Appendix 13).

3.3.2.3 Resting-state functional connectivity and trait curiosity

Left and right ROIs of the VTA, NAcc, anterior and posterior hippocampus were defined, where a series of permutation tests (one-tailed) were conducted correcting for multiple comparisons across the 20 pairs of ROIs when correlated with each subscale of curiosity. The first permutation test indicated that out of the 20 correlations conducted between ROI-to-ROI functional connectivity coefficients and Interest EC, no significant positive correlations were observed (*p*s ≥ 0.369) (Appendix 14A). Similarly, no significant positive correlations were observed in the permutation tests that corrected for multiple comparisons across the 20 pairs of ROIs when correlated with Deprivation EC (*p*s ≥ 0.687) (Appendix 14B), Diversive PC (*p*s ≥ 0.335) (Appendix 14C) or Specific PC (*p*s ≥ 0.581) (Appendix 14D). The positive relationship (non-significant) between Diversive PC and RSFC between the left NAcc and left anterior hippocampus that was found in Experiment 1 does not appear to replicate in this experiment.

With regards to the permutation tests that investigated the relationship between the 5-Dimensional Curiosity subsets and RSFC between selected ROIs, Stress Tolerance showed a positive correlation with RSFC between left NAcc and right VTA ($r(51) = 0.368$, $p_{corr} = 0.050$, 95% CI [0.14, 0.57], **Figure 3.4**, **Table 3.2**). No significant positive correlations were observed in the permutation tests that corrected for multiple comparisons across the 20 pairs of ROIs when correlated with Joyous Exploration (*p*s ≥ 0.625) (Appendix 14E), Deprivation Sensitivity (*p*s ≥ 0.805) (Appendix 14F), Social Curiosity (*p*s ≥ 0.398) (Appendix 14G) and Thrill Seeking (*p*s ≥ 0.529) (Appendix 14H).

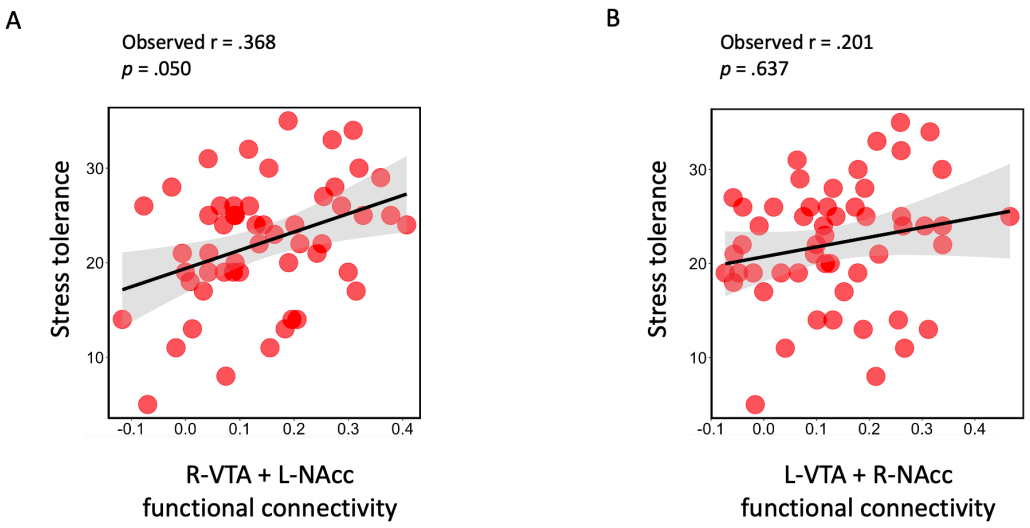


Figure 3.4: (A) Positive correlation between right ventral tegmental area (VTA) and left nucleus accumbens (NAcc) resting-state functional connectivity and Stress Tolerance. **(B)** No significant relationship between left VTA and right NAcc resting-state functional connectivity and Stress Tolerance. The line of best fit and 95% confidence interval are shown on each scatter plot with 53 data points.

Table 3.2: RSFC-behaviour correlations are based on 53 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Stress Tolerance.

ROI-to-ROI functional connectivity	Stress Tolerance		
	r(51)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.252	0.386	[0.004, 0.46]
L-pos. HC + R-NAcc	0.089	0.955	[-0.21, 0.42]
L-pos. HC + L-VTA	-0.041	0.999	[-0.33, 0.25]
L-pos. HC + R-VTA	0.032	0.994	[-0.23, 0.31]
R-pos. HC + L-NAcc	0.045	0.989	[-0.22, 0.30]
R-pos. HC + R-NAcc	-0.236	0.999	[-0.45, -0.01]
R-pos. HC + L-VTA	-0.029	0.999	[-0.30, 0.26]
R-pos. HC + R-VTA	-0.013	0.998	[-0.25, 0.26]
L-ant. HC + L-NAcc	0.135	0.873	[-0.07, 0.32]
L-ant. HC + R-NAcc	-0.073	0.999	[-0.28, 0.14]
L-ant. HC + L-VTA	0.014	0.996	[-0.25, 0.28]
L-ant. HC + R-VTA	0.014	0.996	[-0.25, 0.29]
R-ant. HC + L-NAcc	0.034	0.993	[-0.20, 0.25]
R-ant. HC + R-NAcc	-0.078	0.999	[-0.28, 0.15]
R-ant. HC + L-VTA	0.078	0.969	[-0.13, 0.27]
R-ant. HC + R-VTA	0.124	0.899	[-0.08, 0.32]
L-NAcc + L-VTA	0.007	0.997	[-0.28, 0.31]
L-NAcc + R-VTA	**0.368**	**0.050***	[0.14, 0.57]
R-NAcc + L-VTA	0.201	0.637	[-0.06, 0.43]
R-NAcc + R-VTA	0.003	0.997	[-0.25, 0.26]

***p < 0.1**; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

3.4 Discussion

State curiosity had been linked to hippocampus-dependent learning via increased activation in areas involved in the hippocampal-VTA loop (Chiew & Adcock (2019); Gruber et al., 2014; Kahn & Shohamy, 2013; Kang et al., 2009; Lisman & Grace, 2005; Shohamy & Adcock, 2010). However, the functional mechanism underlying trait curiosity, a stable personality characteristic in which people high in trait curiosity experience states of curiosity more frequently and intensely than individuals low in trait curiosity (Grossnickle, 2016), has yet to be established. In the current study resting-state fMRI was employed as a means to investigate the relationship between individual differences in trait curiosity and variability observed in functional connectivity between brain areas involved in the hippocampal-VTA loop known to regulate learning. Here, greater functional connectivity between specific ROIs was found to positively correlate with curiosity traits. Experiment 1 found that Diversive PC showed a positive relationship with RSFC between the left anterior hippocampus and left NAcc that approached significance. This finding was not confirmed in Experiment 2. Instead, Experiment 2 indicated that Stress Tolerance positively correlated with RSFC between the right VTA and left NAcc.

3.4.1 Individual variability in EC subsets do not relate to RSFC between ROIs involved in the hippocampal-VTA loop

EC describes a persons desire for knowledge and their internal drive to know (Berlyne, 1954), and can be motivated by either a means to reduce feelings of boredom and stimulate positive affect (i.e., Interest EC) or a means to reduce uncertainty by searching for the information that is lacking (i.e., Deprivation EC). The hippocampus is a structure that can be defined into its anterior and posterior segments, where the anterior hippocampus has been found to supply numerous inputs to areas including the NAcc that forms part of the ventral striatum and involved in reward anticipation, whilst the posterior hippocampus is considered to be more involved in spatial navigation and detailed memories (Aggleton et al., 2015; Christiansen et al., 2016; Christiansen et al., 2017; Hartley et al., 2003; Saunders & Aggleton, 2007). Interest EC was expected to positively correlate with functional connectivity between the anterior hippocampus, NAcc,

and VTA, whilst Deprivation EC was expected to positively correlate with functional connectivity between the posterior hippocampus, NAcc, and VTA. Here, no significant association was found between either subset of EC and RSFC between ROIs involved in the hippocampal-VTA loop that facilitates learning, motivation, and memory. Somewhat in line with Chapter 2 that indicated Deprivation EC did not correlate with segments of the fornix – a structure connecting the hippocampus with the ventral striatum – the present findings also indicate that inter-individual differences in functional connectivity within the hippocampal-VTA loop does not predict Deprivation EC. With regards to Interest EC, the findings from Chapter 2 suggest that EC may involve coordination along the entire hippocampal longitudinal axis, however, in the present experiment inter-individual differences in functional connectivity within the hippocampal-VTA loop did not differentiate between individual differences in this subset of EC. Therefore, perhaps it is underlying structure – not functional connectivity within the hippocampal-VTA loop – that relates to Interest EC. Furthermore, it is possible that the functional mechanism underlying trait EC utilizes different structures more involved in the semantic network. For instance, structures implicated in semantic knowledge and control, including the inferior frontal gyrus, parahippocampal gyrus, and amygdala (Catani et al., 2003; Nugiel et al., 2016), which may demonstrate greater functional connectivity in individuals that display a greater tendency to seek out information for enjoyment and/or information that is lacking/deprived from their semantic knowledge.

3.4.2 Individual variability in Diversive PC relates to RSFC between anterior hippocampus and NAcc

Similar to Interest EC, Diversive PC was expected to positively correlate with functional connectivity between the anterior hippocampus, NAcc, and VTA. In Experiment 1, though not quite reaching statistical significance, this curiosity trait showed a positive relationship with the functional connectivity between the left anterior hippocampus and left NAcc, the former structure being one that has been found to supply numerous inputs to the NAcc involved in reward anticipation and motivated behaviours (Fanselow & Dong, 2010; Krebs et al., 2011; Poppenk et al., 2013). One explanation for the possible relationship between Diversive PC and functional connectivity observed between the anterior hippocampus and NAcc may be that those with high Diversive PC traits have a greater drive and tendency to employ exploratory behaviours in search for

general perceptual stimulants to reduce boredom and increase arousal (Berlyne, 1960, 1966; Collins et al., 2004). In contrast to Diversive PC, Specific PC was expected to positively correlate with the functional connectivity between the posterior hippocampus, NAcc, and VTA. Specific PC is a subset of PC in which an individual has a tendency to explore detailed and sensorially stimulating information that is lacking as a means to reduce their uncertainty in their environment (Berlyne, 1960, 1966; Collins et al., 2004). However, inter-individual variation in this subset of PC, that is associated with detailed perceptual information seeking, did not correlate with the functional connectivity between the posterior hippocampus and other ROIs involved in the hippocampal-VTA loop. With regards to the findings in Chapter 2, Specific PC showed an association with the posterior hippocampal fornix microstructure, which suggests that similar to Interest EC, it may be the underlying structure – not functional connectivity – that relates to Specific PC. Alternatively, it may be possible that such traits associated with the desire to seek information to reduce uncertainty, such as Specific PC (and Deprivation EC), utilise other networks such as the semantic network that involves the anterior temporal lobe structures, or perhaps they utilise networks that involve areas including the ACC rather than the hippocampal-VTA loop. For example, Jepma et al. (2012) identified the ACC and anterior insular cortex to be more active when perceptual uncertainty was elicited. Therefore, perhaps it is possible that those high in Specific/Deprivation-based Curiosity are more sensitive to uncertainty in their environment where individual variability in ACC connectivity better predicts trait curiosity that is elicited when information is lacking.

In Experiment 2, no significant relationship was found between ROI-to-ROI RSFC and the subsets of EC nor with the subsets of PC. Despite some methodological differences between Experiment 1 and 2, it is unlikely that the reason why the relationship between Diversive PC and RSFC could not be replicated was due to differences in trait scores (e.g., lower trait scores in Experiment 2 given participants were exposed to experiments that elicited curiosity/salience etc.), as no significant difference in Diversive PC scores were observed between the two experiments (Appendix 4B). An alternative explanation could be that Experiment 2 was underpowered to successfully replicate any true relationships from Experiment 1 (Button et al., 2013; Chen, Lu, & Yan, 2018).

3.4.3 Individual variability in Stress Tolerance relates to RSFC between VTA and NAcc

In Experiment 2, individual variability in the subsets of the 5-Dimensional Curiosity scale (Kashdan et al., 2018) was also examined, in which Stress Tolerance was the only subset to correlate with RSFC between regions involved in the hippocampal-VTA loop. Specifically, greater functional connectivity between the right VTA and left NAcc related to greater scores on Stress Tolerance. This subset of the 5-Dimensional Curiosity scale reflects the perceived ability in coping with anxiety involved in encountering the unknown. This finding suggests that individuals who can successfully cope with anxiety involved in encountering the unknown are likely to show an increased functional connectivity between the right VTA and contralateral NAcc. Previous anatomical evidence supports the direct projections from the VTA to the NAcc in releasing dopamine (Kahn & Shohamy, 2013; Fox et al., 2016; Swanson, 1982). Dopamine release was traditionally thought not to cross hemispheres from the VTA to the NAcc, however some research now indicates that some dopaminergic neurons project and release dopamine in the contralateral hemisphere (Fox et al., 2016; Molochnikov & Cohen, 2014). The present finding that increased functional communication between the right VTA and left NAcc is related to increased Stress Tolerance suggests that better coping ability with anxiety of the unknown may be related to increased dopamine release between these well-connected structures. Further investigation is warranted to examine whether dopamine release within the mesolimbic dopamine system predicts Stress Tolerance say for example, during anticipation for unknown information.

3.4.4 Limitations and future directions

The present study comes with some limitations that should be considered for future research investigating the functional neural mechanisms underlying trait curiosity. It should be noted that the two experiments in this chapter were exploratory as they were the first of its kind. However, given its exploratory nature, examining the relationship between trait curiosity and ROI-to-ROI functional connectivity resulted in a vast number of correlations. As a result, permutation tests were employed separately for each trait measure of curiosity that corrected for multiple comparisons across 20 ROI-to-ROI RSFC measures, arguably a fairly conservative approach. An alternative method to examine

the underlying functional mechanism of trait curiosity would be to use task-based experiments to identify which ROIs are functionally involved during task performance. A potential future study could investigate group differences of participants who score high versus low in trait curiosity and examine regional activation when completing information and/or novelty seeking curiosity-based tasks. Additionally, although RSFC analyses allows us to determine the connectivity between ROIs in the brain, it does not allow for researchers to comment on the influence of one ROI on the other and how this explains subsequent functional connectivity. For instance, whether connectivity between the NAcc and VTA is driven from the NAcc to the VTA, or VTA to the NAcc. Perhaps the use of Dynamic Causal Modelling or Granger Causality Analyses would better provide information about directed connectivity (Friston, Moran, & Seth, 2013). The ROIs selected in the present study were based on previous neuroimaging studies on reward and motivation, where connectivity between the VTA, NAcc, and hippocampus has already been established (Kahn & Shohamy, 2013). Future research using RSFC may benefit from systematically interrogating networks involved in memory, attention, and salience (Beaty et al., 2016; DeYoung et al., 2010) to further understand the functional specialization of trait curiosity. Finally, given the advances in MRI scanning resolution, future studies should aim to carry out fMRI scanning that use ultra-high magnetic fields at 7T, as they offer higher BOLD signal responses and the higher spatial resolution to delineate between small anatomical brain regions compared to 3T (Uğurbil, 2014; Schuler et al., 2019). As such, delineation of hippocampal subfields such as the ventral subiculum that has been found to provide numerous inputs to the NAcc and shown to influence the mesolimbic dopamine system (Floresco, Todd, & Grace, 2001; Groenwegen et al., 1987), can be used as more specific ROIs to examine their role in novelty and reward-based behaviours.

3.5 Chapter Summary

In summary, this study using resting-state fMRI investigated whether individual variability in the functional organisation of the hippocampal-VTA loop that regulates learning is related to individual differences observed in trait curiosity. The present study found that high trait curiosity was associated with increased functional connectivity between brain regions involved in motivation and memory, including the VTA, NAcc and segments of the hippocampus. In particular, Diversive PC showed a positive (though

non-significant) relationship with RSFC between the NAcc and anterior hippocampus in Experiment 1, whilst in Experiment 2 Stress Tolerance positively related to RSFC between the NAcc and VTA. Overall, the present findings indicate that stronger coupling at rest between regions involved in the hippocampal-VTA loop reflect higher trait curiosity and may explain why curiosity is evoked more frequently and/or more intensely in some people but not others (cf., Grossnickle, 2016; Kashdan & Roberts, 2004). However, it should be noted that across the 2 experiments in this chapter, only 2 correlations out of the total number of correlations conducted (i.e., 13 permutation tests that together resulted in a total of 260 correlations) showed trend level significance indicating that stronger coupling at rest within the hippocampal-VTA loop reflects higher trait curiosity. Due to the exploratory nature of this study, it is recommended that future studies aim to further explore the contribution of other regions and networks in supporting the variability observed in trait curiosity.

Chapter 4: The effect of curiosity and information-prediction errors on delayed memory

4.1 Introduction

Trait curiosity is regarded as a dispositional tendency to experience curiosity more frequently under a variety of conditions. State curiosity is another dimension of curiosity and is considered as a momentary experience of curiosity in response to cues such as novelty and surprise (Grossnickle, 2016; Kashdan & Roberts, 2004). In order to investigate the effects of curiosity and in particular manipulate different states of curiosity in a lab setting, studies often employ trivia memory paradigms (or variations of it). One of the earlier studies conducted by Kang et al. (2009) investigating the effects of state curiosity, involved participants viewing a set of trivia-based questions that elicited high and low epistemic curiosity. When presented with these trivia questions, participants were asked to silently guess the answer and rate both their curiosity and confidence in knowing the answer to the question. After submitting their curiosity and confidence ratings, participants were presented with the question for a second time followed by the presentation of the correct answer. Following this initial phase of the experiment, Kang et al. (2009) had participants report their answers to the questions they had guessed earlier. In order to investigate the relationship between curiosity and memory performance, Kang et al. (2009) invited participants to return 1 to 2 weeks later for a follow up study. Here, participants were presented with the same questions received at encoding and asked to recall the correct answers with the incentive of receiving $0.25 for every correct answer. This initial study found that high versus low levels of curiosity resulted in better recollection for correct answers that were initially guessed incorrectly (i.e., surprising answers) (Kang et al., 2009).

In addition to investigating the effects of curiosity on memory for trivia answers, other studies have also investigated the effect of curiosity on immediate and delayed memory for incidental information. One study conducted by Gruber et al. (2014) instructed participants to rate a number of trivia questions on how likely it was that they knew the answer, and how curious they were in learning the answer to the trivia question (Gruber et al., 2014). This was followed by the encoding phase, where participants were presented with a selected number of high and low curiosity trivia questions previously rated in the screening phase. Following the presentation of the trivia question, participants were asked to fixate their gaze and wait for the answer to appear. During this period of anticipation for the answer, a face appeared on the screen to which participants were instructed to make a judgement on whether the person had potential knowledge of the upcoming trivia answer. Shortly after the presentation of the incidental face, the answer was revealed to participants. In both the immediate and one-day-delayed memory tests, participants were presented with the incidental faces from encoding and asked to make old/new confidence judgments, followed by the presentation of trivia questions where participants were asked to write down the answers. Similar to Kang et al. (2009) participants exhibited better recall memory for trivia answers that elicited high-compared to low-curiosity. Gruber et al. (2014) further found this effect for incidental faces, as faces presented during the anticipation of high curiosity trials were better remembered than faces presented during low anticipatory trials. Although the authors suggest that states of high curiosity help participants to remember incidental information, it can be argued that this information may not have been truly incidental. Participants were asked to think about whether the person whose face appeared during anticipation were knowledgeable about the trivia question, and so this process of association between face and trivia question *during* the state of high curiosity could in fact explain why a face memory effect was observed. Other studies examining memory for incidental information have also found that 'task irrelevant faces' presented in temporal proximity to trivia questions that elicit curiosity are better recognized (Galli et al., 2018; Stare et al., 2018). However, similar to Gruber et al. (2014) these studies asked participants to determine whether the presented person knew or could help answer the trivia question (Galli et al., 2018; Stare et al., 2018), raising the question of whether the face presented between trivia question and answer is truly incidental.

When a surprising or rewarding event occurs, we tend to not only remember the event itself, but perhaps even information surrounding it (Wang et al., 2010). The

synaptic tag-and-capture model suggests incidental information can be consolidated when followed by salient experiences (Dunsmoor et al., 2015; Frey & Morris, 1997). Encoding inconsequential information produces a weak tetanisation at the synapse, inducing early long-term potentiation and creating a synaptic tag; this tag subsequently *captures* plasticity-related proteins associated with long-term potentiation of salient experiences that follow it (Frey & Morris, 1997, 1998; Redondo & Morris, 2011; Wang et al., 2010). In line with this hypothesis, behavioural tagging suggests that transient memories for incidental information are strengthened when followed closely by behaviourally salient experiences (Moncada et al., 2015; Moncada & Viola, 2007). Based on the behavioural tagging and the synaptic tag-and-capture hypothesis, salience has been found to retroactively enhance memory following a 24-hour delay versus immediately after encoding (Dunsmoor et al., 2015; Patil et al., 2016). One study conducted by Murayama and Kitagami (2014) involved participants incidentally encoding images of objects by making judgements as to whether the presented object was natural or man-made. After making their judgement of a single object, participants were presented with an unrelated reward or control cue. The authors found that reward cues predicted later memory for the preceding neutral picture. This retrograde memory effect observed after a delay versus immediately after learning is suggestive of a possible mechanism of memory consolidation.

The effect of curiosity on memory has also been investigated in older and younger adults, in which memory was found to be supported by post-answer interest (McGillivray, et al., 2015). Marvin and Shohamy (2016) describe the 'information-as-reward hypothesis', that suggests curiosity follows the basic principles associated with reward motivated behaviour, where prediction errors appear to play a role in such behaviours. A prediction error is when an outcome differs from what was predicted, where rewards exercise their effects via dopaminergic reward prediction errors (Schultz & Dickinson, 2000; Schultz, 2006; Schultz et al., 1997). Similarly, information-gaps (Loewenstein, 1994) can be viewed as eliciting a prediction error, where "the difference between the satisfaction experienced upon receipt of the information and the curiosity experienced in anticipation of information functions as an information prediction error" (Marvin & Shohamy, 2016, p.267), and serves as a key driver of curiosity on memory. Calculating the difference between the value of the received information (via satisfaction ratings) and the expected value of the information (via curiosity ratings), Marvin and Shohamy (2016) found that participants were more likely to remember information that resulted in a more

positive information prediction error, i.e., instances where satisfaction exceeded one's curiosity. This suggests that perhaps it is not just curiosity that predicts memory but also the satisfaction of information that is received.

Although there is a growing body of evidence investigating the neural mechanisms of state curiosity (Gruber et al., 2014; Kang et al., 2009; Jepma et al., 2012), given that trait curiosity may contribute to its manifestation there has been little investigation into the relationship between trait and state curiosity. For instance, previous studies have shown that individual differences in trait curiosity are associated with individual differences in behaviours that manifest in a number of instances including educational settings and work-related settings. One study examining the relationship between each of the Big Five personality traits and learning found that the effect of Openness to Experience and Conscientiousness on learning were mediated by Epistemic Curiosity (Hassan et al., 2015). Regarding behaviours related to work performance and whether curiosity increases the learning of new skills to help overcome challenges and deal with change in the working environment, Mussel (2013b) found that work-related curiosity correlated with job performance. Other behavioural studies have shown that trait curiosity correlates with exploration/information seeking and anticipation of upcoming information (Risko et al., 2012; Baranes et al., 2015, respectively). Although Chapter 2 was not successful in observing a strong relationship between trait curiosity and fornix microstructure, nor did Chapter 3 indicate a strong relationship between trait curiosity and RSFC within the hippocampal-VTA loop, I speculated whether a behavioural relationship manifests between trait curiosity and curiosity-related measures of memory.

In this chapter, two behavioural experiments were conducted that both utilised a trivia memory paradigm to investigate the effect of states of curiosity on subsequent memory for curiosity-related information (i.e., trivia answers) and incidental information (i.e., faces). The paradigms used in the present experiments were similar to that of Gruber et al. (2014) with minor changes such as asking participants to make a male or female judgement when the face appears on the screen (rather than asking if the presented person is knowledgeable about the topic area), and presenting the faces before the state of curiosity is elicited, as a means to investigate memory for truly incidental information and whether the behavioural tagging/the synaptic tag-and-capture hypothesis explains incidental memory enhancements. I predicted that participants would recall significantly more answers to high- compared to low- curiosity questions,

and that participants recognition memory performance would be greater for faces presented prior to a state of high- versus a state of low- curiosity. Furthermore, this chapter also examined whether information prediction errors predicted subsequent memory for trivia answers. Based on Marvin and Shohamy's (2016) findings, I expected that better memory recall would be observed in instances where ratings for post-answer interest exceeds curiosity for the trivia question (i.e., trials that produce positive prediction errors), compared to instances where ratings for post-answer interest is less than or equal to curiosity for the trivia question (negative and zero prediction errors, respectively). Finally, Experiment 2 examined the relationship between measures of memory and sub-scales from questionnaires that measured types of curiosity and information seeking including the 10-item EC scale (Litman, 2008) and the 5-Dimensional Curiosity scale (Kashdan et al., 2018).

4.2 Experiment 1

4.2.1 Materials and Methods

4.2.1.1 Participants

Thirty-four healthy adults (24 females) with a mean age of 20 years (range: 18-25), with normal or corrected-to-normal vision were recruited from Cardiff University. To the best of our knowledge all participants were native speakers of English and naïve to the experimental aims. Participants provided written consent prior to participating in the study, which was approved by the Cardiff University Research Ethics Committee. Participants were compensated with either course credits or payment for their participation.

4.2.1.2 Stimuli

Black and white (greyscale) images of faces were obtained from an online database (Minear & Park, 2004). Three sets of 50 faces were compiled and matched as closely as possible to each other with age (range = 18-84; mean = 35.70), gender (M:F = 20:30), and race (Asian: Caucasian: African-American = 1:35:14). The 3 sets of faces were counterbalanced across participants for high, low curiosity trials (during encoding) and new faces (at retrieval). Trivia questions were compiled from the literature (Galli et al., 2018; Fastrich et al., 2018). Some questions were excluded on the basis that they were based around American culture and/or consisted of answers that would be too difficult to recall at retrieval. Appendix 5 illustrates the list of trivia questions and answers used in the present experiment. The trivia pool was randomised before being administered to each participant during the screening phase of the experiment. Stimuli presentation was programmed with Psychophysics Toolbox (Brainard,1997) interfaced with MATLAB 2015a (The MathWorks, Inc., Natwick, Massachussetts).

4.2.1.3 Experimental procedure

4.2.1.3.1 Screening phase

Participants were given detailed instructions before the start of each phase of the experiment. During a single trial of the screening phase participants were presented with a trivia question (6 seconds) and asked to first rate their curiosity in finding out the answer on a scale from 1-6 (1 = not at all curious; 6 = extremely curious to know the answer to the trivia question), and then how confident they were in knowing the answer on a scale from 1-6 (1 = not at all confident; 6 = extremely confident). Participants were given a set duration of 3 seconds to give a response for each of the ratings. Participants were encouraged to use the full range of keys for the curiosity and confidence ratings and asked to rest their fingers on the relevant keys on the keyboard. Before the start of the experiment participants were guided through a practice run on what to expect during a single trial and to familiarise themselves with the timings. The screening phase took approximately 45 minutes to complete. The screening phase terminated once participants had successfully rated: 50 trivia questions that they were curious in finding

out the answer to (high curiosity trials; ratings 4-6), and 50 questions they were not curious about (low curiosity trials; ratings 1-3), where the confidence rating in knowing the answer ranged between 1-5 (i.e., not including trials where confidence was rated 6, extremely confident) (**Figure 4.1**; Green screening phase).

4.2.1.3.2 Encoding phase

The first 50 high and first 50 low curiosity trials rated successfully were then fed into the encoding phase of the experiment that was administered immediately after the screening phase. Participants were given detailed instructions as well as a short practice run on what to expect before starting this part of the experiment. Participants were told they would be presented with a selection of trivia questions from the previous phase along with their answers. **Figure 4.1** (Purple encoding phase) illustrates that a single trial involved the presentation of an exclamation mark (1 second) followed by a black and white face (2 seconds), in which participants were asked to indicate whether the face was male or female[1] (key 1 = male; key 6 = female). They were then presented with a fixation cross (1 second) followed by the trivia question (4 seconds) and then the anticipatory fixation cross (8 seconds) where they were told to think about what the possible answer to the question could be. They were then presented with the answer (2 seconds) followed by a question asking how interesting they found the answer to the question on a scale from 1-6 (1 = not at all interesting; 6 = extremely interesting) where they had 2 seconds to respond. The inter-trial interval was a fixation cross of 5 seconds. Participants were presented with 5 blocks of 20 trials, where each block consisted of 2 sets of 5 consecutive high curiosity trials and 2 sets of 5 consecutive low curiosity trials. The order that these sets were presented are illustrated in Appendix 6A, where the presentation of high and low curiosity conditions were counterbalanced for odd and even subjects. After each block of 20 trials, participants were encouraged to take a break before starting the next block of trials. The encoding phase of the experiment lasted approximately 50 minutes. Participants returned the following day (~24 hours) to complete the retrieval phase of the experiment, which ran for approximately 40 minutes.

[1] *Across all participants, the average accuracy for male/female judgements was 91%. Three participants had a male/female judgement accuracy of less that 80%. Removing these participants from the analysis in section 4.2.2.2 does not change the statistical significance of the t-test.*

Participants were counterbalanced on whether they completed face retrieval first followed by the recall of answers, or answer recall first followed by retrieval of faces (no significant difference in memory performance (for either faces or answers) was found between those who completed the retrieval of faces first or answers first).

4.2.1.3.3 Retrieval of trivia answers

The 100 trivia questions from encoding were randomised and presented to participants in an excel sheet. Participants were asked to answer the questions in order as best they could in their own time. Participants spent approximately 20 minutes to complete this phase of the experiment (**Figure 4.1**; Blue retrieval phase).

4.2.1.3.4 Retrieval of faces

Participants were presented with 100 faces from encoding and 50 new faces in a randomised order. Participants were asked to give a 'remember' or 'know' response by pressing key 1 or 3, respectively, if they thought the face was 'old' (i.e., seen the day before), or press key 9 if they thought the face was 'new' (**Figure 4.1**; Blue retrieval phase). Participants were given detailed instructions on how to distinguish a 'remember' response from a 'know' response. Specifically, they were instructed that a *remember* response should be given if they could recollect contextual details about the face from the time of encoding, and a *know* response should be given if the face triggers a feeling of familiarity but no specific details from the time of encoding comes to mind (Yonelinas, 2002). Participants were given an unlimited duration to respond to faces, however they were instructed to respond within 2-3 seconds, not spending too long on any one trial. **Figure 4.1** illustrates the sequence of phases on two consecutive days. Finally, participants completed a series of curiosity questionnaires, they were debriefed and then compensated for their participation in the study.

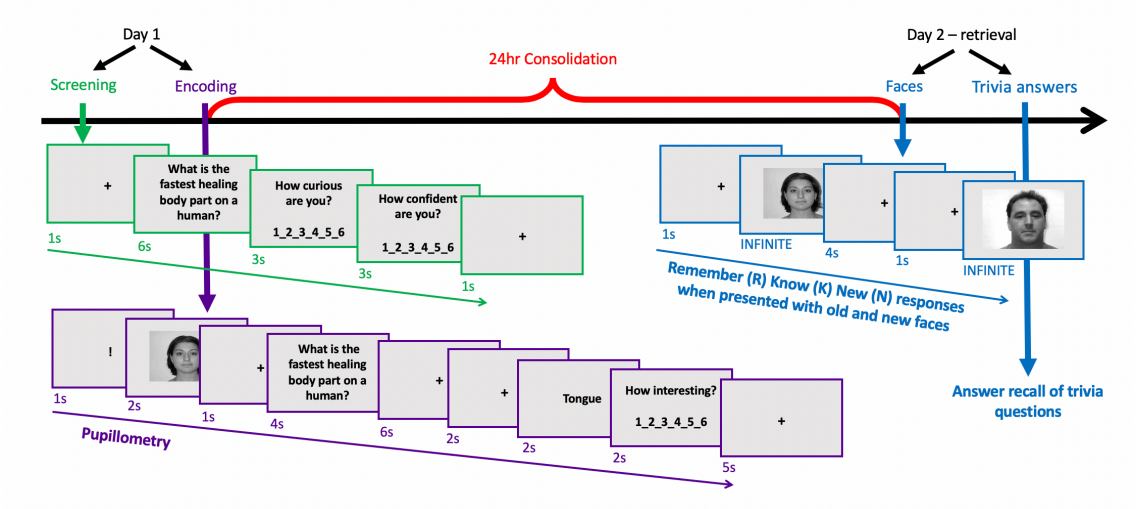


Figure 4.1: Example trials from screening, encoding and retrieval phases of Experiment 1. Participants first completed the screening phase where for each trial, curiosity in finding out the answer to the presented trivia question was rated followed by their confidence rating in knowing the answer (Green screening phase). The first 50 high and low curiosity trials in which participants did not know the answer were used in the encoding phase of the experiment (i.e., Purple encoding phase). Pupil dilation was recorded throughout the encoding phase, where for each trial, participants were first presented with a face (and asked to make a judgement on gender), followed by the presentation a trivia question from the previous phase. Participants then fixated their gaze on a fixation cross which was followed by answer presentation and rating on how interesting the answer was (Purple encoding phase). Participants returned the next day and completed the recognition memory task for faces and the recall of trivia answers to questions that were presented at encoding (Blue retrieval phase).

[1] Pupillometry method and results are not addressed in the thesis.

4.2.1.4 Statistical analysis

4.2.1.4.1 Recall memory for answers

Recall rate was calculated for each curiosity condition by taking the total number of successfully recalled trivia answers and dividing it by the total number of trials in the condition (i.e., 50 trials).

$$Recall\ rate = \frac{total\ number\ of\ successfully\ recalled\ trivia\ answers}{total\ number\ of\ trials\ in\ condition} \times 100$$

4.2.1.4.2 Recognition memory for faces

'Remember' and 'know' responses were collapsed into an 'old' response given the low number of recollection trials for both high and low curiosity conditions. Thus, trials at retrieval were categorised as remembered (participants assigned either a 'remember' or 'know' response to a face that was presented at encoding), forgotten (participants assigned a new response to a face that was presented at encoding), or false alarm (participants assigned a 'remember' or 'know' response to a face not presented at encoding). Recognition memory performance was calculated for each participant, where the data from five participants were removed for having miss and/or false alarms greater than 2SD above the mean of the whole sample.

$$Recogntion\ memory\ performance = \frac{total\ number\ of\ correctly\ recognized - \ false\ alarms}{total\ number\ of\ trials\ in\ condition} \times 100$$

4.2.1.4.3 Information prediction error analysis

Similar to Marvin and Shohamy (2016), information prediction errors (IPEs) were calculated for each trial by subtracting the curiosity rating from the post-answer interest rating.

$$Information\ prediction\ error = \ Post\ answer\ interest\ rating - curiosity\ rating$$

IPEs ranged from -5 to 5, given that the highest rating possible for both curiosity and post-answer interest was 6. Separately, for the high and low curiosity trials, for each participant the total number of positive (+1 to +5 IPE), negative (-1 to -5 IPEs), and zero IPE trials were calculated along with the proportion of these trials that were correctly recalled. The effect of the different IPEs was examined separately for the two types of curiosity trials, given that states of high- versus low-curiosity have been consistently found to enhance learning of trivia answers. One participant was excluded from the IPE analysis of high curiosity trials as their total number of IPE trials was less than 80% (i.e., this participant failed to give a post-answer interest response on more than 10 trials). Similarly, a different participant was excluded from the IPE analysis of low curiosity trials for the same reasons. The final sample for the IPE analysis (for each high and low curiosity trials) consisted of 33 participants. Repeated measures one-way ANOVA's were conducted with three levels of interest (high, zero, and low IPE). Mauchly's test was used to assess the assumption of sphericity. If a significant effect was observed, I next employed post-hoc tests for all possible comparisons and applied a Bonferroni correction by dividing the 0.05 alpha by the number of comparisons (i.e., 0.05/3 = 0.0167).

4.2.2 Results

4.2.2.1 The effect of curiosity on learning of answers to trivia questions

Participants recalled significantly more answers to trivia questions that elicited high curiosity than answers to questions that elicited low curiosity (61.29%, SE ± 2.80 versus 47.18%, SE ± 3.10; $t_{(33)} = 7.36$, $p < 0.001$, Cohens $d = 1.262$; **Figure 4.2A**), replicating findings from the literature (Fastrich et al., 2018; Galli et al., 2018; Gruber et al., 2014; Kang et al., 2009; McGillivray et al., 2015; Mullaney et al., 2014; Stare et al., 2018; Wade & Kidd, 2019).

4.2.2.2 The effect of curiosity on learning of incidental faces

In order to understand how different states of curiosity predicts memory for incidental information, it was hypothesised that recognition memory would be higher for incidental faces presented before a state of high curiosity is elicited. There was no significant difference in recognition memory performance for faces presented prior to states of high curiosity (high trivia question presentation) compared to faces presented prior to states of low curiosity (low trivia question presentation) (high curiosity: 27.66%, SE = ± 2.46; low curiosity: 25.79%, SE = ± 1.93; $t_{(28)} = 1.20$, $p = 0.120$, Cohens $d = 0.223$; **Figure 4.2B**).

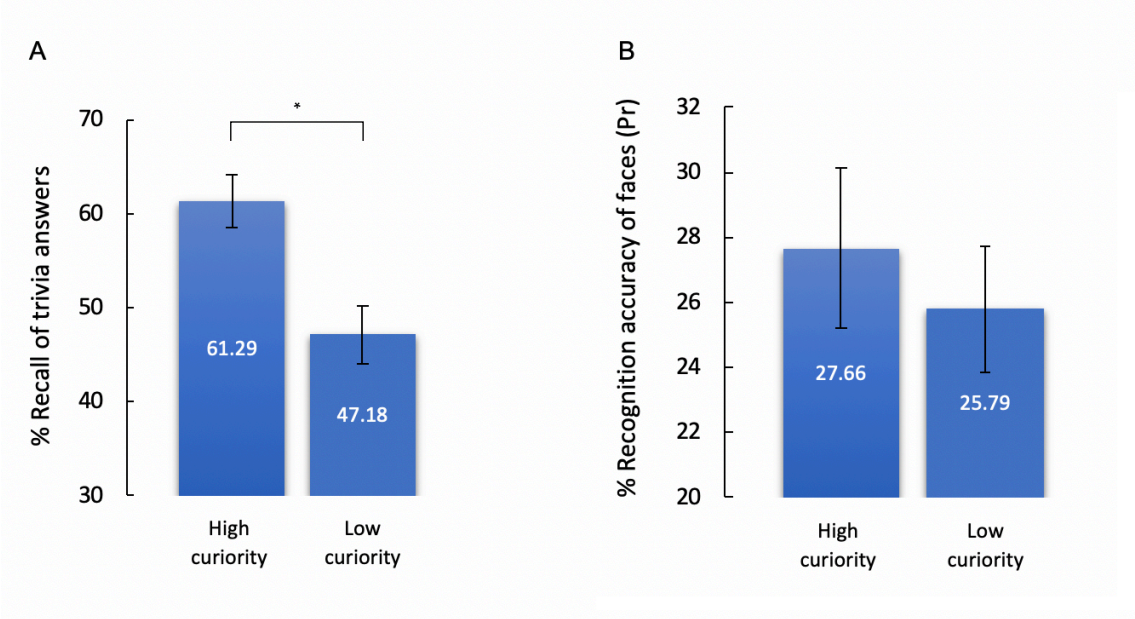


Figure 4.2: High curiosity benefits the learning of trivia answers but not incidental faces. **(A)** Participants recalled more answers to questions that elicited high- versus low-curiosity. **(B)** Participants did not show higher recognition memory for faces encoded in conditions of high- versus low-curiosity. Error bars represent ± 1 SEM. *indicates significant difference between conditions of interest**.**

4.2.2.3 Information prediction errors and its effect on memory for high curiosity trivia answers

The hypothesis that the type of IPE would affect the proportion of high curiosity answers recalled was examined using a repeated measure one-way ANOVA. Mauchly's test indicated that the assumption of sphericity had not been violated ($\chi^2(2) = 1.694$, $p > 0.05$). The ANOVA demonstrated a significant difference between the condition means, $F_{(2, 64)} = 17.975$, $p < 0.001$, **Figure 4.3A**. This represented an effect size (ηp^2) of 0.360, showing that 36.0% of the variation in the number of high curiosity answers recalled was accounted for by type of IPE. Post-hoc comparisons applying Bonferroni correction confirmed that the proportion of high curiosity recalled answers was significantly less for negative IPE trials than zero IPE trials ($p < 0.001$) or positive IPE trials ($p < 0.001$). These differences demonstrated medium effect sizes ($d = 0.773$ and 0.729, respectively). The

difference between zero IPE trials and positive IPE trials was not statistically significant (p = 0.999) and this comparison demonstrated a small effect size (d = 0.003).

4.2.2.4 Information prediction errors and its effect on memory for low curiosity trivia answers

The hypothesis that the type of IPE would affect the proportion of low curiosity answers recalled was examined using a repeated measure one-way ANOVA. Mauchly's test indicated that the assumption of sphericity had not been violated ($\chi^2(2) = 1.402$, $p > 0.05$). The ANOVA demonstrated a significant difference between the condition means, $F_{(2, 64)} = 16.768$, $p < 0.001$, **Figure 4.3B**. This represented an effect size (ηp^2) of 0.344, showing that 34.4% of the variation in the number of low curiosity answers recalled was accounted for by type of IPE. Post-hoc comparisons applying Bonferroni correction confirmed that the proportion of low curiosity recalled answers was significantly less for negative IPE trials than positive IPE trials ($p < 0.001$). This difference demonstrated a medium effect size (d = 0.894). Furthermore, the proportion of low curiosity recalled answers was significantly less for zero IPE trials than positive IPE trials ($p < 0$ .001). This difference demonstrated a medium effect size (d = 0.799). The difference between zero IPE trials and negative IPE trials was not statistically significant (p = 0.700) and this comparison demonstrated a small effect size (d = 0.203). These results suggest that positive IPE trials resulted in greater recall rate for low curiosity answers than negative and zero IPE trials.

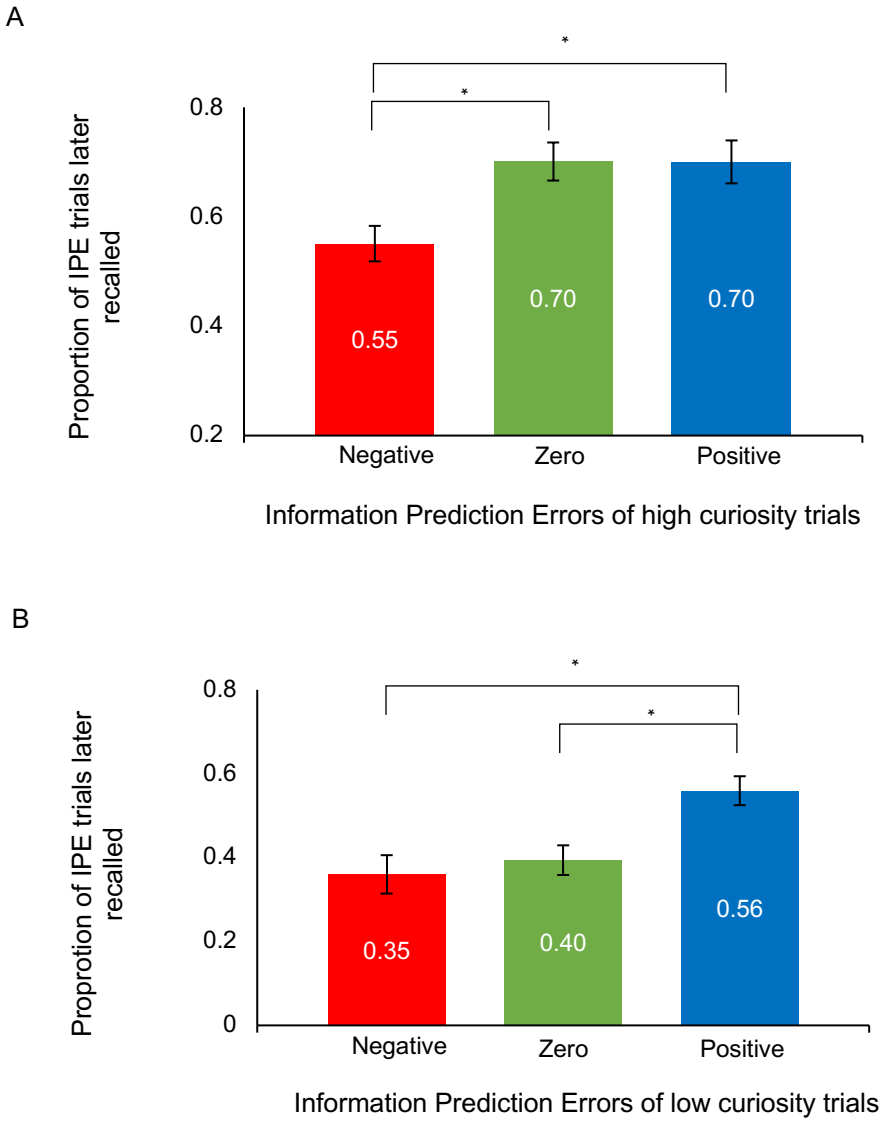


Figure 4.3: For each individual the proportion of trials in which information was later recalled for the three types of information prediction errors (negative, zero, and positive IPEs) of high curiosity trials (**A**) and low curiosity trials (**B**). Graphs A and B show the mean across all individuals and error bars represent ± 1 SEM. *indicates significant difference between conditions of interest**.** The total number of participants included in the IPE analysis (for each high and low curiosity trials) consisted of 33 participants.

4.3 Experiment 2

Experiment 1 suggested that states of high- versus low-curiosity enhances memory for trivia answers, but not incidental faces presented prior to the presentation of the trivia question. Furthermore, for high curiosity trials both positive and zero IPEs resulted in greater recall rate for answers than negative IPE trials, whilst for low curiosity trials positive IPEs resulted in greater recall rate for answers than negative and zero IPE trials. In Experiment 2, small changes in method protocol and stimuli presentation were employed. Despite these changes, Experiment 2 aimed to provide further evidence for the curiosity-answer memory effect and find an effect of curiosity on incidental memory for faces.

First, as Experiment 1 incorporated pupillometry methods during the encoding phase (not discussed in the thesis), the stimuli consisted of black and white (grey scale) images as a means to reduce any fluctuations in pupil size due to visual input. Therefore, in Experiment 2 given that pupillometry methods were not used at any point in the experiment, coloured images identical to that of Gruber et al. (2014) were employed as the incidental images to be presented prior to the presentation of the trivia question (i.e., when a state of curiosity was elicited). Additionally, the number of trials in each curiosity condition was reduced from 50 trials (as in Experiment 1) to 30 trials. Thirty trials were chosen (in each condition) based on a pilot study where a similar curiosity answer memory effect was observed to that of Experiment 1. Furthermore, lowering the trial number to 30 enabled a quicker administration of the experiment and subsequently allowed for more participants to be tested during the testing time frame. Other changes from Experiment 1 included using different stimuli presentation timings such as a shorter anticipation period and shorter presentation of answer. Participants were also given a little more time to make their post-answer interest rating. Furthermore, the duration of the fixation following the face presentation was increased from 1 to 4 seconds (this was done to match the presentation timings to a potential fMRI study that requires longer fixation periods). Finally, given that Experiment 1 indicated there was no significant difference in memory performance when administering retrieval of answers followed by recognition of faces versus administering recognition of faces followed by retrieval of answers, in Experiment 2 all participants first completed the face recognition memory phase followed by the recall of trivia answers.

Identical to Experiment 1, it was hypothesised that participants would recall significantly more answers to high- compared to low- curiosity questions, and that participants recognition memory performance would be greater for faces presented prior to a state of high- versus a state of low- curiosity. Furthermore, I expected that better memory recall would be observed in instances where ratings for post-answer interest exceeds curiosity for the trivia question (i.e., trials that produce positive prediction errors), compared to instances where ratings for post-answer interest is less than or equal to curiosity for the trivia question (negative and zero prediction errors, respectively). Importantly, Experiment 2 also investigated the relationship between trait and state curiosity memory effects. Participants were given a series of questionnaires identical to the ones administered in Chapter 2 and 3 (Experiment 2), to which the analyses focussed on the 2 subscales of EC (Interest and Deprivation EC) and the three subscales of the 5-Dimensional Curiosity scale that were believed to be the most relatable to the curiosity paradigm. These included the Joyous Exploration subscale, reflecting the preference for novel experiences and information where feeling curious and subsequent exploratory behaviours are deemed pleasurable; Deprivation Sensitivity subscale, reflecting the aversive aspect of curiosity, in which individuals seek out information as a means to escape the tension elicited from not knowing something; and Stress Tolerance subscale, reflecting the perceived ability in coping with anxiety involved in encountering the unknown, were considered to better describe the type of curiosity depicted in the present curiosity paradigm. In contrast, the Social Curiosity subscale describing an individual's fascination and fixation in how other people think, act, and feel; and the Thrill Seeking subscale reflecting a person's tendency to seek out adventure and pleasure particularly when significant risks are present, were not descriptive of the type of curiosity elicited in the current curiosity paradigm and hence were not analysed for the present chapter. Furthermore, the subscales of the EC scale in comparison to the subscales of the PC scale were better suited to the curiosity paradigm in which Epistemic Curiosity rather than Perceptual Curiosity was elicited. Based on theories that suggest a positive relationship between trait and state curiosity, where some studies have shown individual differences in trait curiosity relate to individual differences in behaviour (e.g., Grossnickle, 2016; Hassan et al., 2015; Mussel, 2013b; Kashdan & Yuen, 2007), I predicted that participants with higher trait curiosity (i.e., scoring high in subscales of interest: Interest EC, Deprivation EC, Joyous Exploration, Deprivation Sensitivity and Stress Tolerance subscales) would show larger effects of curiosity states on memory. Therefore, subscales of trait curiosity were predicted to positively correlate with the

following measures of memory: **(1)** curiosity-related answer memory benefit (high curiosity answer recall rate - low curiosity answer recall rate), and **(2)** overall answer memory (high answer recall rate + low answer recall rate); **(3)** curiosity-related face memory benefit (high curiosity face recognition memory performance - low curiosity face recognition memory performance), and **(4)** overall face memory (high curiosity face recognition memory performance + low curiosity face recognition memory performance); **(5)** high curiosity IPE-related answer memory benefit (positive IPE – negative IPE); and **(6)** low curiosity IPE-related answer memory benefit (positive IPE – negative IPE).

4.3.1 Materials and Methods

4.3.1.1 Participants

Fifty-five healthy adults (47 females) with a mean age of 19 years (SD ± 1.75, range = 18-25), with normal or corrected-to-normal vision were recruited from Cardiff University. This sample was identical to the sample reported in Chapter 2 and 3 (Experiment 2). To the best of our knowledge all participants were naïve to the experimental aims. Participants provided written consent prior to participating in the study, which was approved by the Cardiff University Ethics Committee, and were compensated with course credits and/or payment for their participation.

4.3.1.2 Stimuli

Coloured images of faces were obtained from Gruber et al (2014). Three sets of 30 faces were compiled and matched as closely as possible to each other with gender (M:F = 15:15). The 3 sets of faces were counterbalanced across participants for high, low curiosity trials (during encoding), and new faces (at retrieval). The pool of trivia questions used in this experiment was identical to that in Experiment 1.

4.3.1.3 Trait curiosity measures

Participants completed a variety of sub-scales from questionnaires that measured types of curiosity and information seeking. Identical to Chapter 2 and 3 (Experiment 2), participants completed the 10-item EC scale (Litman, 2008; Appendix 1) and the 5-Dimensional Curiosity scale (Kashdan et al., 2018; Appendix 3), of which Joyous Exploration, Deprivation Sensitivity, and Stress Tolerance were the three subscales of interest to be correlated with measures of memory. Cronbach's alpha was calculated for each self-report measure using SPSS (version 23) where Cronbach's alpha coefficients for all curiosity subsets of interest were >0.70 and <0.90 suggesting good internal consistency (Tavakol & Dennick, 2011) (Appendix 15).

4.3.1.4 Experimental procedure

Participants were given detailed instructions before the start of each phase of the experiment. The screening and encoding phases were similar to that of Experiment 1, with a few minor changes such as duration of presented stimuli and the number of trials in each curiosity condition. During the screening phase participants were presented with trivia questions and asked to rate their curiosity in finding out the answer on a scale from 1-6 (1 = not at all curious; 6 = extremely curious to know the answer to the trivia question), and then how confident they were in knowing the answer on a scale from 1-6 (1 = not at all confident; 6 = extremely confident). The screening phase took approximately 30 minutes to complete, and terminated once participants had successfully rated: 30 trivia questions that they were curious in finding out the answer (high curiosity trials), and 30 questions they were not curious about (low curiosity trials), where the confidence rating in knowing the answer ranged between 1-5, similar to Chapter 4 Experiment 1 (i.e., not including trials where confidence was rated 6, extremely confident) (**Figure 4.4**; Green screening phase). The first 30 high and first 30 low curiosity trials rated successfully were then fed into the encoding phase of the experiment. At encoding, participants were presented with 4 blocks of 15 trials, where each block consisted of 3 sets of 5 consecutive trials that comprised of either 2 sets of high curiosity trials (and one set of low curiosity trials) or 2 sets of low curiosity trials (and one set of high curiosity trials). The order that these sets were presented are illustrated in Appendix 6B, where the presentation of high and low curiosity conditions were counterbalanced for odd and even

subjects. After each block of 15 trials participants were encouraged to take a break before starting the next block of trials. The encoding phase[1] of the experiment lasted approximately 30 minutes (**Figure 4.4**; Purple encoding phase). Participants were invited back the next day (~24 hours) where they completed the retrieval phase of the experiment (**Figure 4.4**; Blue retrieval phase). The retrieval phase lasted approximately 30 minutes, in which participants first completed the remember/know recognition memory test for faces followed by the recall of trivia answers. Participants were presented with 60 faces from encoding and 30 new faces in a randomised order. After the face recognition memory test, the 60 trivia questions from encoding were randomised and presented to participants in an excel sheet. Participants were asked to answer the questions in order as best they could in their own time. **Figure 4.4** illustrates the timing parameters for the sequences of the three phases carried out over two consecutive days. Finally, participants completed a series of curiosity trait questionnaires, and were debriefed and compensated for their participation in the study. It should be taken into account that this experiment was part of a larger study that involved the administration of MRI scanning procedures and unrelated reward tasks. Participants took part in the MRI scanning sessions on a separate day to the administration of the curiosity-trivia paradigm (MRI findings reported in Chapter 2 and 3), and the other reward tasks were conducted after the screening/encoding phase on day 1, and after the retrieval phase and questionnaires administered on day 2.

[1] *Across all participants, the average accuracy for male/female judgements was 93%. Three participants had a male/female judgement accuracy of less that 80%. Removing these participants from the analysis in section 4.3.2.2 does not change the statistical significance of the t-test.*

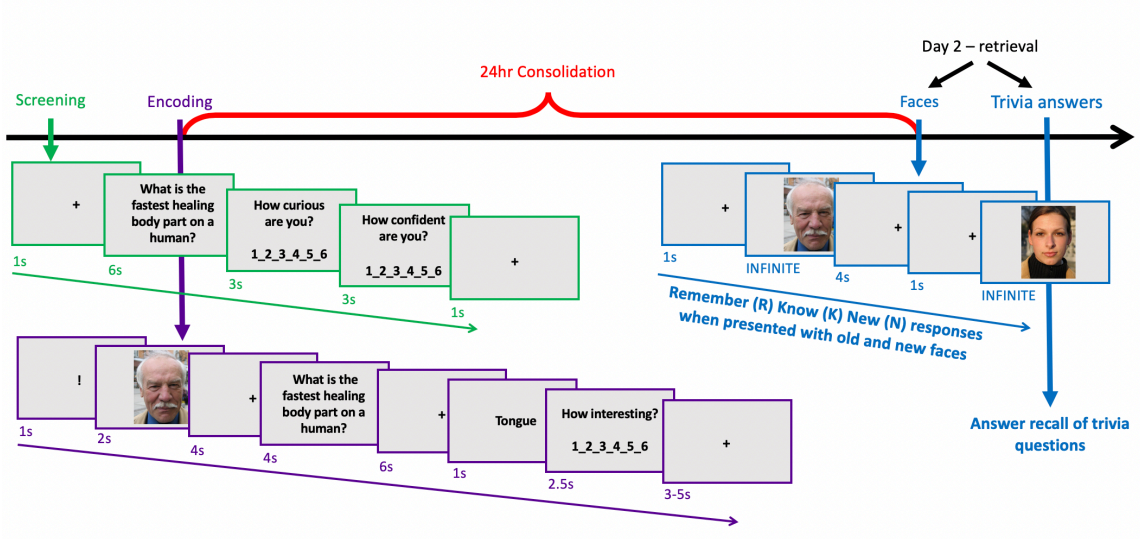


Figure 4.4: Example trials from screening, encoding and retrieval phases of Experiment 2. Participants first completed the screening phase where for each trial, curiosity in finding out the answer to the presented trivia question was rated followed by their confidence rating in knowing the answer (Green screening phase). The first 30 high and low curiosity trials in which participants did not know the answer were used in the encoding phase of the experiment (i.e., Purple encoding phase), where for each trial participants were first presented with a face (and asked to make a judgement on gender), followed by the presentation a trivia question from the previous phase. Participants then fixated their gaze on a fixation cross which was followed by answer presentation and rating on how interesting the answer was (Purple encoding phase). Participants returned the next day and completed the recognition memory task for faces and the recall of trivia answers to questions that were presented at encoding (Blue retrieval phase).

4.3.1.5 Statistical analysis

Statistical analysis of recall memory for trivia answers and recognition memory for faces were identical to that of Experiment 1. The data from three participants were removed from the answer recall analyses and the face memory analyses (one participant failed to complete the retrieval phase of the experiment, 2 participants failed to accumulate enough trials during the screening phase to proceed to the encoding phase of the experiment). Additionally, for the answer recall analyses, 2 participants' data were not successfully saved. The final sample for the answer recall analyses therefore

consisted of 50 participants. The recall rate was calculated for high and low curiosity conditions (i.e., total number of successfully recalled trivia answers/30 trials). In addition to the 3 participants removed for the face memory analyses, 4 participants were excluded for having false alarms and/or misses greater than 2SD above the mean of the whole sample. The final sample for the face memory analyses thus consisted of 48 participants. Due to insufficient trial numbers for remember and know responses, separately, I collapsed remember and know responses and calculated recognition memory performance for high and low curiosity conditions (i.e., hits – false alarms/30 trials).

Identical to Experiment 1, IPEs were calculated for each trial by subtracting the curiosity rating from the post-answer interest rating. Separately, for the high and low curiosity conditions, for each participant the total number of positive (+1 to +5 IPE), negative (-1 to -5 IPEs), and zero IPE trials were calculated followed by the proportion of these trials that were correctly recalled. One participant was excluded from the IPE analysis of low curiosity trials as their total number of IPE trials was less than 80% (i.e., this participant failed to give a 'interestingness' response on more than 6 trials). The final sample for the IPE analysis for high and low curiosity trials were 50 and 49 participants, respectively. Repeated measures one-way ANOVA's with three levels of interest (high, zero, and low IPE) were conducted, where Mauchly's test was used to assess the assumption of sphericity. If a significant effect was observed, I next employed post-hoc tests for all possible comparisons and applied a Bonferroni correction by dividing the 0.05 alpha by the number of comparisons (i.e., 0.05/3 = 0.0167).

To test for associations between curiosity trait scores and measures of memory, directional Pearson's correlations were conducted using MATLAB. For each subset of the EC scale (Interest and Deprivation subscales) and the 3 subscales of interest from the 5-Dimensional Curiosity scale (Joyous Exploration, Deprivation Sensitivity, and Stress Tolerance), the total score for each participant was calculated. Participants' data with trait curiosity scores +/– 3SD beyond the group mean were considered as outliers and removed from respective analyses. This resulted in one participant's data being removed from analyses involving the Joyous Exploration subscale. To test whether the Pearson's correlation coefficient *r,* reflecting the positive association between trait curiosity and each measure of memory, was statistically significant, non-parametric permutation tests (one-tailed) that randomly permute the real data between participants were employed. The following measures of memory included: **(1)** curiosity-related

answer memory benefit (high curiosity answer recall rate - low curiosity answer recall rate); **(2)** overall answer memory (high answer recall rate + low answer recall rate); **(3)** curiosity-related face memory benefit (high curiosity face recognition memory performance - low curiosity face recognition memory performance); **(4)** overall face memory (high curiosity face recognition memory performance + low curiosity face recognition memory performance); **(5)** high curiosity IPE-related answer memory benefit (positive IPE – negative IPE); and **(6)** low curiosity IPE-related answer memory benefit (positive IPE – negative IPE). Permutation tests were conducted separately for the EC scale and the 5-Dimensional Curiosity scale. Each test corrected for multiple comparisons across the subscales within a curiosity scale (e.g., Interest and Deprivation EC; Joyous Exploration, Deprivation Sensitivity, & Stress Tolerance). The methodological steps taken to carry out these non-parametric permutation tests are described in Chapter 2. The 95% confidence intervals (CI) for each correlation was derived using a bootstrapping method based on 1000 iterations.

4.3.2 Results

4.3.2.1 The effect of curiosity on learning of answers to trivia questions

Participants recalled significantly more answers to questions that elicited high curiosity than answers to trivia questions that elicited low curiosity (high curiosity: 61.00% SE ± 2.16; low curiosity: 47.27%, SE ± 2.48; $t_{(49)} = 7.19$, $p < 0.001$, Cohen's $d = 1.02$; **Figure 4.5A**), replicating earlier findings (Chapter 4, Experiment 1).

4.3.2.2 The effect of curiosity on learning of incidental faces

There was no significant difference in recognition memory performance for faces presented prior to states of high curiosity compared to faces presented prior to states of low curiosity (high curiosity: 30.21% SE ± 2.54; low curiosity: 29.58%, SE ± 2.36; $t_{(47)} = 0.362$, $p = 0.360$, Cohen's $d = 0.05$; **Figure 4.5B**).

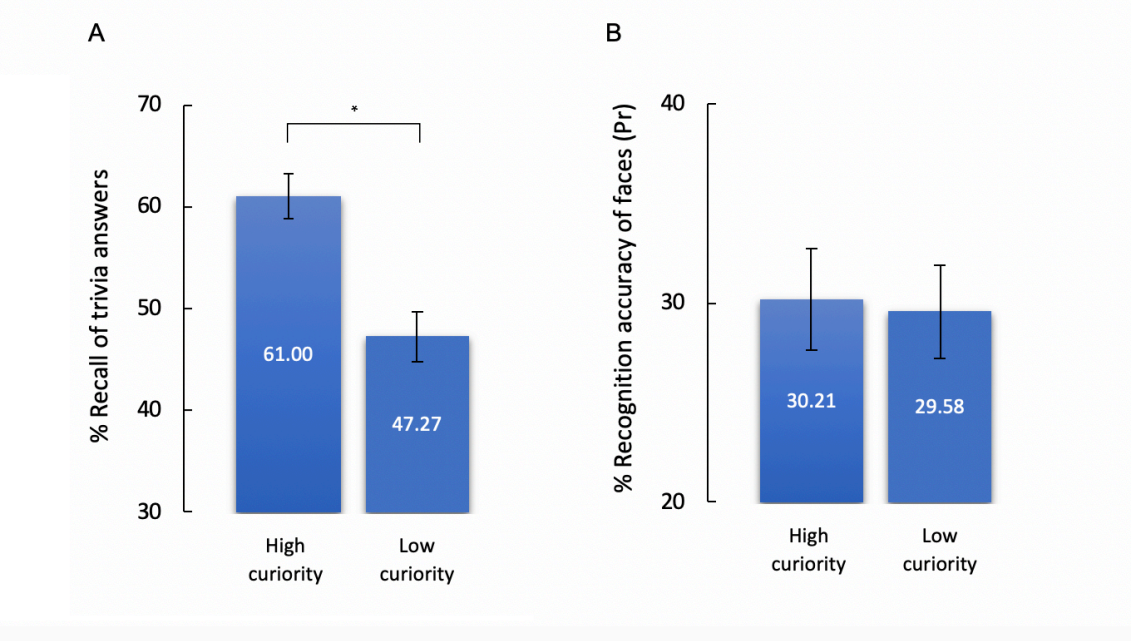


Figure 4.5: High curiosity benefits the learning of trivia answers but not incidental faces. **(A)** Participants recalled more answers to questions that elicited high- versus low-curiosity. **(B)** Participants did not show higher recognition memory for faces encoded in conditions of high- versus low-curiosity. Error bars represent ± 1 SEM. *indicates significant difference between conditions of interest.

4.3.2.3 Information prediction errors and its effect on memory for high curiosity trivia answers

The hypothesis that the type of IPE would affect the proportion of high curiosity answers recalled was examined using a repeated measure one-way ANOVA. Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2(2) = 12.516$, $p < 0.05$) therefore degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.813$). The ANOVA demonstrated a significant difference between the condition means, $F_{(1.63, 79.71)} = 9.410$, $p = 0.001$, **Figure 4.6A**. This represented an effect size (ηp^2) of 0.161, showing that 16.1% of the variation in the number of high curiosity answers recalled was accounted for by type of IPE. Post-hoc comparisons applying Bonferroni correction confirmed that the proportion of high curiosity recalled answers was significantly less for negative IPE trials than zero IPE trials ($p < 0.001$) or positive IPE trials ($p = 0.016$). These differences demonstrated large and medium effect sizes (*d*

= 0.911 and 0.547, respectively). The difference between zero IPE trials and positive IPE trials was not statistically significant (p = 0.100) and this comparison demonstrated a small effect size (d = -0.153).

4.3.2.4 Information prediction errors and its effect on memory for low curiosity trivia answers

The hypothesis that the type of IPE would affect the proportion of low curiosity answers recalled was examined using a repeated measure one-way ANOVA. Mauchly's test indicated that the assumption of sphericity had not been violated ($\chi^2(2) = 5.417$, $p > 0.05$). The ANOVA demonstrated a significant difference between the condition means, $F_{(2, 96)} = 32.680$, $p < 0.001$, **Figure 4.6B**. This represented an effect size (ηp^2) of 0.405, showing that 40.5% of the variation in the number of low curiosity answers recalled was accounted for by type of IPE. Post-hoc comparisons applying Bonferroni correction confirmed that the proportion of low curiosity recalled answers was significantly less for negative IPE trials than positive IPE trials ($p < 0.001$). This difference demonstrated a large effect size (d = 1.178). Furthermore, the proportion of low curiosity recalled answers was significantly less for zero IPE trials than positive IPE trials ($p < 0.001$). This difference demonstrated a large effect size (d = 1.097). The difference between zero IPE trials and negative IPE trials was not statistically significant (p = 0.999) and this comparison demonstrated a small effect size (d = 0.085).

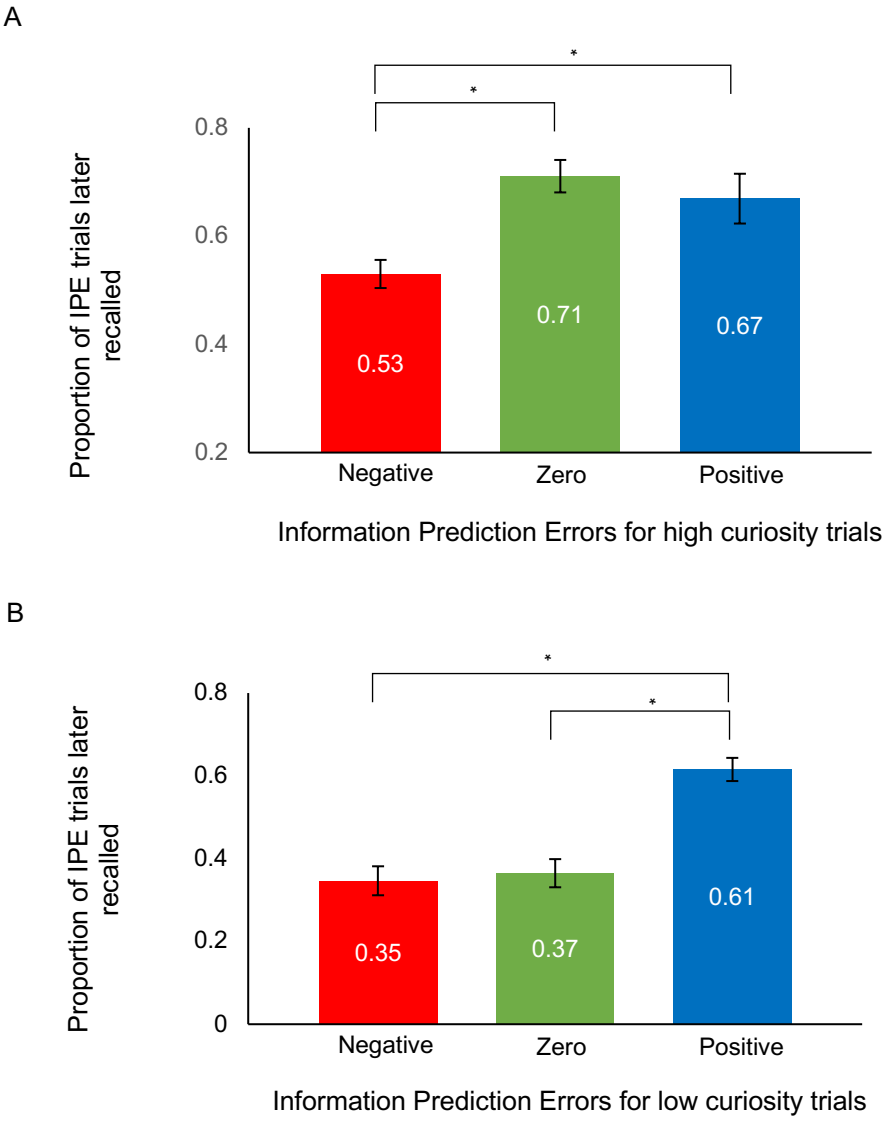


Figure 4.6: For each individual the proportion of trials in which information was later recalled for the three types of information prediction errors (negative, zero, and positive IPEs) of high curiosity trials (**A**) and low curiosity trials (**B**). Graphs A and B show the mean across all individuals and error bars represent ± 1 SEM. *indicates significant difference between conditions of interest. The total number of participants included in the IPE analysis for each high and low curiosity trials consisted of 50 and 49 participants, respectively.

4.3.2.5 State-trait curiosity relationship

A series of permutation tests (one-tailed) that investigated the relationships between trait curiosity scores and measures of memory were conducted. Specifically, two separate permutation tests were conducted for each measure of memory. One permutation test corrected for multiple comparisons for the subscales within the EC scale (Interest and Deprivation EC), the other permutation test corrected for multiple comparisons for the subscales of interest within the 5-Dimensional Curiosity scale (Joyous Exploration, Deprivation Sensitivity, Stress Tolerance). The 6 permutation tests ran between each measure of memory when correlated with subsets of EC indicated no significant positive relationships (**Table 4.1**). With regards to the permutation tests ran between each measure of memory when correlated with the subsets of the 5-Dimensional Curiosity scale, the permutation test that examined the relationship between low curiosity IPE-related answer memory benefit and the three subsets of the 5-Dimensional Curiosity scale indicated that Joyous Exploration showed a positive relationship with low curiosity IPE-related answer memory benefit that approached significance ($r(46) = 0.278$, $p = 0.070$, 95% CI [-0.002, 0.50]), whilst no significant relationships were observed between low curiosity IPE-related answer memory benefit and the two other subsets of interest from this scale (Deprivation Sensitivity, $r(46) = -0.011$; $p_{corr} = 0.839$, 95% CI [-0.26, 0.24]; Stress Tolerance, $r(46) = 0.081$; $p_{corr} = 0.583$, 95% CI [-0.21, 0.35]). The remaining permutation tests ran between each measure of memory when correlated with Joyous Exploration, Deprivation Sensitivity, and Stress Tolerance, indicated no significant positive relationships (**Table 4.2**).

Table 4.1: Separate non-parametric permutation tests were carried out for each measure of memory correlated with the 2 subsets of EC. One-tailed Pearson correlation coefficients, p-values and 95% confidence intervals are reported for each measure of memory when correlated with subsets of EC.

Measures of memory		Epistemic Curiosity scale	
		Interest EC	Deprivation EC
Trivia answer			
Curiosity answer memory benefit	Pearson's *r*(48)	-0.084	-0.013
	p_{corr}	0.856	0.698
	CI [LL,UL]	[-0.45,0.27]	[-0.27,0.25]
Overall answer memory	Pearson's *r*(48)	0.199	0.058
	p_{corr}	0.144	0.504
	CI [LL,UL]	[-0.06,0.41]	[-0.27,0.37]
Faces			
Curiosity face memory benefit	Pearson's *r*(46)	0.001	-0.130
	p_{corr}	0.683	0.932
	CI [LL,UL]	[-0.30,0.30]	[-0.39,0.13]
Overall face memory	Pearson's *r*(46)	-0.030	-0.165
	p_{corr}	0.752	0.961
	CI [LL,UL]	[-0.30,0.25]	[-0.45,0.17]
IPE-related answer memory benefit			
High curiosity trials	Pearson's *r*(48)	0.109	0.115
	p_{corr}	0.348	0.334
	CI [LL,UL]	[-0.17,0.35]	[-0.20,0.39]
Low curiosity trials	Pearson's *r*(47)	0.143	0.049
	p_{corr}	0.253	0.526
	CI [LL,UL]	[-0.20,0.43]	[-0.22,0.33]

EC, *Epistemic Curiosity*; IPE, *information prediction error;* CI, *confidence interval*; LL, *lower level*; UL, *upper level. Curiosity answer memory benefit, overall answer memory and high curiosity IPE-related answer memory benefit correlations are based on 50 participants; curiosity face memory benefit and overall face memory correlations are based on 48 participants; low curiosity IPE-related answer memory benefit correlations are based on 49 participants.*

Table 4.2: Separate non-parametric permutation tests were carried out for each measure of memory correlated with the 3 subsets of the 5-Dimensional Curiosity scale. One-tailed Pearson correlation coefficients, p-values and 95% confidence intervals are reported for each measure of memory when correlated with subsets of interest from the of the 5-Dimensional Curiosity scale.

Measures of memory		Subscales of interest from the 5-Dimensional Curiosity scale		
		Joyous exploration	Deprivation Sensitivity	Stress Tolerance
Trivia answer				
Curiosity answer memory benefit	Pearson's *r*(47)	-0.017	0.182	-0.168
	p_{corr}	0.859	0.261	0.992
	CI [LL,UL]	[-0.34,0.31]	[-0.10,0.42]	[-0.47,0.15]
Overall answer memory	Pearson's *r*(47)	-0.016	0.073	0.141
	p_{corr}	0.843	0.596	0.379
	CI [LL,UL]	[-0.26,0.24]	[-0.22,0.36]	[-0.07,0.38]
Faces				
Curiosity face memory benefit	Pearson's *r*(45)	0.218	-0.343	0.177
	p_{corr}	0.178	0.999	0.274
	CI [LL,UL]	[-0.05,0.46]	[-0.56,-0.10]	[-0.15,0.45]
Overall face memory	Pearson's *r*(45)	-0.043	-0.102	-0.311
	p_{corr}	0.893	0.960	0.999
	CI [LL,UL]	[-0.35,0.29]	[-0.45, 0.31]	[-0.56,-0.01]
IPE-related answer memory benefit				
High curiosity trials	Pearson's *r*(47)	0.111	0.071	-0.116
	p_{corr}	0.477	0.615	0.971
	CI [LL,UL]	[-0.19,0.40]	[-0.28,0.41]	[-0.42,0.23]
Low curiosity trials	Pearson's *r*(46)	0.278	-0.011	0.081
	p_{corr}	**0.070***	0.839	0.583
	CI [LL,UL]	[-0.002,0.50]	[-0.26,0.24]	[-0.21,0.35]

***p < 0.1**; IPE, *information prediction error;* CI, *confidence interval*; LL, *lower level*; UL, *upper level. Curiosity answer memory benefit, overall answer memory and high curiosity IPE-related answer memory benefit correlations are based on 49 participants; curiosity face memory benefit and overall face memory correlations are based on 47 participants; low curiosity IPE-related answer memory benefit correlations are based on 48 participants.*

4.4 Discussion

The present experiments examined the effect of state curiosity on later memory for curiosity-related information. Consistent with the literature, this research found that participants showed increased recall memory for trivia answers to questions that elicited high- versus low-curiosity (Fastrich et al., 2018; Galli et al., 2018; Gruber et al., 2014; Kang et al., 2009; McGillivray et al., 2015; Mullaney et al., 2014; Stare et al., 2018; Wade & Kidd, 2019). These experiments also investigated whether incidental information presented before a state of curiosity is elicited would result in a later memory effect based on the behavioural tagging/synaptic tag-and-capture hypothesis (Dunsmoor et al., 2015; Frey & Morris, 1997; Moncada et al., 2015; Moncada & Viola, 2007; Murayama & Kitagami, 2014; Patil et al., 2016). However, neither experiment found a significant difference in memory performance for faces presented prior to a state of high- versus a state of low-curiosity. In this chapter the effect of IPEs on later memory for trivia answers was also examined, where Experiments 1 and 2 found that for trials which elicited high curiosity, positive and zero IPEs resulted in a significantly greater proportion of trivia answers later recalled than negative IPEs, whilst for low curiosity trials positive IPEs resulted in a significantly greater proportion of trivia answers later recalled compared to zero and negative IPEs. Finally, Experiment 2 further investigated the relationship between trait curiosity and state curiosity measures of memory, where a positive association was found between Joyous Exploration and low curiosity IPE-related answer memory benefit.

4.4.1 High states of curiosity predict memory for trivia answers but not faces

Previous studies have employed versions of the trivia memory paradigm as a means to investigate the effect of state curiosity on immediate and delayed memory performance, where the finding that being in a state of high curiosity benefits later memory for interesting information has consistently been observed (Fastrich et al., 2018; Galli et al., 2018; Gruber et al., 2014; Kang et al., 2009; McGillivray et al., 2015; Mullaney et al., 2014; Stare et al., 2018; Wade & Kidd, 2019). Despite minor differences between Experiments 1 and 2 (i.e., timings of anticipation and answer duration during encoding),

this research provides consistent support for the notion that states of high- versus low-curiosity results in memory consolidation for trivia answers after a 24-hour delay. Specifically, this evidence assists the idea that the anticipation of information facilitates memory specifically when participants are curious to find out the answer. With regards to the incidental faces that were presented to participants prior to when a state of curiosity was elicited, no memory effect was observed in either of the experiments. These experiments categorised a state of curiosity being elicited when the trivia question was presented at encoding and ending when the trivia answer was revealed to participants. According to the behavioural tagging and STC hypothesis, memories for incidental information are retroactively strengthened when followed closely by behaviourally salient experiences (Moncada et al., 2015; Moncada & Viola, 2007; Dunsmoor et al., 2015; Patil et al., 2016). In the present experiments, it is possible that the reason why no face memory effect was observed may be because the presentation of the incidental information was too far removed from the 'salient experience'. Here, the salient experience was defined to be when curiosity was elicited, however, perhaps the salient experience is in fact when the trivia answer (i.e., the source that will resolve a knowledge gap and satisfy curiosity) is presented. Gruber et al. (2014) utilised the sequence of presenting the trivia question, followed by the presentation of a face and then the trivia answer which appeared shortly after. In this instance, faces that were presented before the presentation of a trivia answer associated with high curiosity resulted in better recognition memory performance than faces presented before the presentation of a trivia answer associated with low curiosity (Gruber et al., 2014). However, it can be argued that Gruber et al. (2014) cannot deduce that this anticipatory state of high curiosity drives one to remember incidental information, as participants were also asked to think about whether the person whose face appeared during anticipation were knowledgeable about the trivia question. This process of association between face and trivia question *during* the state of high curiosity in Gruber et al's. (2014) experiment could also contribute to why a face memory effect was observed. In the present paradigms employed, faces were displayed prior to the trivia question rather than during answer anticipation. This was because I believed, based on the STC hypothesis, memories for incidental information are retroactively strengthened when followed closely by behaviourally salient experiences, where a salient experience was perceived to be from when the trivia question was presented to when the answer was revealed. Given the present findings, it is likely that the salient experience is specific to the presentation of the answer. Therefore, future studies wanting to examine the effect of state curiosity on incidental

information may want to consider presenting the face at different timepoints during anticipation (i.e., prior to answer presentation as in Galli et al., 2018; Gruber et al., 2014; & Stare et al., 2018). Ideally, during the presentation of incidental faces, participants would not relate the face to the trivia question, such as in the present study where participants were instructed to make a simple neutral male/female judgement when the face was presented.

Furthermore, future research investigating the effects of curiosity may want to consider the additional effects of prior knowledge. Post-analysis of Experiment 1 and 2 of this chapter indicated that the average confidence rating for high curiosity trials was significantly greater than the average confidence rating for low curiosity trials (Appendix 6C). This could pose difficulty in determining whether curiosity or confidence predicts learning. For instance, it can be argued that trivia answers to questions that were rated as high in curiosity were better remembered because confidence in knowing the answer was also high. However, it is acknowledged in the literature that learning is best predicted by not just curiosity but also prior knowledge. One study by Wade and Kidd (2019) found that participants who believed their guess was close to the correct answer showed a greater level of curiosity in finding out the answer. Similarly, Stare et al. (2018) also found that answers to trivia questions that participants rated as being highly confident in knowing the answer (i.e., having prior knowledge) were better remembered. In order to disentangle the integrative effect of prior knowledge and curiosity, future trivia memory paradigms may want to consider including conditions of high and low curiosity trials that control for confidence/prior knowledge, and/or conditions of high and low confidence trials that control for curiosity to better understand their independent effects on learning. Wade and Kidd (2019) also propose that lower level factors such as salience can influence curiosity. For instance, it is possible that some trivia questions can elicit an emotional response which influences subsequent curiosity self-reports and learning of information that follows. As a means to control for this potential confound, future studies could employ pupillometry methods at the screening phase in order to monitor levels of arousal when a trivia question is first presented, where trials that meet a pre-specified criterion of arousal would then be included in the learning phase. In summary there appears to be a range of factors that can influence levels of curiosity that can range from high level (prior knowledge) to low level factors (salience) (Wade & Kidd, 2019).

4.4.2 Positive information prediction errors result in better memory recall for trivia answers

The effect of IPEs on later answer memory recall was also examined. Marvin and Shohamy (2016) had participants view trivia questions and rate their curiosity in finding out the answer, followed by how satisfied they were when they received the answer. Using these two ratings the authors were able to calculate the participants IPE for each trial, in which calculated IPEs fell into one of three categories (negative, zero, or positive IPE). For each individual the proportion of correctly remembered information was computed for each type of IPE, where Marvin and Shohamy (2016) found that positive IPEs resulted in a greater proportion of correctly remembered information than negative IPEs. Adopting a similar approach in calculating IPEs, Experiment 1 and 2 found some support of the hypothesis that better memory recall would be observed in instances where ratings for post-answer interest exceeds curiosity for the trivia question (i.e., trials that produce positive prediction errors), compared to instances where ratings for post-answer interest is less than or equal to curiosity for the trivia question (negative and zero prediction errors, respectively). This hypothesis was supported for low curiosity trials, where positive IPEs resulted in greater proportions of recall for low curiosity answers than negative and zero IPE trials. However, for high curiosity trials positive and zero IPE trials resulted in greater proportions of recall for high curiosity answers than negative IPE trials. This suggests that in states of both high and low curiosity, when post-answer interest exceeds an individual's initial curiosity to find out the answer, memory for the answer is better than when post-answer interest is worse or less than one's curiosity. Furthermore, extending beyond previous findings, the present study found that for high curiosity trials instances where curiosity and post-answer interest were 'equal', also facilitated later memory recall but not for trials that elicited low curiosity. This suggests that for states of high curiosity even if post-answer interest is similar to initial curiosity, we observe greater recall, but for states of low curiosity post-answer interest has to be greater than initial curiosity for memory to prevail. One thing that should be noted is that in contrast to Marvin and Shohamy's (2016) use of 'satisfaction' rating, the current study asked participants to rate how interesting they found the answer to the trivia questions to calculate IPEs. Similar to the present study, McGillivray et al. (2015) also asked their participants to give post-answer interest ratings, which were subsequently found to support later memory. Additionally, Kang et al. (2009) in their curiosity memory paradigm found that BOLD activations observed in the midbrain and hippocampus during the

presentation of trivia answers that followed incorrect guesses (i.e., violations) were modulated by curiosity, suggesting that high curiosity is perhaps related to the rewarding value of information. Although Kang et al. (2009) did not directly investigate the role of IPEs in supporting later memory, their findings imply that curiosity may stimulate memory regions in response to incorrectly guessed information, where this surprising event subsequently predicts later memory for the correct information. To our knowledge the neural mechanism underlying IPEs are not known, however, based on Kang et al's. (2009) findings it is possible that midbrain and hippocampal activation may be involved in the process of IPEs in predicting later memory.

Critically, the 'information-as-reward hypothesis' (Marvin & Shohamy, 2016) suggests that curiosity follows the basic principles associated with reward motivated behaviour, where information-gaps (Loewenstein, 1994) can be viewed as eliciting a prediction error that subsequently plays a role in learning and memory. In the two experiments reported in this chapter, IPEs were calculated for each trial by subtracting participants' initial curiosity rating from their post-answer interest rating. One interpretation of IPEs, based on its calculation (interest – curiosity rating; difference score method), is that the effect of IPEs is simply driven by post-answer interest. For instance, a significant positive IPE effect fundamentally indicates that interest is a stronger predictor of later memory than curiosity. Furthermore, this index can be argued to be constrained by the initial level of curiosity assigned to the trial, due to the usage of a restricted rating scale, where high curiosity ratings leave little room for surprise or greater interest ratings when presented with the answer to the trivia question. Ultimately, this means that positive IPEs occur more often for low-curiosity trials where there is ample room for surprise/greater interest, and negative IPEs occur more often for high curiosity trials. Despite this discrepancy, it should be noted that this appears to be a key aspect of prediction errors, where positive prediction errors are naturally limited when the value of the expected outcome approaches maximum.

4.4.3 Trait curiosity correlates with some measures of memory

A common assumption is that people high in trait curiosity experience states of curiosity more frequently and intensely than individuals low in trait curiosity (Grossnickle, 2016), where some studies have shown that individual differences in trait curiosity is

associated with individual differences in behaviours in a number of instances, such as in education and in work settings (Hassan et al., 2015; Mussel, 2013b; Kashdan & Yuen, 2007) as well as visual exploratory behaviours (Risko et al., 2012; Baranes et al., 2015). In the present study, a correlation approach was adopted to investigate the relationship between trait curiosity and various measures of memory elicited by states of curiosity. Based on the findings from Chapter 2 and 3 one might expect a relationship between trait curiosity and memory given that the Interest-type aspect of curiosity was found to correlate with fornix microstructure (Chapter 2), and the Diversive aspect of curiosity (albeit PC) was found to show a positive association with RSFC between the NAcc and left anterior hippocampus that approached significance (Chapter 3). Overall, no significant correlations were observed between trait curiosity and measures of memory. However, Joyous Exploration showed a positive trend (non-significant) with IPE-related answer memory benefit for low curiosity trials, such that those scoring high in Joyous Exploration showed a greater benefit of positive IPEs in influencing later memory for low curiosity trivia answers. This finding suggests that perhaps when exposed to a state of low curiosity, individuals who have a greater tendency to seek out novel information (to which the experience itself is deemed pleasurable) are more prone to (positive) surprise (i.e., their post-interest is subsequently greater than their initial curiosity), which subsequently better facilitates memory.

To assess the relationship between trait and the effects of state curiosity, Experiment 2 examined whether participants who score higher in trait curiosity, also benefit more from being in a high curiosity state (i.e., whether they show larger memory benefits). In the current paradigm it can be argued that all participants experienced the same states of high and low curiosity to which we cannot imply that people high in trait curiosity experience states of curiosity more frequently and intensely than individuals low in trait curiosity (Grossnickle, 2016). An alternative measure of state curiosity could be to have participants seek out information ‘naturally’ as a measure of how frequently they expose themselves to states of curiosity. For example, Lydon-Staley et al. (2019a) had participants browse Wikipedia and explore topics that interested them for a duration of 15 minutes a day over 21 days. Participants in this study also completed the Deprivation Sensitivity and Joyous Exploration subscales from Kashdan et al’s. (2018) 5-Dimensional Curiosity scale as a measure of trait curiosity. The authors were able to quantify participants’ qualitative Wikipedia browsing behaviours into tight and loose information seeking networks (i.e., states of curiosity) which were subsequently found to

relate to high- versus low-Deprivation Sensitivity, respectively, and similarly, high- versus low-Joyous Exploration related to loose versus tight knowledge networks (Lydon-Staley et al., 2019a). Other studies have employed eye-tracking methods to investigate the relationship between trait curiosity and state curiosity behaviours. For example, Baranes et al. (2015) found that exposure to high curiosity trials were associated with participants directing their gaze towards the location of the answer, and that eye distance to the answer negatively correlated with trait curiosity. This finding suggests that participants characterised with higher trait curiosity have a stronger tendency to anticipate upcoming information and shift their gaze to the answer location in high- versus low-curiosity states (Baranes et al., 2015). Furthermore, Risko et al. (2012) investigating individual differences in eye movements found that Perceptual Curiosity positively correlated with the number of regions visited in a scene-viewing task. These studies in contrast to the present study measure behaviours 'in the moment' of exploration and/or information seeking that subsequently show an association with trait curiosity. Therefore, future research examining the relationship between trait and state curiosity, testing whether those who show higher trait curiosity experience states of curiosity more frequently and intensely, should consider measuring behaviours that manifest during the state rather than behaviours that are a product of being in a state of curiosity.

4.5 Chapter Summary

The two behavioural experiments in this chapter employed a version of the classic trivia memory paradigm, where states of high- versus low-curiosity resulted in greater memory recall for 'interesting' information – replicating previous findings. In contrast, no curiosity-related memory effects were found for incidental information. A possible reason for the lack of curiosity-related memory effects for incidental faces could be that the incidental information was presented prior to being in a state of curiosity, and thus too far removed from the 'salient experience' of answer presentation, as opposed to previous studies where faces were presented during a state of curiosity. Therefore, the present findings elucidate the boundary conditions of the incidental effect. The current evidence would suggest then that the face memory benefit is only evident when the incidental face image is presented within a curiosity state. This chapter also investigated the effect of IPEs on later memory for answers associated with high and low curiosity, where positive information prediction errors overall appeared to have the greatest effect. In summary

these findings suggest that perhaps it is the most salient part of a curiosity state (i.e., anticipation as well as exposure to 'interesting' information) that is important in facilitating memory. Experiment 2 of this chapter also asked whether participants who scored high in trait curiosity also benefited from being in a high curiosity state. Contrary to expectations, this study did not find any significant relationships between trait curiosity and measures of memory. However, a positive trend (non-significant) was observed between Joyous Exploration and IPE-related answer memory benefit for low curiosity trials. It is advised that future studies wanting to investigate the curiosity state-trait relationship consider measuring state exposure itself when designing their study.

Chapter 5: Multi-modal investigation of state curiosity-related memory effects

5.1 Introduction

The concept of curiosity can be described as a motivational state that shares qualities similar to states of extrinsic motivators such as monetary rewards (Murayama & Kitagami, 2014; Wittmann et al., 2005). Motivational states alone can facilitate learning and memory (Shohamy & Adcock, 2010; Gruber et al., 2014; Kang et al., 2009) where the hippocampus, NAcc and midbrain areas, including the SN/VTA, have been found to show high intrinsic connectivity thought to form a functional loop that regulates learning (Kahn & Shohamy, 2013; Lisman & Grace, 2005). This hippocampal-VTA functional loop theory suggests the presence of direct projections from the VTA to the hippocampus, where the VTA modulates the encoding of salient information in the medial temporal lobes via increased dopaminergic release. In addition to the projections to the hippocampus, the VTA directly projects to the NAcc (Lisman & Grace, 2005), which is involved in reward anticipation and incorporates novel information into the functional circuit. Other projections include the direct connection from the hippocampus to the NAcc and indirect projections from the NAcc to the VTA (Lisman & Grace, 2005).

Previous fMRI evidence using curiosity memory paradigms have provided support for the hippocampal-VTA functional loop theory in relation to curiosity driven learning. For example, Kang et al. (2009) found that both midbrain and hippocampus activations during the presentation of trivia answers (that followed incorrect guesses) were modulated by curiosity, suggesting that high curiosity related to the reward anticipation of information. Gruber et al. (2014) similarly adopted a curiosity memory paradigm to measure brain activity during the study phase of the experiment, where a single trial began with the presentation of a trivia question in which participants waited in anticipation for the presentation of the correct answer. Participants then completed a delayed-memory test where their memory for trivia answers was tested. Consistent with Kang et

al. (2009) participants showed greater memory for answers to questions that elicited high curiosity. Interestingly, both SN/VTA and NAcc activity during the presentation of the trivia question were found to linearly increase with participants' curiosity ratings, indicating that the key structures of the dopaminergic circuit previously found to be associated with levels of reward anticipation additionally correlate with levels of state curiosity (Adcock et al., 2006; Knutson et al., 2001). In addition, Gruber et al. (2014) asked whether the specific circuit involving the VTA, NAcc and hippocampus predicted curiosity-related memory enhancements. The authors found that activation observed in the right hippocampus and NAcc during the anticipation of trivia answers for high- compared to low-curiosity trials subsequently predicted later memory answer recall (Gruber et al., 2014). Finally, activity directly evoked by the trivia answers revealed subsequent memory effects that did not differentiate between high and low curiosity trials, indicating that it is the anticipatory activity elicited in the hippocampus and NAcc during states of high curiosity that facilitates the learning of upcoming information, rather than the activity observed during the processing of the 'interesting' information itself.

In contrast, Ligneul, Mermillod, and Morisseau (2018), manipulating answer uncertainty in a trivia paradigm that was performed under fMRI, found that activity in the NAcc of the ventral striatum was found to be modulated by curiosity-dependent answer delivery rather than when the question was elicited or during anticipation of the answer as indicated by Gruber et al. (2014). Furthermore, this modulation of NAcc activity was observed when curiosity was relieved in 50% of the trials, whilst no modulation of NAcc activity was observed when answers were delivered in 100% of the trials. One possible reason put forward by Ligneul et al. (2018) is that in instances where epistemic curiosity is systematically satisfied (i.e., trials in which question is always followed by an answer), the affective or motivational signalling associated with EC should mainly occur at the stage of the trivia question (i.e., Gruber et al., 2014; Kang et al., 2009), whilst situations with uncertain outcomes (i.e., where the value of the outcome cannot be anticipated), results in ventral striatal signalling when the outcome is revealed (Ligneul et al., 2018). Likewise, Lau, Ozono, Kuratomi, Komiya, and Murayama (2018) found using fMRI that the striatum is activated when participants choose to gamble in order to satisfy their curiosity. Similarly, Oosterwijk, Snoek, Tekoppele, Engelbert, and Scholte, (2019) found that curiosity for morbid stimuli in which participants choose to view negative information which is novel, deviant and rare, activated the striatum compared to when participants viewed negative information they did not actively choose to view.

Furthermore, it is possible that white matter bundles may also facilitate learning and memory. One such white matter structure that may help facilitate the hippocampal-VTA loop in regulating memory is the fornix (Ross et al., 2016). The fornix is a white matter tract that connects the hippocampus, a structure involved in novelty detection, exploration, information seeking and episodic memory, with areas including the PFC, anterior thalamic nuclei, the mammillary bodies and the ventral striatum - where the latter structure is a major portion of the basal ganglia that functions as part of the reward system and consists of the NAcc (Aggleton, 2008, 2012; Catani & Thiebaut de Schotten, 2008; Poletti & Creswell, 1977). Notably, microstructure of the fornix has been found to correlate with memory processes including recognition memory and recall memory performance. For example, Hartopp et al. (2019) found that visual recognition memory for faces and free recall memory positively correlated with fornix FA, and also negatively correlated with fornix MD. Another study that aimed to examine the relationship between fornix microstructure and recognition memory, employed DWI to extract the fornix in a sample of 25 healthy participants, where FA was extracted as the measure of interest (Rudebeck et al., 2009). Here, the authors found that individual differences in fornix FA, in particular the tail region of this tract, reflected recollection but not familiarity memory (Rudebeck et al., 2009). Taken together, this work highlights that individual differences in the microstructure of the fornix are related to variations observed in memory, which arguably supports the role of the fornix in hippocampal-dependent processes.

Additionally, within the animal literature, deep brain stimulation of the fornix has been found to increase BOLD responses in the structures that contribute to the medial limbic and corticolimbic circuits, including the NAcc, hippocampus and VTA (Ross et al., 2016; Shin et al., 2019). The authors also found that fornix stimulation resulted in an efflux of dopamine in the NAcc, suggesting that the fornix may play an important role in providing a pathway for the transmission of neurotransmitters (i.e., glutamate) from the hippocampus to the NAcc, eventually enabling neurons in the NAcc to enter a depolarized active state (Kelley & Domesick, 1982; Ross et al., 2016; O'Donnell & Grace, 1995). This occurs when activated glutamatergic projections from the hippocampus to the NAcc, via the fornix, subsequently activate inhibitory GABAergic inputs from the NAcc to the ventral pallidum, which in turn result in decreased GABAergic inhibition from the ventral pallidum to the VTA, subsequently stimulating dopaminergic neurons in the VTA (Floresco et al., 2001; Lisman & Grace, 2005). Finally, the VTA projects dopamine

to the NAcc and also back to the hippocampus enhancing LTP and learning (Lisman & Grace, 2005; **Figure 5.1**).

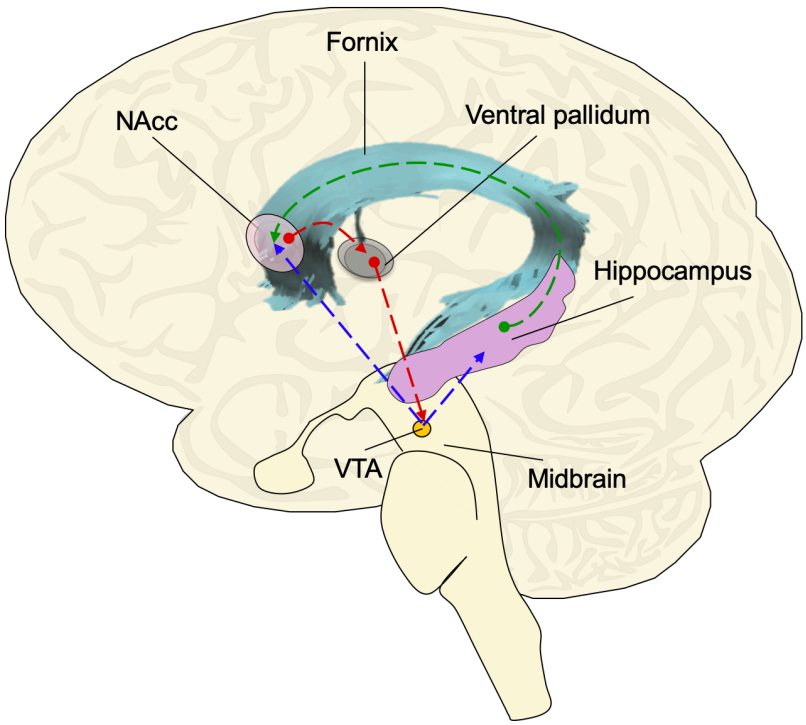


Figure 5.1: The fornix and hippocampal-VTA loop in regulating learning. The ventral tegmental area (VTA) provides dopaminergic input (blue lines) to the hippocampus and nucleus accumbens (NAcc). The hippocampus provides excitatory glutamatergic input (green line) to the NAcc via the fornix white matter structure. The NAcc projects GABAergic inputs to the ventral pallidum, that in turn reduces GABAergic inhibition to the VTA, subsequently stimulating dopaminergic neurons in the midbrain. (*See Floresco et al., 2001; Lisman & Grace, 2005; Shohamy & Adcock, 2010; Kahn & Shohamy, 2013; Figure taken and adapted from Gruber et al., 2019, reproduced with permission*).

So far there is compelling evidence from both human and animal neuroscience for the functional role of the mesolimbic pathway in curiosity-related learning. In addition, although there is a clear relationship between the microstructure of the fornix and the dopaminergic pathway (Ross et al., 2016; Shin et al., 2019), there is no evidence to our knowledge directly examining the relationship between white matter structure, functional connectivity and memory prioritization due to dopaminergic processes nor curiosity-

related memory. Therefore, in a sample of healthy individuals the present experiment examined the functional and structural correlates of curiosity-related memory using resting-state fMRI and DTI, respectively. First, the relationship between white matter microstructure and curiosity-related answer memory benefit was investigated using DTI. Deterministic CSD tractography was employed in which FA and MD for the fornix was extracted for each participant and correlated with curiosity-related answer memory benefit. It was hypothesised that curiosity-related answer memory benefit would positively correlate with fornix FA and negatively correlate with fornix MD (mm^2s^{-1}). Using resting-state fMRI this experiment also examined whether functional connectivity between specific regions involved in the mesolimbic pathway, including the VTA, NAcc and hippocampus related to curiosity-related measures of memory. Given the relationship between the VTA, NAcc and hippocampus and their role in the functional loop in regulating memory for items associated with reward and novelty, this study predicted there to be increased functional connectivity between these ROIs. Given that this study targets a specific type of curiosity, that is epistemic curiosity, and given the findings from Chapter 2 that indicate aspects of EC relate to the whole fornix, I decided not to split the hippocampus into anterior and posterior segments. Furthermore, with regards to their subsequent relationship with behaviour, it was predicted that positive connectivity between the selected ROIs would be positively modulated by curiosity-related answer memory benefit (e.g., the greater the benefit of curiosity in influencing later memory for trivia answers, the stronger the connectivity will be between these ROIs). Next, the ROI-to-ROI correlation that reached significance when correlated with curiosity-related answer memory benefit (i.e., RSFC between right NAcc and left VTA), was consequently correlated with FA and MD of the fornix. Finally, a mediation analysis was employed to investigate a potential three-way relationship between RSFC, fornix microstructure and curiosity-related answer memory benefit.

5.2 Materials and Methods

5.2.1 Participants

Fifty-five healthy adults (47 females) with a mean age of 19 years (range: 18-25), with normal or corrected-to-normal vision were recruited from Cardiff University and were

scanned at the Cardiff University Brain Research Imaging Centre (CUBRIC). This sample of participants were the same subset of participants that took part in Experiment 2 of Chapter 2, Chapter 3 and 4). To the best of our knowledge all participants were naïve to the experimental aims. Participants provided written consent prior to participating in the study, which was approved by the Cardiff University Ethics Committee, and were compensated with course credits and/or payment for their participation.

5.2.2 Imaging acquisition

Imaging data were obtained at CUBRIC, Cardiff University on a 3 Tesla MR scanner (Siemens Magnetom Prisma) with a 32-channel head coil. T1-weighted 3D images were acquired using an MPRAGE sequence (orientation = sagittal; TR = 2250ms; TE = 3.06ms; TI = 900ms; flip angle = 9°; FOV = 256mm²; slice thickness = 1mm; voxel size = 1mm³; number of slices = 224; bandwidth = 230Hz/pixel; total acquisition time = 7 minutes 36 seconds).

Diffusion weighted images were acquired using a multi-shell sequence (orientation = transversal/axial; TR = 9400ms; TE = 70.0ms; FOV = 256mm²; slice thickness = 2mm; voxel size = 2mm³; number of slices = 80). Diffusion gradients were applied in (i) 30 isotropic directions by using a diffusion-weighted factor b=1200sec/mm², (ii) in 60 isotropic directions by using a diffusion-weighted factor b=2400sec/mm², and (iii) a volume without diffusion gradients (b=0sec/mm²) (bandwidth = 1954Hz/pixel; total acquisition time = 15 minutes 51 seconds).

Resting-state fMRI images were acquired using an echo planar imaging sequence (orientation = transversal/axial; TR = 3000ms; TE = 30.0ms; flip angle = 89°; FOV = 192mm²; slice thickness = 2mm; voxel size = 2mm³; number of slices = 50, bandwidth = 2170Hz/pixel; total acquisition time = 10 minutes 11 seconds).

5.2.3 Experimental procedure

Participants were asked to change into MRI scrubs and placed in the scanner where they were asked to keep as still as possible during the duration of the scanning session. During the T1 structural scan and multi-shell diffusion sequence, participants watched an animated DVD to help reduce movement, boredom and nervousness. During the resting-state fMRI scan participants were asked to look at a fixation cross. Participants were taken out of the scanner where they got changed out of the MRI scrubs and into their normal clothing. Participants returned for a duration of two consecutive days and completed the curiosity memory paradigm followed by a series of self-report measures (Chapter 2, 3 and 4 (Experiment 2). Finally, participants were debriefed and compensated for their participation in the study.

5.2.4 Resting-state functional connectivity pre-processing

Following the same pre-processing steps as Chapter 3, resting-state data was pre-processed using CONN toolbox (version 18b; Whitfield-Gabrieli & Nieto-Castanon, 2012; www.nitrc.org/projects/conn) in conjunction with the SPM 12 modules (Wellcome Trust Centre for Neuroimaging, London) executed using MATLAB (version 2015). Using standard parameters in CONN, imaging data were subjected to slice-time correction (Interleaved Siemens) in order to correct for different acquisition times for the different slices in the functional data; realignment and unwarp correcting for head movement; functional outlier detection using Artifact Detection Tool (ART) to identify potential outlier scans due to abrupt movements; segmentation and normalisation to MNI (Montreal Neurological Institute) space; and spatial smoothing with a 6mm full-width-half-maximum (FWHM) Gaussian kernel. In order to remove unwanted motion, physiological, and other artefacts from the BOLD signal before computing functional connectivity, the following were applied to the data: denoising, specific to functional connectivity analyses, was applied to implement band-pass filtering (0.01-0.1Hz), a linear detrending term, an anatomical component based noise correction method (aCompCor) that removed 10 noise components of the signal from white matter and CSF (Behzadi et al., 2007), and motion regression with 12 regressors (6 motion parameters and 6 first-order temporal derivatives that were estimated during realignment). Scans for two participants were removed due to excess motion artefacts identified by CONN.

5.2.5 Diffusion MRI pre-processing and Tractography

The diffusion MRI pre-processing and tractography of the fornix was identical to that in Chapter 2, Experiment 2. Following automated tractography the data from 8 participants were removed from all analyses of interest due to poor white matter reconstructions (<10 reconstructed fibre strands).

5.2.6 Statistical Analysis

The behavioural dataset and behavioural measures of memory included in this chapter are identical to the dataset and behavioural measures described and reported in Chapter 4, Experiment 2. Similarly, the DTI dataset and the resting-state fMRI dataset reported in this chapter are identical to the datasets described and reported in Chapter 2 (Experiment 2), and Chapter 3 (Experiment 2), respectively.

5.2.6.1 Behavioural measures

Curiosity-related answer memory benefit was calculated by subtracting each participants' answer recall rate for low curiosity trials from the answer recall rate for high curiosity trials. Curiosity-related answer memory benefit was subsequently correlated with fornix microstructure and ROI-to-ROI RSFC.

Similarly, to see whether the mediation of RSFC on the relationship between fornix microstructure and behaviour is specific to curiosity-related answer memory benefit or applicable to other behavioural measures as well, this experiment also explored the relationship between fornix microstructure and ROI-to-ROI RSFC with: overall answer memory (high curiosity answer recall rate + low curiosity answer recall rate); curiosity-related face memory benefit (high curiosity face recognition memory performance - low curiosity face recognition memory performance); overall face memory (high curiosity face recognition memory performance + low curiosity face recognition memory performance). IPE-related answer memory benefit was also calculated by subtracting each participants' proportion of negative IPE trials that were later recalled from the proportion of positive IPE trials that were later recalled (i.e., positive IPE – negative IPE). This was calculated

for each high and low curiosity conditions and subsequently correlated with fornix white matter microstructure and ROI-to-ROI RSFC.

5.2.6.2 Regions of interest and functional connectivity analysis

For the ROI-to-ROI based functional connectivity analyses, the functional connectivity between two ROIs during rest was examined. Based on evidence for possible cross-hemispheric projections between the VTA, hippocampus and NAcc (Floresco, Seamans & Phillips, 1997; Fox et al., 2016; Molochnikov & Cohen, 2014; Jurkowlaniec, Tokarski & Trojniar, 2003), left and right hemispheric ROIs were employed to investigate RSFC within the hippocampal-VTA loop. The following ROIs were selected for the current analyses: the left and right VTA (Murty et al., 2014), the left and right NAcc (Harvard-Oxford atlas), and left and right hippocampus (these ROIs were derived from tracing the hippocampus based on the average participant brain (using DARTEL) from the Gruber et al. (2016) dataset). Source and target areas represented ROIs included in the ROI-to-ROI functional connectivity analysis. When conducting functional connectivity analysis between two ROIs, one ROI is typically treated as the source area and the other is treated as the target area in CONN **(Figure 5.2)**.

ROI based functional connectivity analysis was carried out using CONN where, for each pre-defined ROI mask, the BOLD time series was computed by averaging the voxel time series across all voxels within the ROI. Fisher-transformed bivariate correlation coefficients were computed between source and target ROI BOLD time series as a measure of functional connectivity. For each ROI-to-ROI analysis a one sample t-test was performed to test whether the means of connections were greater than zero. To correct for multiple tests a FDR correction (Benjamini & Hochberg, 1995) was applied over the set of target ROIs. Results were thresholded at $p<0.001$, one tailed, as it was believed that positive functional connectivity between the selected ROIs were modulating curiosity-related answer memory benefit. Finally, the fisher-transformed ROI-to-ROI connectivity values for each subject were extracted and subsequently correlated with white matter microstructure and curiosity-related answer memory benefit.

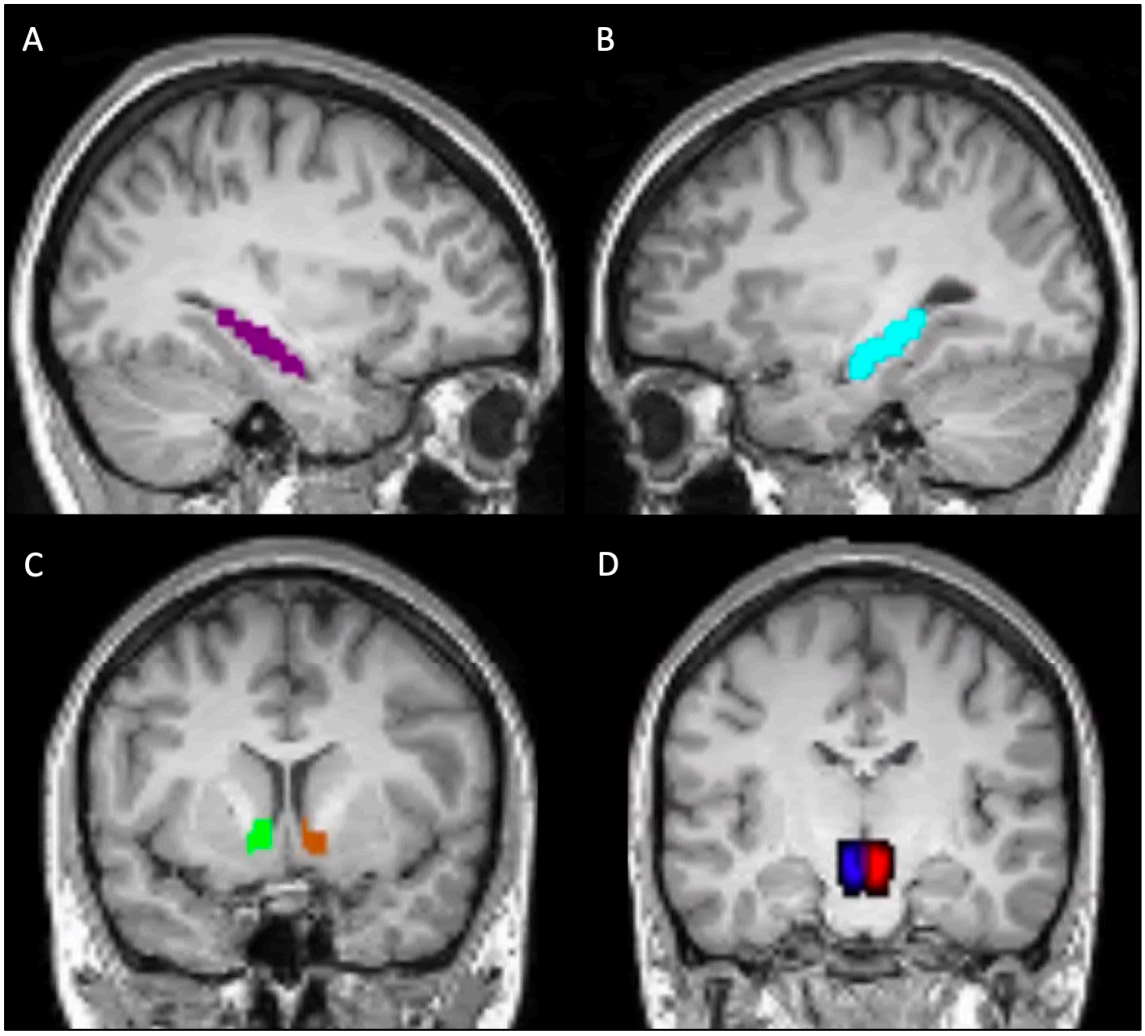


Figure 5.2: Regions of interest (ROI) included in the RSFC analyses. **(A)** left hippocampus (purple, x = -26, y = -26, z = -12); **(B)** right hippocampus (cyan, x = 28, y = -23, z = -13); **(C)** Left nucleus accumbens (bright green, x = -9, y = 11, z = -7) and right nucleus accumbens (brown, x = 9, y = 12, z = -7); **(D)** left ventral tegmental area (navy blue, x = -3, y = -15, z = -15) and right ventral tegmental area (red, x = 4, y = -16, z = -14).

To test whether the Pearson's correlation coefficient *r,* reflecting the association between a) RSFC between selected ROIs, b) curiosity-related answer memory benefit and c) FA/MD of the fornix, was statistically significant, non-parametric permutation tests (one-tailed) that randomly permute the real data between participants were employed. First, permutation tests were conducted separately for the two microstructure metrics (i.e., FA and MD) with curiosity-related answer memory benefit, where a positive

association with fornix FA and a negative association with fornix MD was predicted. The next permutation test corrected for multiple comparisons across the selected 12 ROI-to-ROI RSFC measures and were correlated with curiosity-related answer memory benefit, where positive associations were expected. Finally, any ROI-to-ROI RSFC measures that significantly correlated with curiosity-related answer memory benefit were subsequently correlated with fornix microstructure in which two separate permutation tests for the two microstructure metrics (i.e., fornix FA and MD) were employed. For instance, if 3 pairs of ROI-to-ROI RSFC measures were found to significantly correlate with curiosity-related answer memory benefit, these were then correlated with fornix microstructure (e.g., fornix FA) correcting for multiple comparisons across three RSFC measures. The methodological steps taken to carry out these non-parametric permutation tests are described in Chapter 2. The 95% confidence intervals (CI) for each correlation was derived using a bootstrapping method based on 1000 iterations.

Finally, to test for the indirect effect via RSFC on the relationship between fornix microstructure and behaviour, a mediation analysis (PROCESS for SPSS (version 23)) using a bootstrapping method (Preacher & Hayes, 2008) was employed. In this experiment, fornix microstructure was used as the predictor/independent variable, curiosity-related answer memory benefit was used as the outcome/dependent variable and ROI-to-ROI functional connectivity was used as the mediator variable in cases where relationships were observed between these three variables.

5.3 Results

5.3.1. Behaviour

Identical to the procedure in Experiment 2 of Chapter 4, curiosity-related answer memory benefit was calculated for each participant (Mean = 13.73, SD = 13.51) and subsequently correlated with fornix microstructure and ROI-to-ROI RSFC reported below.

5.3.2 DTI and curiosity-related answer memory benefit

Based on the directional hypotheses summarised above, separate permutation tests (one-tailed) were conducted for each DTI metric (fornix FA and MD) to be correlated with curiosity-related answer memory benefit. The analyses reported in this section are based on 42 participants as 8 datasets were removed due to poor white matter reconstructions following automated tractography and an additional 5 datasets were removed due to incompletion/missing behavioural measures. No significant correlations were observed between fornix microstructure and curiosity-related answer memory benefit (**Table 5.1**).

Table 5.1: DTI-behaviour correlations are based on 42 participants. Separate non-parametric permutation tests were carried out for each DTI metric to be correlated with curiosity-related answer memory benefit. One-tailed Pearson correlation coefficients, p-values and 95% confidence intervals are reported for each diffusion metric (i.e., FA and MD) of the fornix when correlated with curiosity-related answer memory benefit.

		Curiosity answer memory benefit		
		r(40)	p_{corr}	CI [LL, UL]
Fornix	FA	0.011	0. 476	[-0.27, 0.29]
	MD	-0.060	0.346	[-0.41, 0.35]

FA, *fractional anisotropy*; MD, *mean diffusivity*; CI, *confidence interval*; LL, *lower limit*; UL, *upper limit*

5.3.3 Resting-state functional connectivity results

The analyses reported in this section are based on 53 participants as data from two participants were removed due to excess motion artefacts. Average fisher-transformed bivariate correlation coefficients were calculated between source and target ROI BOLD time series, where source and target ROIs showed positive functional connectivity at a FDR-corrected threshold of p<0.001 (Appendix 16).

5.3.4 RSFC and curiosity-related answer memory benefit

Here, left and right ROIs of the VTA, NAcc, and hippocampus were defined, where a permutation test (one-tailed) correcting for multiple comparisons across the 12 pairs of ROIs when correlated with curiosity-related answer memory benefit was conducted. From the 53 participants used in the previous resting-state analysis, 49 of these had complete behavioural results and so were included in the subsequent behavioural-RSFC analysis (data from 4 participants were removed due to incomplete/missing behavioural measures. Out of the 12 correlations conducted[1] between ROI-to-ROI functional connectivity coefficients and curiosity-related answer memory benefit, curiosity-related answer memory benefit positively correlated with functional connectivity between right NAcc and left VTA ($r(47) = 0.382$, $p_{corr} = 0.030$, 95% CI [0.13, 0.58]), **Figure 5.3**. This correlation survived the multiple comparison corrections across 12 correlations, whilst the remaining correlations did not reach significance at $p<0.05$ (Appendix 17).

[1]Twelve comparisons that include the left and right hippocampus each being correlated with each left and right NAcc and VTA, left and right NAcc each correlated with each left and right VTA.

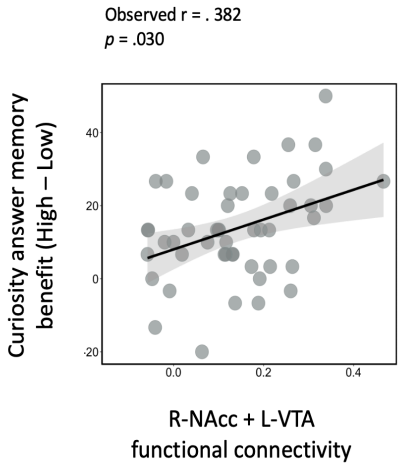


Figure 5.3: Significant positive correlation between curiosity-related answer memory benefit and resting state functional connectivity between right nucleus accumbens (NAcc) and left ventral tegmental area (VTA). The line of best fit and 95% confidence interval is shown on the scatter plot with 49 data points.

5.3.5 RSFC and DTI

The analyses reported in this section are based on 45 participants as 8 datasets were removed due to poor white matter reconstructions following automated tractography and an additional 2 datasets were removed due to excess motion artefacts during the resting state fMRI scan. Based on the single ROI-to-ROI functional connectivity coefficient found to significantly correlate with curiosity-related answer memory benefit in the analysis above, separate permutation tests (one-tailed) were conducted for each DTI metric (fornix FA and MD) to be correlated with RSFC between right NAcc and left VTA. It was expected that RSFC between the right NAcc and left VTA would show a positive relationship with fornix FA and a negative relationship with fornix MD. A summary of correlations between right NAcc and left VTA functional connectivity and fornix FA and MD is summarised in **Table 5.2**. The results indicated that RSFC between the right NAcc and left VTA positively correlated with fornix FA ($r(43) = 0.309$, $p_{corr} = 0.017$, 95% CI [0.11, 0.51], **Figure 5.4**). No significant correlation was observed between right NAcc and left VTA functional connectivity and fornix MD.

Table 5.2: DTI-RSFC correlations are based on 45 participants. Separate non-parametric permutation tests were carried out for each DTI metric to be correlated with resting-state functional connectivity between the right NAcc and left VTA. One-tailed Pearson's correlation coefficients, p-values and 95% confidence intervals are reported for each diffusion metric (i.e., FA and MD) of the fornix when correlated with right NAcc and left VTA functional connectivity coefficient.

Fornix microstructure		R-NAcc + L-VTA
FA	*r*(43)	0.309
	p_{corr}	***0.017***
	CI [LL, UL]	[0.11, 0.51]
MD	*r*(43)	-0.117
	p_{corr}	*0.227*
	CI [LL, UL]	[-0.39, 0.16]

FA, *fractional anisotropy*; MD, *mean diffusivity*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; L, *left*; R, *right*; CI, *confidence interval*; LL, *lower limit*; UL, *upper limit*. Correlations are based on 45 participants. Significant results are denoted by bold text.

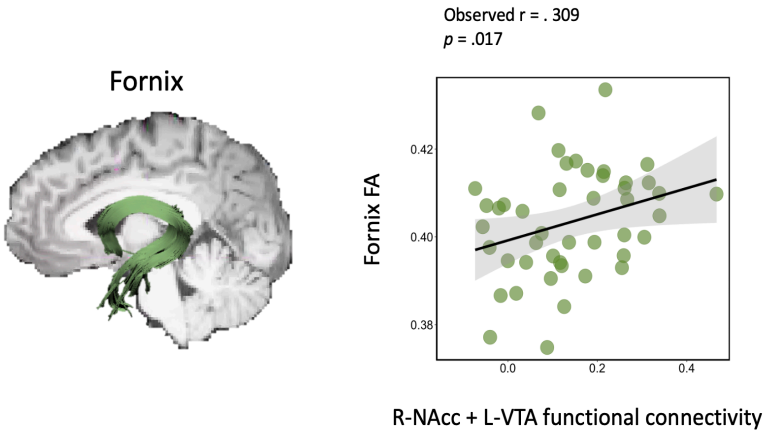


Figure 5.4: Significant positive correlation between fornix fractional anisotropy (FA) and resting-state functional connectivity between right nucleus accumbens (NAcc) and left ventral tegmental area (VTA). The line of best fit and 95% confidence interval is shown on the scatter plot with 45 data points.

5.3.6 Mediation analysis: RSFC, DTI and behaviour

From the correlation analyses above, right NAcc and left VTA RSFC correlated with fornix FA and curiosity-related answer memory benefit. Therefore, a single mediation model was employed, in which RSFC between the right NAcc and left VTA was treated as the mediator for the hypothesised relationship between fornix FA and curiosity-related answer memory benefit. Traditionally, when conducting a mediation analysis, the predictor variable (i.e., fornix FA) should significantly correlate with the outcome variable (e.g., curiosity-related answer memory benefit) (Baron & Kenny, 1986). However, in the present experiment, white matter microstructure was not found to significantly correlate with curiosity-related answer memory benefit (see section 5.3.2). Shrout and Bolger (2002) stipulate that establishing a bivariate relationship between predictor and outcome variable is not necessary, if this process to be mediated is theoretically distal or weak. With regards to the present variables, the relationship between microstructure and behaviour can be argued to be more distal compared to the relationship between RSFC and behaviour. For example, in the literature it is acknowledged that anatomical connections between regions in the brain afford the structural platform for functional interactions between these areas (Huang and Ding, 2016), and that resting-state fMRI (compared to diffusion MRI) is better able to predict behaviours given that brain function (rather than structure) produces behaviour (Dubois et al., 2018). In other words, structural connectivity provides the platform for functional connectivity to occur, to which functional interactions between brain areas subsequently generates behaviour (structure → function → behaviour). Additionally, it is likely that the hypothesised microstructure-behaviour relationship was not observed due to inadequate statistical power (n=42) to detect this distal relationship (Fairchild & McDaniel, 2017; Shrout & Bolger, 2002). Therefore, I continued to run the mediation analysis with RSFC between the right NAcc and left VTA as the possible mediator of the relationship between fornix microstructure and behaviour.

The first mediation model conducted using ordinary least squares path analysis indicated that fornix FA may indirectly influence curiosity-related answer memory benefit through its relationship with right NAcc and left VTA functional connectivity activity. As illustrated in **Figure 5.5**, participants with high fornix FA values had significantly increased right NAcc and left VTA functional connectivity (a = 0.39), and individuals with increased right NAcc and left VTA functional connectivity showed a greater curiosity-

related answer memory benefit for trivia answers (*b* = 0.45). The bootstrap CI for the indirect effect (*ab* = 0.18) based on 1000 iterations was entirely above zero (95% CI [0.06, 0.32]), suggesting that the hypothesized relationship between fornix FA and curiosity-related answer memory benefit is mediated by RSFC between the right NAcc and left VTA. There was no evidence that fornix FA directly influenced curiosity-related answer memory benefit independent of its effects on functional connectivity between right NAcc and left VTA (*c'* = -0.17, *p* = 0.306).

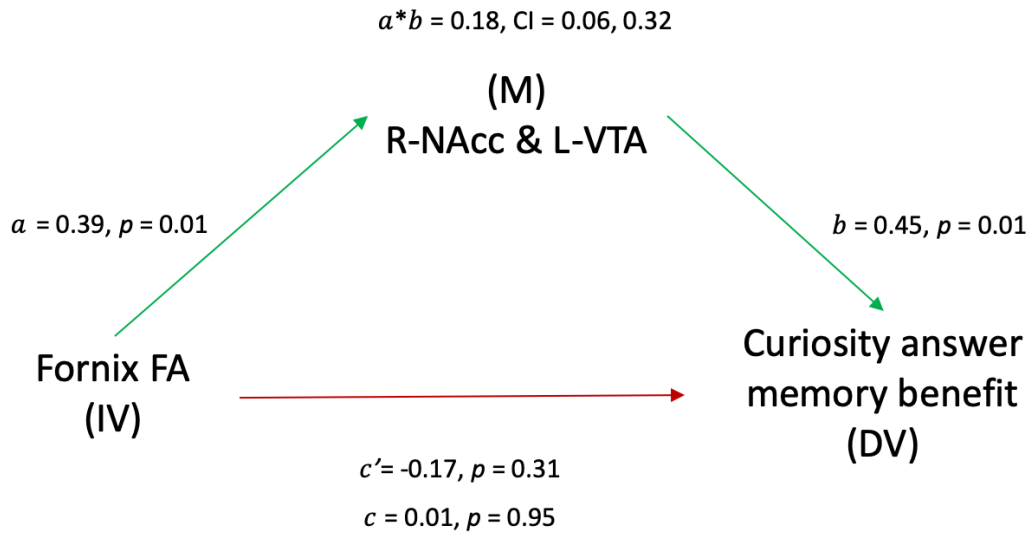


Figure 5.5: Mediation analysis investigating the three-way relationship between resting-state fMRI, white matter microstructure, and curiosity memory benefit. This model tests the extent to which the relationship between fornix FA (predictor variable or independent variable, IV) and curiosity-related answer memory benefit (outcome variable or dependent variable, DV) is mediated by functional connectivity between right nucleus accumbens (R-NAcc) and left ventral tegmental area (L-VTA) (mediator variable, M). Coefficients and corresponding p values are depicted for each path of interest: a, b, a*b, c′, and c. These paths represent the following: path a reflects the effect of the IV on the M path, path b reflects the causal effect of M on the DV, c represents the total effect of the IV on the DV, and path c′ is the direct effect of the IV on the DV that also partials out the effect of the M, finally a*b reflects the indirect effect of the IV on the DV. The bootstrap 95% CI is displayed for the indirect effect (a*b). Models above are based on 41 subjects.

5.3.7 Exploratory investigation of the relationship between DTI, RSFC and other behavioural measures

To see whether the mediation of RSFC on the relationship between fornix microstructure and behaviour is specific to curiosity-related answer memory benefit or applicable to other behavioural measures as well, including overall answer memory, curiosity-related face memory and IPE-related answer memory benefit, this experiment also explored the relationship between fornix microstructure and ROI-to-ROI RSFC with: overall answer memory (high curiosity answer recall rate + low curiosity answer recall rate; Mean = 54.13, SD = 15.00), curiosity-related face memory benefit (high curiosity face recognition memory performance – low curiosity face recognition memory performance; Mean = 0.62, SD = 11.96) and overall face memory (high curiosity face recognition memory performance + low curiosity face recognition memory performance; Mean = 29.90, SD = 15.89). IPE-related answer memory benefit was also calculated by subtracting each participants' proportion of negative IPE trials that were later recalled from the proportion of positive IPE trials that were later recalled (i.e., positive IPE – negative IPE). This was calculated for each high (Mean = 0.14, SD = 0.34) and low curiosity (Mean = 0.26, SD = 0.26) conditions and were subsequently correlated with fornix matter microstructure and ROI-to-ROI RSFC measures.

Employing an identical analysis approach as with curiosity-related answer memory benefit described above, permutation tests (one-tailed) were first conducted for each DTI metric (fornix FA and MD) correlated with each behavioural measure separately. Next, permutation tests (one-tailed) were employed, that corrected for multiple comparisons across the 12 pairs of ROIs when correlated with each behavioural measure separately. Finally, any ROI-to-ROI RSFC measures that significantly correlated with the behavioural measure of interest, were subsequently correlated with fornix microstructure using two separate permutation tests (one-tailed) for the two microstructure metrics (i.e., fornix FA and MD). If, any ROI-to-ROI RSFC measure was found to correlate with both measure of memory and fornix microstructure, a mediation analysis was employed in which the ROI-to-ROI RSFC was treated as the mediator for the hypothesised relationship between fornix microstructure and measure of memory.

5.3.7.1 Relationship between DTI, RSFC and overall answer memory

The 2 separate permutation tests conducted for each DTI metric indicated that neither fornix FA nor MD significantly correlated with overall answer memory (Appendix 18A). Next, a permutation test that corrected for multiple comparisons across the 12 pairs of ROIs, revealed no significant relationship between overall answer memory and any of the 12 ROI-to-ROI functional connectivity coefficients (Appendix 19A). This suggests that the relationship between left VTA-right NAcc RSFC and curiosity-related answer memory benefit (reported above) cannot be explained by overall answer memory.

5.3.7.2 Relationship between DTI, RSFC and face memory

The 2 separate permutation tests conducted for each DTI metric indicated that neither fornix FA nor MD significantly correlated with curiosity-related face memory benefit (Appendix 18B). Similarly, 2 separate permutation tests conducted for each DTI metric indicated neither fornix FA or MD significantly correlated with overall face memory (Appendix 18C). Next, permutation tests that corrected for multiple comparisons across the 12 pairs of ROIs, revealed no significant relationship between the 12 ROI-to-ROI functional connectivity coefficients and curiosity-related face memory benefit (Appendix 19B), or overall face memory (Appendix 19C).

5.3.7.3 Relationship between DTI, RSFC and IPE-related answer memory

The 2 separate permutation tests conducted for each DTI metric indicated that neither fornix FA or MD (**Figure 5.6B**) significantly correlated with high curiosity IPE-related answer memory benefit (Appendix 18D). Following this, a permutation test that corrected for multiple comparisons across the 12 pairs of ROIs, revealed no significant relationship between high curiosity IPE-related answer memory benefit and any of the 12 ROI-to-ROI functional connectivity coefficients (Appendix 19D; **Figure 5.6D**).

Alternatively, with regards to low curiosity IPE-related answer memory benefit, fornix MD was found to significantly correlate with this behavioural measure ($r(39)$ =

-0.288, p_{corr} = 0.036, 95% CI [-0.54, -0.03]; **Figure 5.6A**). Fornix FA did not significantly correlate with low curiosity IPE-related answer memory benefit (r(39) = 0.148, p_{corr} = 0.175, 95% CI [-0.12, 0.38]). Next, a permutation test that corrected for multiple comparisons across the 12 pairs of ROIs, revealed low curiosity IPE-related answer memory benefit positively correlated with functional connectivity between left NAcc and left hippocampus (r(46) = 0.401, p_{corr} = 0.021, 95% CI [0.10, 0.63]; **Figure 5.6C**). The remaining correlations did not reach significance at p<0.05 (Appendix 19E). Based on this single ROI-to-ROI functional connectivity coefficient found to significantly correlate with low curiosity IPE-related answer memory benefit, separate permutation tests were conducted for each DTI metric (fornix FA and MD) to be correlated with RSFC between left NAcc and left hippocampus. No significant correlation was observed between left NAcc and left hippocampus functional connectivity and fornix MD (r(43) = 0.033, p_{corr} = 0.595, 95% CI [-0.24, 0.33]), nor with fornix FA (r(43) = -0.149, p_{corr} = 0.164, 95% CI [-0.43, 0.17]). Given no significant correlation was observed between fornix microstructure (potential IV) and functional connectivity between the left NAcc and left hippocampus (potential mediator), conducting a mediation analysis with the left NAcc and left hippocampus as the mediator for the relationship between fornix microstructure and low curiosity IPE-related answer memory benefit was not appropriate. Given that that left NAcc and left hippocampal RSFC did not correlate with fornix microstructure, both functional and anatomical connections might have a separate effect on the low curiosity IPE-related answer memory benefit.

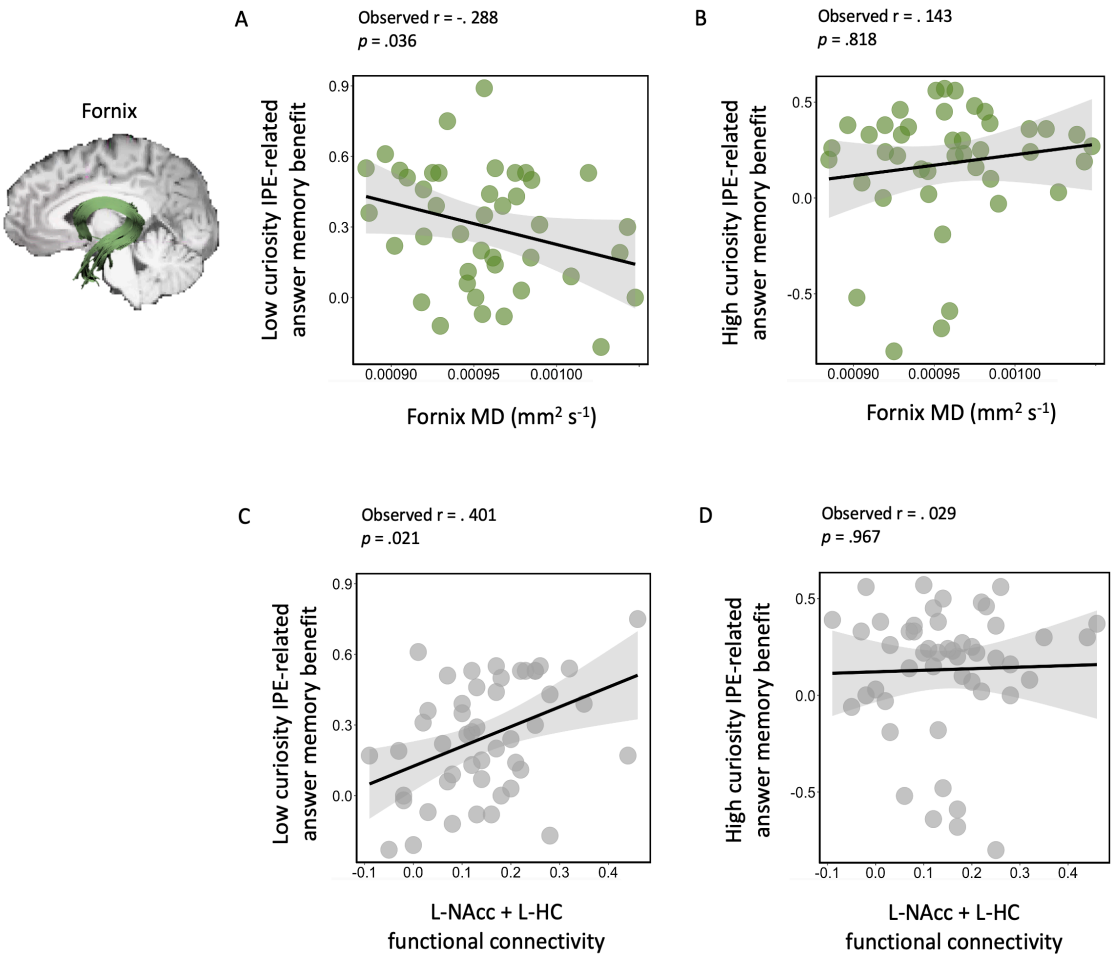


Figure 5.6: (A) Significant negative correlation between low curiosity IPE-related answer memory benefit and fornix MD (mm^2 s^{-1}) (n=41); **(B)** No significant correlation between high curiosity IPE-related answer memory benefit and fornix MD (n=42); **(C)** Significant positive correlation between low curiosity IPE-related answer memory benefit and resting-state functional connectivity between left nucleus accumbens (NAcc) and left hippocampus (n=48); **(D)** No significant correlation between high curiosity IPE-related answer memory benefit and resting-state functional connectivity between left (NAcc) and left hippocampus (n=49). The line of best fit and 95% confidence interval is shown on the scatter plots.

5.4 Discussion

This study investigated individual differences in structural and functional connections underlying curiosity-related memory. Focussing the analyses on the white matter microstructure of the fornix (i.e., fornix FA and MD) as potential correlates of curiosity-related memory, no direct association was found between fornix microstructure and behaviour. With regards to functional connectivity at rest between ROIs involved in the functional loop, curiosity-related answer memory benefit was found to positively correlate with RSFC between the right NAcc and left VTA. Furthermore, RSFC between the right NAcc and left VTA positively correlated with FA of the whole fornix. Given that RSFC between the right NAcc and the left VTA correlated with fornix FA and curiosity-related answer memory benefit, this variable was used as the potential mediator of the hypothesized relationship between fornix microstructure and curiosity-related memory. This study found that the relationship between fornix FA and curiosity-related answer memory benefit was in fact mediated by functional connectivity between the right NAcc and left VTA, suggesting that fornix microstructure does not predict later curiosity-related memory alone.

5.4.1 Indirect effect via functional connectivity on the relationship between microstructure and curiosity-related memory

First, this experiment examined the relationship between microstructure and behaviour. The fornix is a structure that connects the hippocampus, involved in information seeking and episodic memory, to the ventral striatum - a structure that functions as part of the reward system and consists of the NAcc. Therefore, it was predicted that fornix FA reflective of high myelin density and histological orientation would predict curiosity-related answer memory benefit. Despite previous evidence supporting the role of the fornix in predicting episodic memory performance (Rudebeck et al., 2009; Metzler-Baddeley et al., 2011), no significant relationship between fornix microstructure and curiosity-related answer memory benefit was found.

Although the current study did not find a relationship between fornix microstructure and curiosity-related answer memory benefit, I tested for a positive correlation between

curiosity-related answer memory benefit and functional connectivity between selected ROIs. For example, a positive association was expected between curiosity-related memory and functional connectivity observed between the NAcc and the hippocampus, based on evidence that suggests that hippocampal and NAcc communication is important for memory consolidation and retrieval (Adcock et al., 2006; Kahn and Shohamy, 2013; Lisman and Grace, 2005; Gruber et al., 2014). The ROI-to-ROI RSFC analysis confirmed first that there was high functional connectivity between the VTA, NAcc and hippocampus, in line with the hippocampal-VTA functional loop theory that postulates high intrinsic connectivity between these regions (Lisman & Grace, 2005). Next, correlating ROI-to-ROI RSFC with participant's curiosity-related answer memory benefit, right NAcc functional connectivity with the left VTA was found to positively correlate with curiosity-related answer memory benefit. However, no significant correlation was found between curiosity-related answer memory benefit and functional connectivity observed between the VTA and the hippocampus, where based on the hippocampal-VTA functional loop theory that supports learning, such a relationship was expected (Adcock et al., 2006; Gruber et al., 2014, 2016; Kahn & Shohamy, 2013). These findings suggest that at rest, increased functional connectivity between the NAcc and the VTA predicts a greater benefit of curiosity in influencing later memory for trivia answers, where the NAcc appears to play a pivotal role in bridging the communication between the VTA and hippocampus. Previous evidence suggests that when a person is exposed to a novel stimulus, the hippocampus detects this information that is not already stored in long-term memory and conveys a novelty signal through to the NAcc, ventral pallidum and then to the VTA (Kahn & Shohamy, 2013). In the present study, the increased functional connectivity between the NAcc and the VTA observed at rest reflects a pattern of communication that may facilitate the transmission of neurotransmitters when novel information is encountered, supporting the entry of information that bridges a knowledge gap into long term memory. The present study provides some evidence in support of the hippocampal-VTA functional loop theory; however, it also highlights that although there is a loop, the utility of its subsections are not all equal and some portions of the loop may be more critical in triggering the loop for information processing.

Next, whether RSFC between ROIs that significantly correlated with curiosity-related answer memory benefit also correlated with fornix microstructure was investigated. These results indicated that right NAcc functional connectivity with the left

VTA positively correlated with FA of the whole fornix. Previous evidence illustrates there being a strong relationship between the NAcc and VTA where activated glutamatergic projections from the hippocampus to the NAcc via the fornix activate inhibitory GABAergic inputs from the NAcc to the ventral pallidum, which in turn results in decreased GABAergic inhibition from the ventral pallidum to the VTA, subsequently stimulating dopaminergic neurons in the VTA that project directly to the NAcc (Floresco et al., 2001; Lisman & Grace, 2005). This evidence is in line with the relationship found in the present study between fornix microstructure and RSFC between the NAcc and VTA. One interpretation of the observed relationship between fornix white matter structure and RSFC is that the fornix facilitates aspects of the functional loop, supporting the communication between the NAcc and VTA. Specifically, the fornix structure delivers the necessary neurotransmitters from the hippocampus to the NAcc that subsequently offsets communication between the NAcc and VTA (Floresco et al., 2001; Lisman & Grace, 2005).

So far, the results of this experiment indicate a relationship between fornix microstructure and NAcc-VTA RSFC, and a relationship between NAcc-VTA RSFC and curiosity-related answer memory benefit. However, although evidence leads us to believe there would be a relationship between fornix microstructure and memory performance (Rudebeck et al., 2009; Hartopp et al., 2019) no direct relationship between fornix microstructure and curiosity-related answer memory benefit was found in the present study. The evidence thus far suggests that RSFC may possibly help explain and/or facilitate the effect of microstructure on behaviour, since ultimately it is structure that affords the hardware for functional connectivity to emerge, and brain function, rather than structure, that produces behaviour (Dubois, et al., 2018; Straathof, Sinke, Dijkhuizen, & Otte, 2019). Hence, to see any effect of structure on behaviour, it is possible that functional mechanisms need to be involved. Therefore, this study subsequently investigated whether the theorised effect of white matter microstructure on curiosity-related answer memory benefit is operated through functional connectivity between selected ROIs – specifically the RSFC between the right NAcc and left VTA (ROI-to-ROI RSFC that were found to be associated with both fornix microstructure and behaviour). Traditionally, mediation analysis has been practiced with the precondition that the predictor variable correlates with the outcome variable (Hayes, 2013). However, there is now a growing consensus that examining indirect effects is not reliant on a significant relationship between the IV(X) and DV(Y) as a pre-requisite (e.g., Cerin &

MacKinnon, 2009; Hayes, 2009; Rucker, Preacher, Tormala, & Petty, 2011; Shrout & Bolger, 2002; Zhao, Lynch & Chen, 2010). The present mediation model indicated that although no direct effect of fornix microstructure on behaviour was observed, an indirect effect of microstructure on behaviour through RSFC between the NAcc and VTA was present. In other words, the effect of microstructure on behaviour can be thought to be relayed via the mechanism characterised by the microstructure → RSFC → behaviour causal chain of events (Hayes, 2013; Hayes & Rockwood, 2017). The mediation model employed in the present study indicated the presence of an indirect effect of fornix microstructure on curiosity-related memory. This model tested the extent to which the relationship between fornix FA and curiosity-related answer memory benefit was mediated by functional connectivity between right NAcc and left VTA, suggesting that fornix microstructure does not predict later curiosity-related memory alone. It appears that the effect of fornix microstructure on later curiosity-related behaviour is explained through the functional connectivity between the right NAcc and left VTA, where it is established that the transmission of dopamine from the VTA to the NAcc modulates motivation, arousal, and also plays a role in the manifestation of reward seeking behaviours (Fox et al., 2016; Sombers, Beyene, Carelli & Wightman, 2009). With the mediation model carried out in the present experiment, the analysis indicates that RSFC between the right NAcc and left VTA mediates the hypothesized structure-behaviour relationship. Traditionally, it has been thought that dopamine release (e.g., dopamine release from VTA to NAcc) is likely not to cross hemispheres, however evidence suggests that some dopaminergic neurons project and release dopamine in the contralateral hemisphere (Fox et al., 2016; Molochnikov & Cohen, 2014). For instance, D2 autoreceptors from projections of the contralateral VTA have been found to exert more control over dopamine release in the NAcc relative to ipsilateral projections (Fox et al., 2016). The present finding that contralateral functional connectivity between the VTA and NAcc showed a statistically significant relationship with curiosity-related answer memory benefit is in line with the idea that cross-hemispheric connections facilitating the neurotransmission of dopamine modulates motivation and arousal-based behaviours (Fox et al., 2016). Furthermore, this observed contralateral functional communication between the right NAcc and left VTA was found to mediate the hypothesised relationship between fornix microstructure and curiosity-related answer memory benefit, indicating that it is perhaps brain function, rather than structure, that produces behaviour as stated by Dubois et al. (2018).

As well as investigating the relationship between RSFC between the selected ROIs, fornix microstructure and curiosity-related answer memory benefit, the present experiment also explored individual differences in structural and functional connections underlying other behavioural measures including overall answer memory, curiosity-related face memory and IPE-related answer memory benefit. No significant correlations were observed between any of the ROI-to-ROI RSFC measures and overall answer memory. Importantly, this suggests that the relationship between left VTA-right NAcc RSFC and curiosity-related answer memory benefit cannot be explained by overall answer memory. Furthermore, fornix microstructure did not correlate with any of the other behavioural measure except low curiosity IPE-related answer memory benefit, which negatively correlated with fornix MD. A possible explanation for this might be that those participants with reduced diffusivity (i.e., lower MD values) in the fornix show a greater benefit of positive IPEs in influencing later memory for low curiosity trivia answers. Additionally, this was the only other behavioural measure to significantly correlate with the ROI-to-ROI RSFC measures. Specifically, low curiosity IPE-related answer memory benefit positively correlated with functional connectivity between left NAcc and left hippocampus. These correlations are somewhat in line with Pine, Sadeh, Ben-Yakov, Dudai, and Mendelsohn (2018) that suggest the ventral striatum encodes prediction errors, and Jang, Nassar, Dillon, and Frank (2019) that show positive prediction errors increase memory encoding. Despite the relationship between low curiosity IPE-related answer memory benefit with each fornix MD and RSFC between the left NAcc and left hippocampus, no subsequent correlation was observed between microstructure and functional connectivity, which suggests overall, the mediation of RSFC on the relationship between fornix microstructure and behaviour is specific to curiosity-related answer memory benefit.

5.4.2 Limitations and future directions

It is acknowledged that the present study only recruited a sample of 55 participants, where for the separate analyses carried out some datasets were removed for various reasons when analysing the data. This meant that the final mediation analysis consisted of fewer people than at the beginning of the study. Therefore, it is suggested that future studies base their sample size on a calculated power analysis, taking into account the possibility of having to exclude participants based on the criteria for their different

measures, in order to make accurate and reliable statistical judgements. However, compared to diffusion studies that correlate diffusion measures with task-based findings (e.g. perception or memory tasks) (Hodgetts et al., 2015, 2017; Reggente et al., 2018), the present sample is slightly larger and comparable to other recent studies that investigated brain-trait relationships (e.g., Privado et al., 2017). Nevertheless, further correlational studies would need to validate the present findings in a larger sample.

The present study used a mediation analysis that indicated a mediating effect of RSFC on the underlying effect of structure on behaviour. Here, it is explained that establishing a significant relationship between the independent and dependent variable is not necessary – such that two variables that are not significantly related, does not mean that X does not affect Y (Hayes & Rockwood, 2017). For instance, a mediation analysis where the bootstrap confidence intervals for the indirect effect is entirely above zero suggests that the effect of say structure (x) on behaviour (y) is better explained when taking into account the effect of functional connectivity (m). The modern use and interpretation of mediation analysis can therefore be used to help understand the complex relationships that exist between neural mechanisms and their subsequent influence on behaviour.

Extending beyond this mediation analysis, the possible effect of trait curiosity on the three-way relationship between structure, functional connectivity and curiosity-related behaviour was not investigated. I decided not to incorporate the trait curiosity data (see Experiment 2 of Chapter 2-4) in the present study given that the trait questionnaires were administered after participants completed the curiosity memory paradigm. Based on recent evidence showing trait curiosity levels fluctuate across time even within-individuals (Lydon-Staley et al., 2019a, 2019b), I considered that exposure to the curiosity memory paradigm may have influenced participants' self-report ratings compared to say if the trait measures were administered when participants had not been subjected to a behavioural task that elicits different levels of curiosity. Furthermore, the use of the subsets from the 5-Dimensional Curiosity scale rather than subsets from the EC and PC scales would be more beneficial as they provide a better representation of Interest/Diversive and Deprivation/Specific aspects of curiosity that are not limited to whether exploratory behaviours and information seeking is epistemic or perceptually related. Therefore, as a means to obtain a better representation of trait curiosity not confounded by states of curiosity or limited to dimensions of Epistemic or Perceptual

Curiosity, future studies may want to consider utilising the 5-Dimensional Curiosity scale, and for it to be administered before exposing participants to behavioural tasks. This would enable researchers to subsequently investigate the additional effect of trait curiosity on the mediated relationship between structure and curiosity-related behaviours.

5.5 Chapter Summary

This chapter employed combined methods to investigate the relationship between brain structure, function and curiosity-related behaviour. First, no direct relationship was found between fornix microstructure and curiosity-related behaviour. Next, a positive correlation was found between curiosity-related answer memory benefit and resting-state functional connectivity between the right NAcc and left VTA; that could not be explained by overall answer memory. Based on this finding, functional connectivity between the right NAcc and left VTA was correlated with fornix microstructure revealing a positive association with fornix FA. Finally, a mediation analysis revealed an indirect effect, via NAcc-VTA functional connectivity, on the relationship between fornix FA and curiosity-related answer memory benefit. In summary, using combined methods has enabled the investigation of the three-way relationship between structure, function and behaviour, where the effect of fornix FA on curiosity-related answer memory benefit is believed to operate through RSFC between the right NAcc and left VTA, such that for structure to have an effect on behaviour, function needs to be involved.

Chapter 6: General Discussion

6.1 Overview

This thesis set out to examine the neural mechanisms underlying curiosity and the ways in which curiosity benefits memory. Despite the growing and promising research into the concept of curiosity, the majority of this research has focussed on curiosity as a state and the regional activations observed during these states of curiosity. Curiosity motivates us to learn, yet curiosity varies strikingly between individuals. Such individual differences have been shown for two distinct dimensions of curiosity: Epistemic Curiosity, the desire to acquire knowledge about facts, and Perceptual Curiosity, the desire for sensory information. It is not known, however, whether these aspects of curiosity depend on different brain networks and whether inter-individual differences in curiosity depend on variations in anatomical and functional connectivity within these networks. Therefore, this thesis explored the possible neural mechanisms underlying trait curiosity. To achieve this, Chapter 2 and 3 examined the brain networks related to different types of curiosity traits. Next, transitioning the focus of the thesis from trait to state curiosity, where state and trait curiosity are proposed to be positively associated, Chapter 4 investigated whether people high in trait curiosity benefit more from being in a state of curiosity. This chapter also employed a modified version of the classic trivia memory paradigm to determine the effect of curiosity on memory for curiosity-related information as well as incidental information presented prior to being in a state of curiosity. The final experimental chapter aimed to assess how individual variations in structural-functional brain connections predict curiosity-related memory.

This thesis identified potential structural and functional correlates of different types of trait curiosity. Furthermore, in line with the previous literature this research has also shown that high versus low states of curiosity enhance memory for information that people want to know the answer to. In contrast, no evidence was found in support of the effects of curiosity states on memory for incidental information that holds no motivation-based value to the participant. This thesis has also shown that people who display high

trait curiosity do not benefit more from being in a curiosity state than people low in trait curiosity. Finally, one of the more significant findings to emerge from this thesis is that it appears that the effect of white matter microstructure on curiosity-related memory operates through functional connections (measured during rest). In this general discussion I will discuss the findings of this thesis, consider the methodology employed to answer my research questions, discuss the associated limitations to this work, and finally propose future directions that extend the work of this thesis.

6.2 Main findings of the thesis

6.2.1 Inter-individual variation in microstructure relates to specific subsets of trait curiosity

Chapter 2 set out to identify the structural network related to different types of curiosity traits. DWI was employed to investigate underlying microstructure, specifically white matter pathways that connect regions believed to be involved in the manifestation of curiosity and its subsequent behaviours. To date, little evidence has been found associating trait curiosity and the neuroanatomical substrates underpinning individual differences in trait levels of curiosity. Examining the correlates of the ILF, Interest and Deprivation subscales of EC (i.e., subscales that are likely to involve semantic processing and/or cognition) were expected to significantly correlate with ILF microstructure (FA, positive relationships; MD, negative relationships). In Experiment 1 of Chapter 2, it was found that both aspects of EC correlated with ILF MD, a long-distance structural fibre connecting posterior and anterior structures. In contrast, no significant associations were observed between ILF microstructure and subsets of PC. This finding illustrates that individual differences in EC is associated with individual variability underlying white matter pathways involved in higher level cognitive processes (Privado et al., 2017) such as knowledge acquisition. Other evidence suggests that the fornix, a white matter structure interconnecting the hippocampus with areas including the mamillary bodies, PFC and the ventral striatum is associated with behaviours such as novelty and reward dependence (Catani & Thiebaut de Schotten, 2008; Christiansen et al., 2016; Cohen et al., 2009; Poletti & Creswell, 1977). Examining the relationship

between fornix microstructure and subscales of EC and PC, Experiment 1 of Chapter 2 found that fornix FA positively correlated with Interest EC, and fornix MD showed a negative correlation with Specific PC that approached significance. Next examining anterior and posterior segments of the fornix that correspond to the functional subdivisions of the anterior and posterior hippocampus, respectively (Christiansen et al., 2017; Saunders & Aggleton, 2007), contrary to the prediction that individual differences in Interest EC would be associated with variability in microstructure of the anterior hippocampal fornix, individual differences in Interest EC was related at a trend-level to white matter microstructure of two segments that make up the fornix (posterior and left anterior hippocampal fornix FA). In contrast, as expected Specific PC significantly correlated with the posterior hippocampal fornix (MD) only, which could explain why no significant correlation was observed with microstructure of the whole fornix (MD).

In Experiment 2, a similar protocol was conducted in which the aim was to replicate the findings from Experiment 1. Somewhat in line with the findings from Experiment 1, ILF microstructure (FA but not MD) showed a relationship (though non-significant) with both subsets of EC. Together, these initial observations suggest that there may be a link between trait EC and regions that involve the processing of semantic information motivated by positive affect but also the search for specific information in order to close a knowledge gap (Litman, 2005, 2008; Loewenstein, 1994; Lauriola et al., 2015). With regards to the fornix, neither subsets of EC or PC showed significant associations with fornix microstructure (FA or MD). However, with regards to the relationship between fornix FA and Interest EC, it should be noted that the replication Bayes factor indicated only anecdotal evidence in support of a spurious effect. In Experiment 2, the underlying structural correlates of the 5-Dimensional Curiosity scale was also explored. The Joyous Exploration and Deprivation Sensitivity subsets potentially capture Interest/Diversive and Deprivation/Specific aspects of curiosity respectively, without specifying whether information gathering is related to exploratory behaviours that results in increased perception of the environment (i.e., Perceptual Curiosity), or related to the desire for knowledge and drive to know (i.e., Epistemic Curiosity). Joyous Exploration, which was found to significantly correlate with Interest EC, was the only trait measure to show a positive relationship (though non-significant) with fornix FA, such that participants high in Joyous Exploration showed ‘stronger’ fornix white matter connectivity. In Chapter 2, although the second experiment was unable to replicate the findings from the original experiment, this is the first study of its kind to

investigate the underlying brain structure that supports trait curiosity. Together, the findings of these two experiments suggest that the individual variability in fornix microstructure is related to the aspect of curiosity that reflects exploring and information gathering as a means to increase arousal and positive affect, whilst efficient information transfer along the ILF reflects the desire to fill a knowledge gap in instances of Interest and/or Deprivation.

6.2.2 Functional connectivity within the hippocampal-VTA loop shows some relationship with trait curiosity

In Chapter 3, the purpose of the two experiments conducted were to determine whether the hippocampal-VTA functional network related to different types of curiosity traits. Prior studies have noted the functional neural mechanism underlying state curiosity; however, the functional network underlying trait curiosity is less well investigated. This chapter therefore employed resting-state fMRI to investigate whether individual variability in the functional organisation of the hippocampal-VTA loop that regulates learning is related to individual differences observed in trait curiosity. The target network which was examined included regions involved in the mesolimbic pathway, including the VTA, NAcc and hippocampus, with the hippocampus being defined into its anterior and posterior segments. Experiments 1 and 2 of Chapter 3 predicted there to be a positive association between this functional network and scores obtained on subscales of EC and PC. In particular, it was expected that Interest/Diversive aspects of curiosity would show stronger positive correlations with inter-individual differences in functional connectivity involving the anterior hippocampus versus the posterior hippocampus, and Deprivation/Specific aspects of curiosity would show stronger positive correlations with inter-individual differences in functional connectivity involving the posterior hippocampus versus the anterior hippocampus. Furthermore, functional connectivity between the NAcc and the VTA were expected to show significant positive correlations with all subscales of curiosity. Using a ROI/seed-based functional connectivity analysis, Experiment 1 found that individual variability in subsets of EC were not associated with RSFC between ROI's involved in the hippocampal-VTA loop. However, individual variability in Diversive PC, that describes the tendency to employ exploratory behaviours in search for general perceptual stimulants to reduce boredom and increase arousal (Berlyne, 1960, 1966; Collins et al., 2004), was found to show a

positive relationship that approached significance with RSFC between the anterior hippocampus and the subcortical region that it supplies the most numerous inputs to, the NAcc. In Experiment 2, individual variability in Stress Tolerance was found to positively correlate with RSFC between VTA and NAcc. This subset of the 5-Dimensional Curiosity scale was also found to positively correlate with Diversive PC, where based on the findings from Experiment 1, one might have expected a positive association with the RSFC between anterior hippocampus and NAcc instead. Additionally, when correlating the EC and PC subsets of curiosity with RSFC between ROI's involved in the hippocampal-VTA loop, no significant associations were found. A probable explanation for these inconsistent findings across the two experiments could be that the replication study was underpowered (Button et al., 2013; Chen et al., 2018). Taken together, the two experiments of this chapter suggest that stronger coupling at rest between regions involved in the hippocampal-VTA loop reflect higher trait curiosity and may explain why curiosity is evoked more frequently and/or more intensely in some people but not others.

6.2.3 State but not trait curiosity benefits memory

This thesis next examined how different states of curiosity influenced memory for curiosity-related and unrelated information. The experiments in Chapter 4 were designed to determine the effect of high versus low curiosity states on later memory for trivia answers presented after an anticipation period, and incidental faces presented prior to the question eliciting curiosity. In line with the literature, the two experiments in this chapter found that high states of curiosity resulted in better recall for curiosity-related information. With regards to memory for incidental information, previous studies in the literature have typically chosen to present incidental information prior to knowledge acquisition (i.e., during anticipation), where they also ask participants to rate whether the person whose face appeared during anticipation are knowledgeable about the trivia question (Galli et al., 2018; Gruber et al., 2014; Stare et al., 2018). These studies examining the curiosity memory effect for incidental information do not consider whether the faces presented at encoding were truly incidental. In this thesis, truly incidental information describes stimuli that is presented incidentally, such that when presented to the participant it holds no value related to the conditions of interest. Therefore, based on the synaptic tag-and-capture hypothesis that stipulates incidental information can be consolidated when followed by salient experiences (Dunsmoor et al., 2015; Frey &

Morris, 1997), the purpose of the present paradigm was to determine whether truly incidental information, unrelated to the trivia question or answer, were better remembered under conditions of high versus low curiosity conditions. However, the two experiments described in this chapter did not detect any evidence in support of a curiosity memory effect for the incidental faces. These findings suggest that perhaps the salient experience is specific to processes during the anticipation period rather than the presentation of the question. Future studies may want to investigate how presenting truly incidental information at different points during anticipation (leading up to answer presentation) differentially affects later memory, in order to determine the prime time of where a 'tag' is placed before encountering the salient/novel experience that is the trivia answer. This paradigm also investigated the effects of information prediction errors on later memory for trivia answers, where in line with the results of Marvin and Shohamy (2016), the findings indicate that in states of both high and low curiosity, memory for the trivia answer is better when post-answer interest exceeds an individual's initial curiosity to find out the answer than when post-answer interest is less than one's curiosity.

It is a widely held view that those high in trait curiosity engage in information seeking and exploratory behaviours more frequently and intensely than those low in trait curiosity (Grossnickle, 2016; Litman, 2005; Litman et al., 2005; Kashdan & Steger, 2007), with several strong relationships between trait and state curiosity being reported in the literature. In Chapter 4, it was also hypothesised that participants scoring high in trait curiosity would benefit more from being in a state of curiosity than individuals scoring low in trait curiosity. Here, the curiosity-trivia paradigm was employed, to which subsequent measures of memory were correlated with self-report measures related to epistemic curiosity. Contrary to expectations, this study did not find a significant relationship between trait curiosity and curiosity-related memory benefits. The reason for this is not clear but may be due to lack of power and/or the possible bias in the trait curiosity self-report responses.

6.2.4 Effect of microstructure on curiosity-related memory operates through RSFC

The final question in this thesis sought to determine how individual variations in structural-functional brain connections predict curiosity-related memory. To date, there

is no evidence directly examining the relationship between white matter structure, functional connectivity and memory prioritization due to curiosity-related memory. Based on the findings from Chapter 2 (Experiment 1), where white matter microstructure of the whole fornix related to individual differences in Interest EC; as well as previous fMRI evidence that provide support for the hippocampal-VTA functional loop theory in relation to curiosity driven learning (Kang et al., 2009; Gruber et al., 2014), this final aspect of the thesis investigated the three-way relationship between fornix white matter microstructure, RSFC between ROI's involved in the hippocampal-VTA loop and curiosity-related behaviours. The results of this study indicate that although no direct relationship was observed between fornix microstructure and curiosity-related answer memory benefit, functional connectivity between the right NAcc and the left VTA appears to facilitate the hypothesised relationship between fornix microstructure and curiosity-related behaviour. This combined imaging approach has proven useful in expanding our understanding of how functional connectivity in the brain affects the impact of structural connectivity on curiosity-related behaviours.

6.3 Methodological considerations and limitations

6.3.1 Administration of questionnaires

One drawback of this thesis is that in Experiment 2 of Chapters 2-4 the trait curiosity questionnaires were administered at the end of the experiment once participants had completed a series of curiosity and reward-based behavioural tasks. In contrast, Experiment 1 (of Chapters 2-3) involved participants first completing the EC and PC curiosity scales followed by other self-report measures and behavioural tasks that did not tap into processes related to curiosity or reward (these questionnaires/tasks are not discussed in this thesis). It is possible that trait curiosity levels fluctuate across time even within-individuals. For example, Lydon-Staley et al. (2019a) had their participants rate their level of sensation seeking on a daily basis immediately before their daily browse on Wikipedia, where it was found that sensation seeking self-reports that were higher than usual related to looser knowledge networks being created. Given that trait curiosity levels can fluctuate across time, it is possible that trait measures of curiosity administered after completing the curiosity trivia memory paradigm, results in dissimilar

self-reports to when administering curiosity trait measures prior to any behavioural task that elicit reward/salience. Therefore, when administering questionnaires, it is important to consider how a state of a person could influence the self-report ratings they subsequently make (Lydon-Staley et al., 2019a).

Furthermore, it is important to consider the number of questionnaires that were administered at any one time. It is possible that the large number of questionnaires administered in Experiment 2 (of Chapters 2-4) caused participants to become fatigued resulting in less reliable curiosity trait scores. For instance, Experiment 1 involved administering questionnaires of interest separately to other questionnaires not relevant to the thesis, whilst in Experiment 2 all the scales were part of a bank of questionnaires that were administered back-to-back in a randomised order. It is possible that in Experiment 2 where a larger number of questionnaires were administered back-to-back may have resulted in respondent fatigue in which participants become tired and provide perfunctory responses (Ben-Nun, 2008; Porter et al., 2004).

Overall, it is possible that Experiment 1 might have produced much cleaner questionnaire data, as how and when the questionnaires were administered in Experiment 2 compared to Experiment 1 (of Chapters 2 and 3) could explain why the findings with regards to structural connectivity (Chapter 2) and functional connectivity (Chapter 3) underlying trait curiosity could not be replicated.

6.3.2 Statistics and multiple comparisons correction method

This thesis employed non-parametric permutation tests based on Pearson's linear correlation coefficient *r* that corrected for multiple comparisons, as a means to investigate the strength of the relationship between brain measures and behavioural measures. Permutation tests control the family-wise-error rate. This describes the probability that a false positive appears in the entire family of tests, where the ‘family’ denotes all the tests that relate to a specific criterion (Groppe et al., 2011). In the present thesis the ‘family of tests’ consisted of pairs of variables that resulted in the highest number of comparisons. For instance, in Chapter 3 when correlating curiosity traits and functional connectivity measures, separate permutation tests were conducted for each measure of trait curiosity correcting for functional connectivity measures to which there

were 20 measures. This 'family of tests' also resulted in fewer permutation tests being carried out. For instance in Chapter 3 (Experiment 1), a total of 4 permutation tests were ran (each permutation test correcting for 20 RSFC measures), rather than 40 separate permutation tests correcting for the 2 subsets of a specific type of trait curiosity (e.g., 20 permutation tests correcting for the 2 subsets of EC, and 20 permutation tests correcting for the 2 subsets of PC). The only instance where the 'family of tests' did not follow this rule was in Chapter 4, when investigating the relationship between trait curiosity and measures of memory. Here, instead of correcting for measures of memory (6 measures), trait curiosity was corrected for (e.g., 6 permutation tests correcting for the 2 subsets of EC, and 6 permutation tests correcting for the 3 subsets of the 5-Dimensional Curiosity scale). The justification for this was because running a permutation test correcting for measures of memory would have resulted in the removal of 9 participants from each permutation test conducted.

One limitation of running permutation tests throughout this thesis, is that given the vast number of comparisons in some of the pre-defined family of tests, this increased the chance of getting more extreme *r* observations which as a result increased the spread, for example, of the trait-$RSFC_{max}$ distribution (Groppe et al., 2011). This subsequently increased the critical correlation coefficient for the family-wise alpha level of 0.05, meaning that correlation coefficients that did not reach or exceed this critical correlation coefficient value did not significantly deviate from the null hypothesis (Groppe et al., 2011). Unfortunately, this means that in the present thesis some permutation tests were more conservative than others. The adoption of conservative approaches that attempt to reduce the number of type 1 errors (i.e., false positives), runs the risk of making type 2 errors (i.e., false negatives) (Lieberman & Cunningham, 2009). For example, it is possible that in Chapter 3, permutation tests conducted for a single trait measure of curiosity when correlated with the 20 RSFC measures resulted in correlations not reaching significance, despite a correlation coefficient greater than 0.30 (e.g. Experiment 1, left NAcc and left VTA RSFC correlation with Interest EC (Appendix 12A) and Diversive PC (Appendix 12C)). Alternative to conducting such conservative correction methods to avoid type 1 errors (and consequently risk making type 2 errors), Lieberman and Cunningham (2009) recommend replication and meta-analysis, where false positives found in the original study will simply not replicate. It should be noted that Chapter 2 and 3 included a second replication study of their respective original studies, however, due to the lack of power and several methodological differences between the

two experiments, such as how and when the trait questionnaires were administered, it is not conclusive that the results found in the original studies were truly false positives. Further studies are needed to test (or even replicate) the associations between trait curiosity and the structural/functional networks in the brain.

6.3.3 Measuring curiosity states

In this thesis, a momentary experience of curiosity in response to cues such as novelty and surprise was regarded as state curiosity (Grossnickle, 2016; Kashdan & Roberts, 2004). In Chapter 4 and 5, all participants who participated in the trivia memory paradigm experienced the same frequency of high and low curiosity states, where later memory for the items encoded during these states of curiosity were taken as the outcome of being in a state of curiosity. State curiosity is often measured through behavioural outcomes; however, the benefits that come from being in a state of curiosity can be debated to be an indirect measure of state curiosity. For instance, in the current paradigm employed in this thesis it can be argued that all participants experienced the same states of high and low curiosity to which it cannot be said that people high in trait curiosity experience *states* of curiosity more frequently and intensely than individuals low in trait curiosity (Grossnickle, 2016). Alternative methods to quantitively measure states of curiosity could be to employ eye-tracking methods and examine what happens when one is actually in a state of curiosity. For instance, one study that examined the relationship between trait curiosity and individual differences in state curiosity behaviours, found that Perceptual Curiosity positively correlated with the number of regions visited in a scene-viewing task (Risko et al., 2012). Similarly, Baranes et al. (2015) found that exposure to high curiosity states was associated with participants directing their gaze towards the location of the answer, where eye distance to the answer was also found to negatively correlated with trait curiosity. Additionally, an approach similar to Lydon-Staley et al's. (2019a) measure of how frequently participants expose themselves to states of curiosity would better inform us on 'in the moment' exploration and/or information seeking and their subsequent relationship with trait curiosity.

6.3.4 Limitations of DTI and resting-state fMRI

Although, the use of DTI method employed in this thesis has its advantages, some of the issues emerging from this method relate specifically to the measure of structural connectivity. In this thesis, structural connectivity that is white matter was assessed using FA and MD scalar measures, where I found that FA and MD measures do not always relay the same information. These DTI indices are believed to reflect a number of biological properties such as axon diameter and density, myelination and the arrangement of fibres in a given voxel (Beaulieu, 2002). For instance, high FA has been found to reflect high myelin density and structured histological orientation whereas high values of MD are more likely to reflect low myelin density and diffuse histological orientation (Seehaus et al., 2015). However, in the present thesis an inverse relationship between these two measures when correlated with curiosity was not always observed. For example, in Experiment 1 of Chapter 2, whilst Deprivation EC negatively correlated with ILF MD, no significant positive associations were observed with ILF FA. It is thought that FA and MD are sensitive, but non-specific, measures of microstructural architecture (Alexander et al., 2011; Winston, 2012). For example, FA is sensitive to changes in tissue structure and MD is sensitive to characteristics such as necrosis, edema and cellularity, however, these measures do not specify the type of change (Alexander et al., 2011). Nonetheless, these measures are still informative with regards to overall microstructural integrity of white matter tracts, where it is argued that examining one diffusion measure over the other may not be sufficient to characterise tissue change (Alexander et al., 2007). Given the difficulty in interpreting FA and MD measures of connectivity, future work on the microstructural correlates of curiosity could employ more sensitive and meaningful measures of white matter change such as the hindrance modulated orientational anisotropy (HMOA) index that, unlike conventional DTI indices, can detect small white matter tract changes in the microstructural architecture (Dell'Acqua et al, 2013). Other modelling techniques more advanced than the DTI model (Basser et al., 1994), such as the NODDI model, evaluates two specific measures of tissue microstructure: the orientation dispersion index (of neurites) that measures the fanning and bending of axons, and the neurite density index that estimates the fraction of tissue that comprises of dendrites and axons (Zhang et al., 2012). These indices of neurites provide more specific microstructural information than the standard FA and MD values used in diffusion MRI research. Furthermore, the use of correlation analysis is limited to the strength of a relationship between FA/MD measures of microstructure and trait

curiosity. When examining the structural and functional network that underlies behaviour, correlational analyses fails to establish causality in brain-behaviour relationships. The next step in better understanding the brain structure-trait relationship could be to conduct longitudinal studies to determine whether trait curiosity shapes white matter connections, vice versa, or whether both reinforce each other in a bidirectional manner. For instance, Bechler et al. (2018) found that change in myelination through activity-dependent adaptation of an initially hard-wired process occurs in response to experiences and contributes to learning.

Similar to DWI, prior studies have noted the importance of employing resting-state fMRI as a measure of functional brain connectivity in order to best predict individual differences in personality traits (Adelstein et al., 2011; Dubois et al., 2018). In this thesis, a seed-based approach was employed to examine the correlations between selected *a priori* ROI's (Smitha et al., 2017; Van den Heuvel & Pol, 2010). Although there is beauty in the simplicity of this correlational analysis method, a limitation of this approach is that the information obtained about the level of co-activation between brain regions was restricted to the functional connections between selected ROIs involved in the hippocampal-VTA loop, where the pre-selection of target and source ROIs can be argued to induce selection bias (Damoiseaux & Greicius, 2009). However, in this thesis the selection of ROIs was guided by the literature, where the hippocampal-VTA loop merited an investigation. Future research may consider a whole brain approach or explore other brain networks, such as the default mode network, that could be related to curiosity. Furthermore, a general limitation of correlation-based approaches used in resting-state fMRI is that causality cannot be established. Other methods that offer information about directed connectivity and better elucidate the functional brain architecture underlying curiosity traits include the Granger Causality Analyses or Dynamic Causal Modelling (Friston et al., 2013). Within the research of functional integration, the different types of connectivity include functional and effective connectivity (Friston et al., 2013). Ultimately, functional connectivity assesses the shared information or statistical dependence between two neuronal systems of interest, whilst effective connectivity evaluates the causal influences that one neural unit exerts over another (Friston et al., 2013; Stephan & Friston, 2010). Future studies should consider the use of effective connectivity methods of analysis in order to better understand and establish causality in brain-trait relationships.

6.3.5 Participants and sample size

In Experiments 1 of Chapters 2 and 3, a sample of 51 female participants were recruited, whilst in Experiment 2 of these respective chapters, a sample of 55 male and female participants were recruited. One possible reason for the lack of replication in Experiment 2 (Chapter 2) could be due to gender differences in trait curiosity. For instance, one study that examined gender differences in the Big Five found that whilst no gender differences were observed on the global level of the Big Five, women appeared to score higher than men in the Openness aspect of the Openness trait, whilst men scored higher than women in the intellect aspect of the Openness trait (Weisberg, DeYoung & Hirsh, 2011). In Chapter 2, when exploring the correlations between trait curiosity measures and white matter microstructure for only the female participants of Experiment 2, it appeared that correlation coefficients were greater (though not significant) than when male and female participants were included in the sample. Therefore, it is possible that gender differences may also help explain why structural-trait relationships were not replicated in Chapter 2. Furthermore, even though Experiment 2 was intended as a replication of the findings from Experiment 1, the replication study in Chapter 2 resulted in fewer participants than in the original study. Though the final sample was not considerably less, it is encouraged that replication attempts use larger sample sizes as a means to further decrease the uncertainty held for the replicability of these effects/relationships (Boekel et al., 2015; Masouleh et al., 2019). Being limited to a small sample, Experiment 2 (Chapter 2 and 3) lacked the necessary power for a successful replication (Button et al., 2013; Chen et al., 2018). Furthermore, with any correlational or neuroimaging study investigating individual differences, a large sample size is always advised and preferable (Dubois et al., 2018). Based on a power calculation that specifies directional correlations with a medium effect size, an alpha level set at 0.05 and power at 80%, a sample of 64 participants is necessary. However, Dubois and Adolphs (2016) propose that studies investigating brain-behaviour relationships should increase the typical sample size used in the literature (n = 10-50) to reflect n > 100, as a means of increasing power to detect individual differences. Therefore, the sample sizes employed throughout this thesis can be argued to lack sufficient power in detecting individual differences in brain correlates of curiosity related behaviours.

6.4 Implications

This thesis attempts to examine the relationship between structural/functional brain indices and higher-level behaviour/personality traits. The novelty of this thesis provides a starting point and platform for future research in further elucidating the underlying neural mechanism of trait curiosity, its potential relationship with state curiosity and the structural-functional interactions that predict curiosity-related behaviours. Furthermore, this thesis showcases the benefits of mutli-modal imaging methods in better understanding the neural mechanisms of higher-level cognitive processes. For instance, Chapter 5 utilised resting-state fMRI and DTI methods to examine the functional and structural correlates of curiosity-related memory, where a mediation analysis revealed that for structure to have an effect on behaviour, function needs to be involved. In contrast, previous studies in the literature often employ either DTI or resting-state fMRI methods to investigate memory-related behaviours/personality traits, rarely employing both structural and functional measures and ultimately reporting only part of the 'bigger picture'.

A further implication of this thesis is developing a better understanding of the similarities and differences between personality traits and state-related behaviours. Based on models of curiosity, it is proposed that state and trait curiosity are positively related whereby those high in trait curiosity experience states of curiosity – engaging in information seeking and exploratory behaviours – more frequently and intensely than those low in trait curiosity (Grossnickle, 2016; Litman, 2005; Litman et al., 2005; Kashdan & Steger, 2007). This implies that state and trait curiosity are related, however, there is little or no research investigating their relatedness/differences with regards to their underlying neural mechanism. For instance, Chapter 2 of this thesis indicated there to be a relationship between microstructure and traits (i.e., dispositional tendencies to experience some behaviours more frequently under a variety of conditions) whilst in Chapter 5 the relationship between microstructure and momentary experiences/behaviours (e.g. state curiosity) appeared to be more of a distal relationship that relies on RSFC in facilitating the behavioural outcome. This begs the question as to why the structural correlate of state-related behaviour is 'more' distal than the structural correlate of personality traits, and 'more' distal than the functional correlate of state-related behaviours. It is possible that trait and state curiosity differentially utilise structural

and functional mechanisms, where personality traits that reflect characteristics/tendencies that eventually produce a specific behaviour rely on the structural network more than functional connections, and state-related behaviours (e.g., curiosity-related memory) are more dependent on functional connections than structure. Dubois et al. (2018) used resting-state fMRI to predict Openness to Experience on the basis that "ultimately it is brain function, not structure, that generates the behavior on the basis of which we can infer personality" (p.6). With this being said, in Chapter 3 only trend level relationships are observed between trait curiosity and RSFC, whilst in Chapter 2 stronger relationships between trait curiosity and microstructure are observed. Although it holds true that personality traits produce later behaviours (to which we would most likely observe functional interactions between ROIs), the trait measure itself does not produce a behaviour but rather reflects characteristics/tendencies that eventually produce a specific behaviour. Therefore, it is possible that trait personality is more dependent on the structural mechanism whilst behaviours that persevere as a product of personality traits depend more on the functional mechanism compared to the structural mechanism that provides the basis for functional interactions. The novelty of this thesis in investigating the anatomical and functional neural mechanism of trait and state curiosity has brought to light the potential differences between personality traits and state-related behaviours.

6.5 Conclusions and future directions

This was the first study, to our knowledge to investigate the neural correlates of trait curiosity. Chapter 2 found that inter-individual differences in white matter microstructure are associated with specific subsets of trait curiosity. The use of a range of trait curiosity measures made it possible to examine how different types of trait curiosity relate to different brain networks. For instance, Specific-based Curiosity and Interest-based Curiosity appear to map onto fornix microstructure, but in different ways. Furthermore, Deprivation-based Curiosity appears to have a stronger association with microstructure of the ILF than Specific-based Curiosity. This thesis also found that individual differences in functional connectivity within the hippocampal-VTA loop shows a relationship with trait curiosity, such that people high in trait curiosity show greater communication between regions involved in the reward, memory and anticipation. Moreover, Chapter 2 and 3 involved replication attempts, where although the thesis was unable to produce

successful replications it highlights the need for neuroimaging research investigating brain-behaviour correlations to continue to replicate findings, as a single attempt at replication cannot be conclusive in confirming or refuting a finding. Additionally, the replication studies in this thesis emphasise that the failure in replicating the findings from the original experiments may not necessarily be failures but rather the replication study having low statistical power. Future studies wanting to further elucidate the underlying relationship between the brains microstructural architecture and trait curiosity should consider running replication studies that are appropriately powered. Moreover, this thesis speculates that gender may play a role in the relationship between trait curiosity and white matter microstructure. Previous research indicates there being gender differences in white matter microstructure including the ILF and the fornix, where some differences in tract microstructure offer an explanation as to why gender differences are observed in certain types of tasks (Kanaan et al., 2014). Future research is warranted into whether gender differences in trait curiosity exist and whether such difference are accounted for in the brains structural network.

Informatively, Chapter 4 sheds new light on the effects of state curiosity on memory for incidental information. The two experiments in this chapter employed a modified version of the classic curiosity-trivia paradigm to test the synaptic tag-and-capture hypothesis that claims memories for incidental information are retroactively strengthened when followed closely by behaviourally salient experiences. Here, a salient experience was considered to occur when the trivia question was presented, however, the findings in this chapter indicated that incidental information presented prior to a state of high curiosity did not predict better recognition memory. These findings raise intriguing questions regarding the nature and extent of salient experiences and that perhaps they are specific to the process of satisfying curiosity. Future research investigating the effects of curiosity on memory for truly incidental information may find it beneficial to present incidental information at different timepoints during anticipation (e.g., 6, 4 or 2 seconds prior to knowledge acquisition), ideally where the participant does not relate the face to the question that elicits curiosity. Such changes in the experimental design would be informative in showing how memory for incidental information changes as anticipation builds towards a salient experience that is knowledge acquisition.

Surprisingly, despite what has been found in the literature, Chapter 4 indicated no significant relationship between trait curiosity and the benefits of being in a state of

curiosity. This contradictory finding could be due to unreliable self-reports from participants or due to the lack of power. Nevertheless, this finding encourages research to further investigate how trait curiosity can facilitate future knowledge acquisition, which could subsequently be applied to educational and work settings. Alternatively, studies driven to investigate the relationship between curiosity traits and state curiosity itself should design their study in a way that the administration of questionnaires are kept separate to experiment measuring curiosity states. Additionally, when quantifying state curiosity, researchers may want to adopt a paradigm that measures the state itself rather than the benefits of being in a curiosity state. Future studies wanting to investigate the curiosity state-trait relationship are advised to consider these prospects when designing their study.

Finally, the methods and findings from Chapters 2-4 led to the use of multimodal neuroimaging in Chapter 5, where data obtained from resting-state fMRI and DWI were combined to acquire more detailed information about the brain dynamics associated with curiosity. The findings in this chapter help to better understand the relationship between the brains structure, its functional network, and how they relate to curiosity-related behaviours. Specifically, how the effects of the brain's microstructural architecture on curiosity-related memory is dependent on the functional communication between reward and memory related brain regions. Conclusively, there is abundant room for further progress in developing a full picture of the neural mechanisms underlying curiosity. Further work is required to establish the possible effect of trait curiosity on the three-way relationship between structure, functional connectivity and curiosity-related behaviour.

This thesis examines inter-individual differences in the brain's structural and functional network, and how differences in these two modalities relate to individual differences in curiosity. Employing different neuroimaging methods has provided promising evidence that contributes to a better understanding of the neurobiological mechanisms underlying curiosity traits and curiosity-mediated memory. This thesis suggests potential avenues for developing more sophisticated methods that inform researchers on the directionality of the relationship between structural and functional networks and their subsequent effects of curiosity-related behaviours. Further insight into how individual differences in curiosity and the neural mechanisms facilitating this phenomenon, may have important implications in educational and work-related environments.

Appendices

Appendix 1

Epistemic Curiosity Scale (Litman, 2008)

A number of statements that people use to describe themselves are given below. Read each statement and then select the appropriate response using the scale below to indicate how you generally feel. There are no right or wrong answers. Do not spend too much time on any one statement.

For the statements below rate yourself on the following 4-point scale:

1 = Almost Never 2 = Sometimes 3 = Often 4 = Almost Always

1. I enjoy exploring new ideas.

1 2 3 4

2. Difficult conceptual problems can keep me awake all night thinking about solutions.

1 2 3 4

3. I enjoy learning about subjects that are unfamiliar to me.

1 2 3 4

4. I can spend hours on a single problem because I just can't rest without knowing the answer.

1 2 3 4

5. I find it fascinating to learn new information.

1 2 3 4

6. I feel frustrated if I can't figure out solution to a problem, so I work harder to solve it.

1 2 3 4

7. When I learn something new, I would like to find out more about it.

1 2 3 4

8. I brood for a long time in an attempt to solve some fundamental problem.

1 2 3 4

9. I enjoy discussing abstract concepts.

1 2 3 4

10. I work like a fiend at problems that I feel must be solved.

1 2 3 4

Appendix 2

Perceptual Curiosity Scale (Collins, Litman, & Spielberger, 2004)

Several statements that people use to describe themselves are given below. Read each statement and indicate how you generally feel using the scale below. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer that seems to describe how you *generally* feel.

For the statements below rate yourself on the following 4-point scale:

1 = Almost Never 2 = Sometimes 3 = Often 4 = Almost Always

1.	*I like exploring my surroundings.*			
	1	2	3	4
2.	*When I smell something new, I try and find out what the odour is coming from.*			
	1	2	3	4
3.	*I like to discover new places to go.*			
	1	2	3	4
4.	*If I hear something rustling in the grass I have to see what it is.*			
	1	2	3	4
5.	*I like visiting art galleries and art museums.*			
	1	2	3	4
6.	*When I see a new fabric, I like to touch and feel it.*			
	1	2	3	4
7.	*I like to listen to new and unusual kinds of music.*			
	1	2	3	4
8.	*When I hear a musical instrument and I am not sure what it is, I like to see it.*			
	1	2	3	4
9.	*I enjoy trying different kinds of ethnic foods.*			
	1	2	3	4
10.	*When I hear a strange sound, I usually try to find out what caused it.*			
	1	2	3	4
11.	*I enjoy travelling to places that I have never been to*			
	1	2	3	4
12.	*When I see a vocal group, I pick out the different voice types*			
	1	2	3	4

Appendix 3

5-Dimensional Curiosity scale

(Kashdan, Stiksma, Disabato, McKnight, Bekier, Kaji & Lazarus, 2018)

Below are a number of statements that describe ways in which people act and think. For each of the statements below, circle the number (from 1-7) that best describes yourself.

1 = *Does not describe me at all*
2 = *Does not describe me*
3 = Somewhat does not describe me
4 = Neutral
5 = Somewhat describes me
6 = Describes me
7 = Completely describes me

1. *I view challenging situations as an opportunity to grow and learn.*
2. *I am always looking for experiences that challenge how I think about myself and the world.*
3. *I seek out situations where it is likely that I will have to think in depth about something.*
4. *I enjoy learning about subjects that are unfamiliar to me.*
5. *I find it fascinating to learn new information.*
6. *I like to try to solve problems that puzzle me.*
7. *Thinking about solutions to difficult conceptual problems can keep me awake at night.*
8. *I can spend hours on a single problem because I just can't rest without knowing the answer.*
9. *I feel frustrated if I can't figure out the solution to a problem, so I work even harder to solve it.*
10. *I work relentlessly at problems that I feel must be solved.*
11. *The smallest doubt can stop me from seeking out new experiences.*
12. *I cannot handle the stress that comes from entering uncertain situations.*
13. *I find it hard to explore new places when I lack confidence in my abilities.*
14. *I cannot function well if I am unsure whether a new experience is safe.*
15. *It is difficult to concentrate when there is a possibility that I will be taken by surprise*
16. *I like to learn about the habits of others.*
17. *I like finding out why people behave the way they do.*
18. *When other people are having a conversation, I like to find out what it's about.*
19. *When around other people, I like listening to their conversations.*
20. *When people quarrel, I like to know what's going on.*
21. *The anxiety of doing something new makes me feel excited and alive.*
22. *Risk-taking is exciting to me.*
23. *I would like to explore a strange city or section of town, even if it means getting lost.*
24. *When I have free time, I want to do things that are a little scary.*
25. *Creating an adventure as I go is much more appealing than a planned adventure.*

Appendix 4

4A: One-tailed Pearson correlations (uncorrected) conducted between curiosity trait measures and fornix white matter microstructure in the entire sample (male and female participants) of Chapter 2, Experiment 2 and only female participants of Chapter 2, Experiment 2.

Correlation between trait curiosity and fornix microstructure	Male and female participants (n = 47)	Female participants only (n = 40)
Interest EC		
Fornix FA	r = 0.118, p = 0.215	r = 0.186, p = 0.125
Posterior hippocampal fornix FA	r = 0.061, p = 0.341	r = 0.090, p = 0.291
Left lateral hippocampal fornix FA	r = 0.155, p = 0.149	r = 0.157, p = 0.166
Right lateral hippocampal fornix FA	r = 0.168, p = 0.129	r = 0.295, p = 0.032
Interest EC		
Fornix MD	r = -0.114, p = 0.223	r = -0.219, p = 0.087
Posterior hippocampal fornix MD	r = -0.043, p = 0.388	r = -0.143, p = 0.190
Left lateral hippocampal fornix MD	r = -0.148, p = 0.160	r = -0.227, p = 0.080
Right lateral hippocampal fornix MD	r = -0.044, p = 0.385	r = -0.173, p = 0.143
Specific PC		
Fornix FA	r = 0.030, p = 0.421	r = 0.162, p = 0.159
Posterior hippocampal fornix FA	r = 0.065, p = 0.332	r = 0.180, p = 0.133
Left lateral hippocampal fornix FA	r = 0.025, p = 0.433	r = 0.071, p = 0.331
Right lateral hippocampal fornix FA	r = -0.035, p = 0.406	r = 0.115, p = 0.239

EC, *Epistemic Curiosity*; PC, *Perceptual Curiosity*; FA, *fractional anisotropy*; MD, *mean diffusivity.*

4B: It is possible that trait measures of curiosity administered after a behavioural task, especially one that elicits different levels of curiosity (Chapter 2, Experiment 2), could result in dissimilar self-reports to when administering curiosity trait measures prior to behavioural tasks such as in Chapter 2, Experiment 1. Independent t-tests were employed to test for differences in the curiosity trait scores obtained in these two experiments.

The hypothesis that Interest EC scores would differ significantly between participants in Experiment 1 and participants in Experiment 2 was examined using an independent samples t-test. Descriptive statistics showed that Interest EC scores in Experiment 1 (mean 15.18; standard deviation 2.40) was greater than Interest EC scores in Experiment 2 (mean 13.96; standard deviation 2.64). This difference was shown to be statistically significant, $t_{(104)} = 2.47$, $p = 0.015$, 95% CI [0.24, 2.19]. The difference demonstrated a medium effect size, $d = 0.48$.

The hypothesis that Deprivation EC scores would differ significantly between participants in Experiment 1 and participants in Experiment 2 was examined using an independent samples t-test. Descriptive statistics showed that Deprivation EC scores in Experiment 1 (mean 11.92; standard deviation 3.51) was greater than Deprivation EC scores in Experiment 2 (mean 10.24; standard deviation 2.76). This difference was shown to be statistically significant, $t_{(104)} = 2.76$, $p = 0.007$, 95% CI [0.47, 2.90]. The difference demonstrated a medium effect size, $d = 0.54$.

The hypothesis that Diversive PC scores would differ significantly between participants in Experiment 1 and participants in Experiment 2 was examined using an independent samples t-test. Descriptive statistics showed that Diversive PC scores in Experiment 1 (mean 18.90; standard deviation 3.16) was greater than Diversive PC scores in Experiment 2 (mean 18.09; standard deviation 3.37). This difference was not shown to be statistically significant, $t_{(104)} = 1.28$, $p = 0.205$, 95% CI [-0.45, 2.07]. The difference demonstrated a small effect size, $d = 0.25$.

The hypothesis that Specific PC scores would differ significantly between participants in Experiment 1 and participants in Experiment 2 was examined using an independent samples t-test. Descriptive statistics showed that Specific PC scores in Experiment 1 (mean 15.86; standard deviation 3.50) was greater than Specific PC scores in Experiment 2 (mean 14.44; standard deviation 3.71). This difference was shown to be statistically significant, $t_{(104)} = 2.03$, $p = 0.045$, 95% CI [0.03, 2.82]. The difference demonstrated a small effect size, $d = 0.39$.

Appendix 5

Trivia questions

1.	"What is the first country that used postcards?"	"Austria"
2.	"Who was the first Twitter user to reach 20 million followers?"	"Lady Gaga"
3.	"Which animal has the largest eye in the world?"	"Giant squid"
4.	"On average how many babies have been born from people who met on Match.com?"	"Over One million"
5.	"What sport was first filmed in 1894?"	"Boxing"
6.	"Where is the windiest place on Earth?"	"Port Martyin, Antarctica"
7.	"How old was the world's youngest pope?"	"11 years old"
8.	"If you had pogonophobia what would you be afraid of?"	"Beards"
9.	"In which part of a shrimp's body can you find its heart?"	"Head"
10.	"On average how long does a person wait at the traffic lights in their lifetime?"	"2 weeks"
11.	"Who was the last English king to be killed in battle?"	"Richard III"
12.	"What is the world's fastest car?"	"Hennessey Venom GT"
13.	"What is the longest word with one vowel?"	"Strengths"
14.	"What are the longest cells in the body?"	"Motor neurons"
15.	"Which is the most abundant element in the universe?"	"Hydrogen"
16.	"By number of films made which country has the largest film industry?"	"India"
17.	"The human brain is 80% what?"	"Water"
18.	"What is the busiest single-runway airport in the world?"	"London Gatwick"
19.	"What is the oldest university in Britain?"	"Oxford University"
20.	"What football club is the oldest in London?"	"Fulham"
21.	"Which animal has a brain smaller than its eye?"	"Ostrich"
22.	"Which British prime minister was awarded the Nobel Prize of Literature?"	"Churchill"
23.	"What was the first planet to be discovered using a telescope, in 1781?"	"Uranus"
24.	"The Empire State Building is composed of how many bricks?"	"10 million"
25.	"Where is the hottest place on Earth?"	"Dallol, Ethiopia"
26.	"What is the most dangerous chemical?"	"Digoxin"
27.	"On average how much time do women take to put makeup on in their life time?"	"Over one year"
28.	"In what city was chewing gum invented?"	"New York"
29.	"What sauce was once sold as medicine?"	"Ketchup"

30. "How many hours worth of videos are uploaded on YouTube every minute?"	"100 hours"
31. "What is the main symptom for the virus Ebola?"	"Vomiting"
32. "How many primary school pupils worldwide dropped out of school in 2012?"	"31 million"
33. "Where would you find the Sea of Tranquillity?"	"Moon"
34. "What is the life span of a dragon fly?"	"24 hours"
35. "Granadilla is another name for which fruit?"	"Passion fruit"
36. "What type of creature is a dugite?"	"Snake"
37. "In which country is it illegal to produce and distribute adult movies?"	"North Korea"
38. "Which body part stays the same size since birth?"	"Eyes"
39. "How much time does a person spend in the toilet in their lifetime?"	"3 years"
40. "To prevent damage, what did soldiers during World War II use to cover their rifles?"	"Condoms"
41. "Which animal doesn't grow old and die?"	"Lobster"
42. "What made Hugh Hefner go deaf?"	"Viagra"
43. "Which colour can the human eye distinguish the most shades of?"	"Green"
44. "What is the fear of being buried alive known as?"	"Taphephobia"
45. "A team of scientists found a way to turn peanut butter into what?"	"Diamonds"
46. "Which mammal holds the records of having the quickest sexual intercourse?"	"Chimpanzee"
47. "If you lived on the planet Mercury, how long would a year last?"	"88 days"
48. "If a human eats a polar bear's liver, what would happen?"	"Death"
49. "What was the game bingo originally called?"	"Beano"
50. "Falling in love has a similar neurological effect to what drug?"	"Cocaine"
51. "What are the smallest types of bird?"	"Hummingbird"
52. “Which body parts never stop growing?"	"Ears and nose"
53. "On average how long do we sleep in our life time?"	"26 years"
54. "What is the strongest bone in a human body?"	"Femur (thighbone)"
55. "What was the bloodiest war in U.S. history?"	"Civil War"
56. "What fruit is efficient in waking you up in the morning?"	"Apple"
57. "Where would you find the smallest bone in a human body?"	"Ear"
58. "What is four times hotter than the sun?"	"A lightning bolt"
59. "What was ketchup used to treat in the 1800s?"	"Diarrhoea"

60. "How does Ebola spread?"	"Through body fluids"
61. "In the human body what is the hallux?"	"Big toe"
62. "What is the best selling music album of all time?"	"Thriller"
63. "Which country has a national anthem that consists of only 32 syllables?"	"Japan"
64. "Which planet in the solar system is the only one that rotates clockwise?"	"Venus"
65. "Which product, after oil, is the most frequently traded product around the world?"	"Coffee"
66. "Which country has the world's only non-quadrilateral national flag?"	"Nepal"
67. "What is the country with the highest population density?"	"Monaco"
68. "Which fish can produce more eggs than any other known vertebrate?"	"Sunfish"
69. "What disability did Thomas Edison suffer from?"	"Deafness"
70. "What breed of dog is the only animal whose evidence is admissible in some USA courts?	"Bloodhound"
71. "What Beatles song remained the longest on the music charts?"	"Hey Jude"
72. "What is the only lizard that has a voice?"	"Gecko"
73. "Which chemical element belongs in the Halogen Family with fluorine, chlorine, bromine and astatine?"	"Iodine"
74. "What island country lies off the south-east coast of India?"	"Sri Lanka"
75. "What is the longest river in Asia?"	"Yangtze"
76. "What is the monetary unit in Korea?"	"Won"
77. "What is the name of the artist who painted the 'Tahitian Women on the Beach'?"	"Paul Gauguin"
78. "What is Spain's national flower?"	"Carnation"
79. "In which country is Angel Falls, the tallest waterfall, located?"	"Venezuela"
80. "What is the largest temple in Egypt?"	"Karnak"
81. "In which country is the temple of 'Angkor Wat' located?"	"Cambodia"
82. "What is the abbreviated name of the political and economic integration in Southeast Asia?"	"ASEAN"
83. "What is the largest freshwater lake in the world by surface area?"	"Lake Superior"
84. "which popular Greek philosopher is said to have tutored Alexander the Great?"	"Aristotle"
What colour are cranberries before they turn red?"	"White"
85. "Which company is the largest manufacturer of tires?"	"Lego"

86.	"In which country is the city Marrakech located?"	"Morocco"
87.	"Which Australian state was formerly known as Van Diemen's Land?"	"Tasmania"
88.	"What insulates the ice cream to prevent it from melting in the hot dish 'Baked Alaska'?"	"Meringue"
89.	"What body of water does the Danube River flow into?"	"Black Sea"
90.	"Which Disney cartoon character's love interest is named Faline?"	"Bambi"
91.	"What was the original Dutch name of New York City?"	"New Amsterdam"
92.	"What purpose did the Coliseum serve when first built?"	"Amphitheatre"
93.	"What is the largest bear on Earth?"	"Polar Bear"
94.	"What is added to white sugar to make brown sugar?"	"Molasses"
95.	"What fiber-producing plant is attacked by the boll weevil?"	"Cotton"
96.	"What is the name of Beethoven's only opera?"	"Fidelio"
97.	"What is the largest known animal to have ever existed?"	"Blue Whale"
98.	"In which city would you find the Hermitage art gallery?"	"Saint Petersburg"
99.	"Which country has the longest coastline?"	"Canada"
100.	"What is the last name of the cosmonaut who first orbited around the Earth?"	"Gagarin"
101.	"What is the name of the smallest state surrounded by Italy other than Vatican City?"	"San Marino"
102.	"What Spanish city is the capital of Catalonia?"	"Barcelona"
103.	"What does an ichthyologist study?"	"Fish"
104.	"What is the name of the company that produces 'Baby Ruth' candy bars?"	"Nestle"
105.	"In which European city is the Pantheon located?"	"Athens"
106.	"What is the last name of the man who first studied genetic inheritance in plants?"	"Mendel"
107.	"What was the name of the zeppelin that exploded in Lakehurst N.J. in 1937?"	"Hindenburg"
108.	"What is the name of the palace built in France by King Louis XIV?"	"Versailles"
109.	In what ancient city were the 'Hanging Gardens' located?"	"Babylon"
110.	"What is the capital city of Australia?"	"Canberra"
111.	"What is the name of the ship on which Charles Darwin made his scientific voyage?"	"HMS Beagle"
112.	"What is the name of the fountain in Rome into which coins are thrown in for good luck?"	"Trevi"
113.	"In which city is Michelangelo's statue of David located?"	"Florence"

114.	"Of which country is Nairobi the capital?"	"Kenya"
115.	"What is the last name of the first person to complete a solo flight across the Atlantic Ocean?"	"Lindbergh"
116.	"What is the name of the Roman emperor who played the fiddle while Rome burned?"	"Nero"
117.	"What is the last name of the scientist who discovered radium?"	"Curie"
118.	"What was the last piece of music Mozart composed?"	"Requiem
119.	"What is the last name of the author of the James Bond novels?"	"Fleming"
120.	"What was the name of the Apollo lunar module that landed the first man on the moon?"	"Eagle"
121.	"What was the name of the goldfish in the story of Pinocchio?"	"Cleo"
122.	"What is the name of the submarine in Jules Verne's '20,000 Leagues Beneath the Sea'?"	"Nautilus"
123.	"What is the last name of the European author who wrote 'The Trial'?"	"Kafka"
124.	"What is the last name of the poet who originally wrote 'Don Juan'?"	"Byron"
125.	"Who was the first ruler of the Holy Roman Empire?"	"Charlemagne"
126.	"What is the name of the brightest star in the sky, excluding the sun?"	"Sirius"
127.	"What is the name of Germany's largest battleship that was sunk in World War II?"	"Bismarck"
128.	"What is the name of the mountain range that separates Asia from Europe?"	"Ural"
129.	"What is the name of the instrument used to measure wind speed?"	"Anemometer"
130.	"Which planet in our solar system was the last to be discovered?"	"Neptune"
131.	"Which sport uses the terms 'stones' and 'brooms'?"	"Curling"
132.	"What is the name of the unit of measure that refers to a six-foot depth of water?"	"Fathom"
133.	"Who is known as 'the father of geometry'?"	"Euclid"
134.	"What flavor is the extract of fermented and dried pods of several species of orchids?"	"Vanilla"
135.	"Which is the only continent without a desert?"	"Europe"
136.	"Where is the largest Volcano on Earth located?"	"Hawaii"

137.	"What animal's milk does not curdle?"	"Camel"
138.	"What wild animal in Africa has killed the most people?"	"Hippo"
139.	"What is the only domestic animal not mentioned in the Bible?"	"Cat"
140.	"What spice is extremely poisonous if injected intravenously?"	"Nutmeg"
141.	"Who was the first winner of the Fifa World Cup?"	"Uruguay"
142.	"What animal can eat only when its head is upside down?"	"Flamingo"
143.	"Which bird is the international symbol of happiness?"	"Bluebird"
144.	"Which is the largest joint in the body?"	"Knee"
145.	"What was once called brimstone?"	"Sulfur"
146.	"Ankara is the capital city of which country?"	"Turkey"
147.	"In which country are the ruins of the City of Carthage situated?"	"Tunisia"
148.	"What is the only food that never spoils?"	"Honey"
149.	"In food, E330 is better known by what name?"	"Citric acid"
150.	"What did Joseph Priestley discover in 1774?"	"Oxygen"
151.	"Who is the Greek God of music?"	"Apollo"
152.	"What is the name of the largest island in the world?"	"Greenland"
153.	"Which fruit was previously known as a Chinese gooseberry?"	"Kiwi"
154.	"What is the correct term for a female elephant?"	"Cow"
155.	"What colour is octopus' blood?"	"Blue"
156.	"What is a baby oyster called?"	"Spat"
157.	"In which city was the Titanic built?"	"Belfast"
158.	"What is the most common blood type in humans?"	"O positive"
159.	"What was the first internal human organ to be successfully transplanted?"	"Kidney"
160.	"Which poisonous snake secretes an odor like cucumbers?"	"Copperhead Snake"
161.	"What does the Scoville scale of food measure?"	"Spicy Heat"
162.	"Which land mammal has the highest blood pressure?"	"Giraffe"
163.	"What was the first nation to give women the right to	
164.	vote?"	"New Zealand"
165.	"What is the name of the biggest constellation in the sky?"	"Hydra"
166.	"What is the longest common English noun without any vowels?"	"Rhythm"
167.	"What musical note do most American car horns beep in?"	"F"
168.	"Who was the first Christian emperor of Rome?"	"Constantine"

169.	"The Gold Coast is now known as what country?"	"Ghana"
170.	"What is the only country in the world that has a bible on its flag?"	"Dominican Republic"
171.	"What trade was Greek philosopher Socrates trained for?"	"Stonecutting"
172.	"What reptile, according to ancient legend, was able to live in fire?"	"Salamander"
173.	"What unit of measurement is used for fuel wood?"	"Cord"
174.	"What did the D in DC comics originally stand for?"	"Detective"
175.	"What is the most abundant gas in the atmosphere?"	"Nitrogen"
176.	"Which city is the most expensive city in the world to live in?"	"London"
177.	"Which country is the world's biggest producer of olive oil?"	"Spain"
178.	"Which animal has the shortest lifespan?"	"Mayfly"
179.	"What is the only fish that can blink with both eyes?"	"Shark"
180.	"What is the more common name of the plant Hedera?"	"Ivy"
181.	"What is the last letter of the Greek alphabet?"	"Omega"
182.	"What is the only internal human organ capable of natural regeneration of lost tissue?"	"Liver"
183.	"Which city is the only one in the world to be situated in two continents?"	"Istanbul"
184.	"Disney's Lion King movie/musical is generally said to be based on what Shakespeare play?"	"Hamlet"
185.	"Where in the world is the world's largest building (the Burj Khalifa) located?"	"Dubai"
186.	"The hot condiment wasabi is generally from what part of the plant?"	"Root"
187.	"What language has the largest vocabulary?"	"English"
188.	"What colour flag was historically first displayed to indicate sickness aboard a ship?"	"Yellow"
189.	"Which famous religious leader is depicted in the largest statue in the world?"	"Buddha"
190.	"Until 2008, what country was the only one to display a map of their country on their flag?"	"Cyprus"
191.	"What is an ice hockey puck made from?"	"Rubber"
192.	"Which animal tastes with its feet?"	"Butterfly"
193.	"What colour is vermilion a shade of?"	"Red"
194.	“Broccoli belongs to what family of plants?"	"Cabbage"
195.	"What is the National Bird of India?"	"Peacock"
196.	"What was the first country to leave the United Nations?"	"Indonesia"

197.	"Which animal sleeps with one eye open?"	"Dolphin"
198.	"73% of what country is covered by forest?"	"Finland"
199.	"Scooby Doo is based on what breed of dog?"	"Great Dane"
200.	"What is measured with an ombrometer?"	"Rainfall"
201.	"The linden tree is more commonly known as what?"	"Lime Tree"
202.	"Viticulture is the growing of what plant?"	"Grapes"
203.	"What food did the Aztecs reckon was the food of the Gods?"	"Chocolate"
204.	"What bird has the most feathers per square inch?"	"Penguin"
205.	"In which ocean are the Canary Islands located?"	"Atlantic"
206.	"Which city was the first in the world to have a public bus service?"	"Paris"
207.	"What is the world's fifth largest religion?"	"Sikhism"
208.	"At the end of what period did dinosaurs become extinct on Earth?"	"Cretaceous"
209.	"What nationality was Picasso?"	"Spanish"
210.	"What is the highest range of the male singing voice?"	"Countertenor"
211.	"What type of acid is used in car batteries?"	"Sulfuric"
212.	"What is the colour of mourning in Turkey?"	"Violet"
213.	"Which islands wildlife is 90% unique?"	"Madagascar"
214.	"Where in the body would you find the pisiform bone?"	"Wrist"
215.	"What colour are Amazon river dolphins?"	"Pink"
216.	"What dog breed has the best eyesight?"	"Greyhound"
217.	"Barajas is the main airport in what city?"	"Madrid"
218.	"What Polish political movement got the support of Pope John Paul II in the 1980's?"	"Solidarity"
219.	"What was the surname of the first democratically elected president of Russia?"	"Yeltsin"
220.	"The forint is the monetary unit of what central European country?"	"Hungary"
221.	"In what century was Leonardo da Vinci born?"	"15th"
222.	"What is the name of the composer who wrote Don Giovanni?"	"Mozart"
223.	"Along with chitin, what strengthens the exoskeleton of bugs?"	"Calcium"
224.	"What do birds rely on to swallow?"	"Gravity"
225.	"What animal is the 'Turdus migratorius' better known as?"	"American Robin"
226.	"What radioactive element is extracted from carnotite and pitchblende?"	"Uranium"

227.	"Who was the first physician to record case histories of patients?"	"Hippocrates"
228.	"Copper and what else are the two main constituents of bronze?"	"Tin"
229.	"What body part is low-density lipoprotein most likely to clog?"	"Arteries"
230.	"What are you shopping for if you're sized up by a Brannock Device?"	"Shoes"
231.	"What chemical compound comes from the Greek word for 'primary'?"	"Protein"
232.	"Hydrogen and what are thought to be the primary elements of which Jupiter is composed?"	"Helium"
233.	"What was the name of the first probe to send back pictures from Mars?"	"Viking"
234.	"Yapping Deng was a world champion in which sport?"	"Table Tennis"
235.	"Coconut and what other fruit were Hawaiian women once forbidden by law to eat?"	"Banana"
236.	"From what vegetable were jack-o-lanterns originally carved?"	"Turnips"
237.	"What was the first war in which one jet plane shot down another?"	"Korean War"
238.	"What nation started giving gas masks to its citizens before the Persian Gulf War?"	"Israel"
239.	"What was the surname of the first president to appear on a U.S coin?"	"Lincoln"
240.	"What food is the leading source of salmonella poisoning?"	"Chicken"
241.	"What is the second largest island in Europe?"	"Iceland"
242.	"What was the poison used at Socrates' execution?"	"Hemlock"
243.	"Who was first to publish the theory that the Earth revolves around the sun?"	"Copernicus"
244.	"What studio did the Beatles use to record 191 songs?"	"Abbey Road"
245.	"What is the longest venomous snake?"	"King Cobra"
246.	"What common insect depends the most on sight, rather than sound, to locate mates?"	"Firefly"
247.	"What taste are cats unable to detect?"	"Sweet"
248.	"Christopher Columbus introduced what animal to North America?"	"Pig"
249.	"What was the first bird domesticated by man?"	"Goose"
250.	"The title of what animal literally means 'Terrible lizard'?"	"Dinosaur"

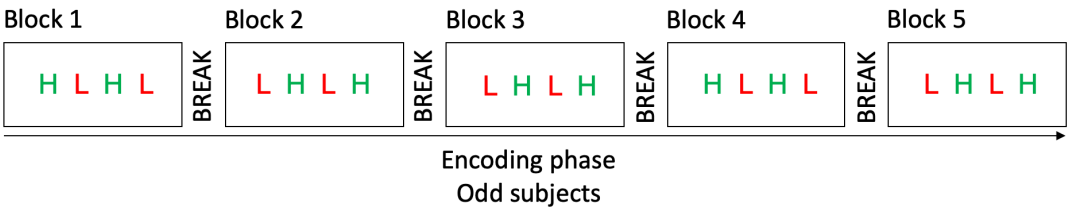
251.	"In what century did mathematicians first use plus and minus signs?"	"16th"
252.	"What unit of measure was once defined as the length of 3 grains of barley laid end to end?"	"Inch"
253.	"The element Manganese gives what crystal its famous violet colour?"	"Amethyst"
254.	"What were thermometers filled with in the 17th century, before mercury?"	"Alcohol"
255.	"What is the only living part of the human body that has no blood supply?"	"Cornea"
256.	"What illegal hallucinogen naturally occurs in many plants and mammals including humans?"	"DMT"
257.	"What was the name of the first chimpanzee sent into space by America?"	"Ham"
258.	"Which planet has a hexagon shaped cloud formation on its north pole?"	"Saturn"
259.	"Neptune gets its blue colour from what gas?"	"Methane"
260.	"What is the only country to have won at least one gold in every Olympic Games?"	"Great Britain"
261.	"What kind of fruit basket was used for the first game of basketball?"	"Peach"
262.	"What is the proper name of a badminton bird?"	"Shuttlecock"
263.	"South America first saw the cultivation of what vegetable in 200 A.D.?"	"Potato"
264.	"Which animal's milk is used to make authentic Italian mozzarella cheese?"	"Water Buffalo"
265.	"What added ingredient keeps confectioners' sugar from clumping?"	"Cornstarch"
266.	"What flavor is the liqueur Cointreau?"	"Orange"
267.	"What type of fruit would you pick from a Mirabelle tree?"	"Plum"
268.	"Which drink gets its name from a town on the Red Sea coast of Yemen?"	"Mocha"
269.	"What food product did Hippolyte Mege-Mouries invent by treating oils with hydrogen?"	"Margarine"
270.	"On what vegetable did an ancient Egyptian place his right hand when taking an oath?"	"Onion"
271.	"What is the only country with a national dog?"	"Netherlands"
272.	"What is the side of a hammer called?"	"Cheek"
273.	"What is the term for rainforests higher than 3000 feet	

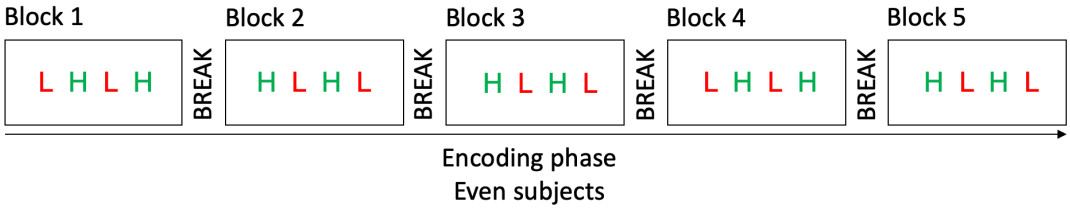
	above sea level?"	"Cloud forests"
274.	"What is the only breed of dog that can get gout?"	"Dalmatian"
275.	"What is the world's smallest mammal?"	"Bumblebee Bat"
276.	"What is the only cat in the world that cannot retract its claws completely?"	"Cheetah"
277.	"What was the world's first National Park?"	"Yellowstone"
278.	"What is the only mammal native to Iceland?"	"Arctic Fox"
279.	"What type of spider wasp eats tarantulas?"	"Tarantula hawk"
280.	"What is a group of goats called?"	"Trip"
281.	"What is the only rock that floats in water?"	"Pumice"
282.	"What gland makes hormones that trigger puberty?"	"Pituitary"
283.	"What part of a cola tree is used to flavour beverages?"	"Nuts"
284.	"Which member of the ginger family is used to colour curries?"	"Turmeric"
285.	"Ingesting large amounts of what type of unripe berry can cause moderate hallucinations?"	"Mulberry"
286.	"What type of animal was the Snickers candy bar named after?"	"Horse"
287.	"What type of bean must be cooked thoroughly for all the cyanide to be extracted?"	"Lima bean"
288.	"The liquid found in what fruit can be used as a substitute for blood plasma in emergencies?"	"Coconut"
289.	"What American State has the highest percentage of people who walk to work?"	"Alaska"
290.	"What is the surname of the former Soviet Russian leader who endorsed Louis Vuitton and Pizza Hut?"	"Gorbachev"
291.	"What animal's antlers are the fastest growing animal cells in nature?"	"Moose"
292.	"What water-dwelling creature can make a sound loud enough to break glass?"	"Pistol Shrimp"
293.	"What is the only animal that can turn its stomach inside out?"	"Starfish"
294.	"What is the fastest healing body part on a human?"	"Tongue"

Appendix 6

Chapter 4, Experiment 1: trial order

6A: 100 trials (50 high and 50 low curiosity trials) were presented during the encoding phase of Experiment 1. Participants were presented with 5 blocks of 20 trials, where each block consisted of 2 sets of 5 consecutive high curiosity trials and 2 sets of 5 consecutive low curiosity trials. The order that these sets were presented were counterbalanced for subjects. After each block of 20 trials participants were encouraged to take a break before starting the next block of trials.

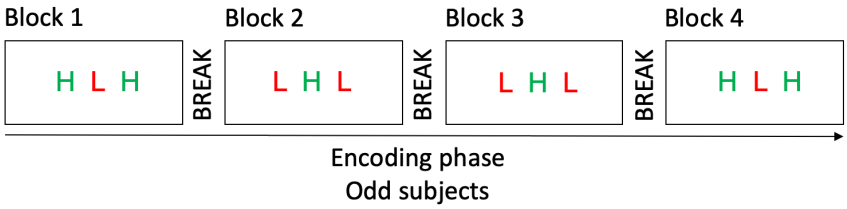


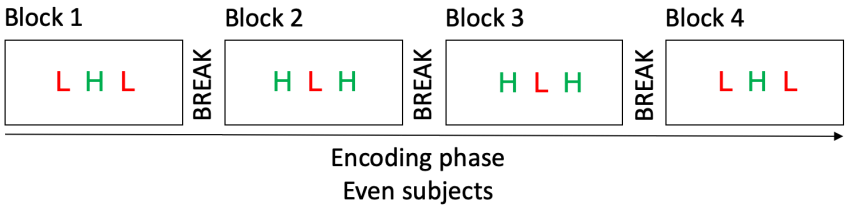


Note: Each letter displayed in the boxes above represent 5 consecutive trials of high curiosity trials (H) or low curiosity trials (L).

Chapter 4, Experiment 2: trial order

6B: 60 trials (30 high and 30 low curiosity trials) were presented during the encoding phase of Experiment 2. Participants were presented with 4 blocks of 15 trials, where each block consisted of 3 sets of 5 consecutive trials that consisted of either 2 sets of high curiosity trials (and one set of low curiosity trials) or 2 sets of low curiosity trials (and one set of high curiosity trials). The order that these sets were presented were counterbalanced for subjects. After each block of 15 trials participants were encouraged to take a break before starting the next block of trials.

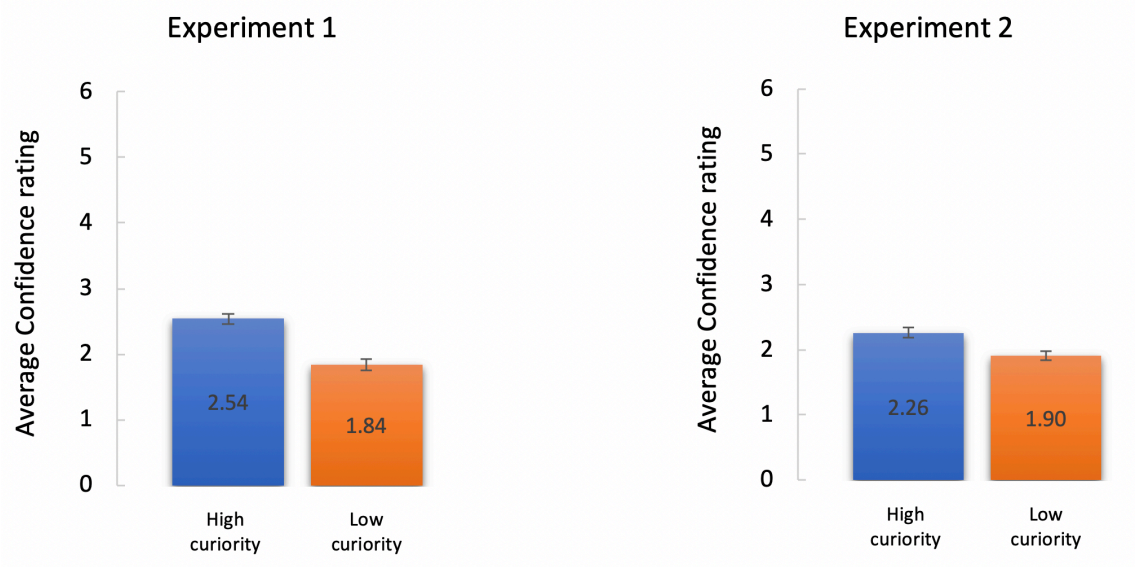




Note: Each letter displayed in the boxes above represent 5 consecutive trials of high curiosity trials (H) or low curiosity trials (L).

Chapter 4, Experiment 1 and Experiment 2: Confidence ratings

6C: Average confidence rating for high curiosity trials was significantly greater than the average confidence rating for low curiosity trials.



Experiment 1:

High curiosity: 2.54, SE = ± 0.08; Low curiosity: 1.84, SE = ± 0.09; $t(_{33}) = 10.56$, $p < 0.001$

Experiment 2:

High curiosity: 2.26, SE = ± 0.08; Low curiosity: 1.90, SE = ± 0.07; $t(_{51}) = 4.79$, $p < 0.001$

Appendix 7

Chapter 2, Experiment 1; Chapter 3, Experiment 1: Cronbach's alpha

The mean (SD) total score across participants (N=51) and Cronbach's alpha (α) coefficients for each curiosity self-report measure.

Self-report measure	Mean (SD)	**α**
Epistemic Curiosity (EC) subscales		
Interest EC	15.18 (2.40)	0.73
Deprivation EC	11.92 (3.52)	0.88
Perceptual Curiosity (PC) subscales		
Diversive PC	18.90 (3.16)	0.70
Specific PC	15.86 (3.50)	0.77

α, *Cronbach's alpha coefficient*; EC, *Epistemic Curiosity*; PC, *Perceptual Curiosity*.

Appendix 8

Chapter 2, Experiment 2; Chapter 3, Experiment 2: Cronbach's alpha

The mean (SD) total score across participants (N=55) and Cronbach's alpha (α) coefficients for each curiosity self-report measure.

Self-report measure	Mean (SD)	**α**
Epistemic Curiosity (EC) subscales		
Interest EC	13.96 (2.64)	0.80
Deprivation EC	10.24 (2.76)	0.82
Perceptual Curiosity (PC) subscales		
Diversive PC	18.09 (3.37)	0.73
Specific PC	14.44 (3.71)	0.75
5-Dimensional Curiosity subscales		
Joyous Exploration	25.00 (4.60)	0.78
Deprivation Sensitivity	21.44 (5.61)	0.83
Stress Tolerance	22.25 (6.52)	0.89
Social Curiosity	27.29 (4.81)	0.81
Thrill Seeking	22.62 (5.71)	0.82

α, *Cronbach's alpha coefficient*; EC, *Epistemic Curiosity*; PC, *Perceptual Curiosity*.

Appendix 9

Chapter 2, Experiment 2: Separate non-parametric permutation tests (one-tailed) correcting for multiple comparisons across the three individual fornix FA segmentations when correlated with each subset of curiosity

Permutation tests	Hippocampal fornix FA		
	Left anterior	Right anterior	Posterior
Interest EC			
Pearson's *r*(45)	0.155	0.168	0.061
p_{corr}	0.309	0.276	0.594
CI [LL, UL]	[-0.11, 0.43]	[-0.19, 0.47]	[-0.24, 0.39]
Deprivation EC			
Pearson's *r*(45)	-0.063	0.029	-0.022
p_{corr}	0.870	0.673	0.792
CI [LL, UL]	[-0.31, 0.26]	[-0.21, 0.28]	[-0.32, 0.29]
Diversive PC			
Pearson's *r*(45)	-0.091	-0.150	0.049
p_{corr}	0.910	0.963	0.606
CI [LL, UL]	[-0.36, 0.26]	[-0.43, 0.14]	[-0.25, 0.38]
Specific PC			
Pearson's *r*(45)	0.025	-0.036	0.065
p_{corr}	0.684	0.834	0.570
CI [LL, UL]	[-0.23, 0.28]	[-0.30, 0.23]	[-0.22, 0.32]

EC, *Epistemic Curiosity*; PC, *Perceptual Curiosity*; FA, *fractional anisotropy;* CI, *confidence interval*; LL, *lower level*; UL, *upper level; DTI-behaviour correlations are based on 47 participants.*

Appendix 10

Chapter 2, Experiment 2: Separate non-parametric permutation tests (one-tailed) correcting for multiple comparisons across the three individual fornix MD segmentations when correlated with each subset of curiosity

Permutation tests	Hippocampal fornix MD		
	Left anterior	Right anterior	Posterior
Interest EC			
Pearson's *r*(45)	-0.148	-0.044	-0.043
p_{corr}	0.254	0.540	0.542
CI [LL, UL]	[-0.43, 0.17]	[-0.36, 0.28]	[-0.36, 0.28]
Deprivation EC			
Pearson's *r*(45)	0.023	-0.118	0.054
p_{corr}	0.722	0.350	0.790
CI [LL, UL]	[-0.27, 0.31]	[-0.37, 0.14]	[-0.23, 0.33]
Diversive PC			
Pearson's *r*(45)	-0.066	0.003	0.025
p_{corr}	0.485	0.664	0.715
CI [LL, UL]	[-0.38, 0.32]	[-0.35, 0.35]	[-0.30, 0.40]
Specific PC			
Pearson's *r*(45)	0.031	0.159	0.120
p_{corr}	0.745	0.942	0.897
CI [LL, UL]	[-0.28, 0.37]	[-0.16, 0.43]	[-0.19, 0.43]

EC, *Epistemic Curiosity*; PC, *Perceptual Curiosity*; MD, *mean diffusivity,* CI, *confidence interval*; LL, *lower level*; UL, *upper level; DTI-behaviour correlations are based on 47 participants.*

Appendix 11

Chapter 3, Experiment 1: Resting state functional connectivity (RSFC) results

Second level analysis (one sample t-test) across 49 subjects during rest. All source ROIs show high connectivity to respective target ROIs.

Source ROI	Connection to target ROI	L/R	Fisher-transformed correlation coefficient	T(48)
Left posterior HC				
	NAcc	L	0.12	9.27
		R	0.10	8.24
	VTA	L	0.09	6.22
		R	0.09	6.06
Right posterior HC				
	NAcc	L	0.10	8.76
		R	0.10	8.00
	VTA	L	0.10	6.80
		R	0.10	6.76
Left anterior HC				
	NAcc	L	0.11	7.85
		R	0.12	8.02
	VTA	L	0.13	8.28
		R	0.12	8.33
Right anterior HC				
	NAcc	L	0.15	10.41
		R	0.16	10.38
	VTA	L	0.16	8.74
		R	0.15	7.60
Left NAcc				
	VTA	L	0.10	6.19
		R	0.09	4.91
Right NAcc				
	VTA	L	0.11	6.82
		R	0.11	6.51

ROI-to-ROI functional connectivity reported at p-FDR<0.001, one sided, positive contrasts. All source ROIs had a high connectivity to respective target ROIs. VTA, *ventral tegmental area*; NAcc, *nucleus accumbens*; HC, *hippocampus*; L, *left*; R, *right*.

Appendix 12

Chapter 3, Experiment 1: Relationship between ROI-to-ROI functional connectivity coefficients and Interest EC, Deprivation EC, Diversive PC and Specific PC.

12A. RSFC-behaviour correlations are based on 49 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Interest EC.

ROI-to-ROI functional connectivity	Interest EC		
	r(47)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.079	0.963	[-0.16, 0.33]
L-pos. HC + R-NAcc	0.040	0.989	[-0.25, 0.31]
L-pos. HC + L-VTA	0.087	0.955	[-0.12, 0.27]
L-pos. HC + R-VTA	-0.029	0.999	[-0.27, 0.23]
R-pos. HC + L-NAcc	0.029	0.994	[-0.21, 0.32]
R-pos. HC + R-NAcc	0.121	0.902	[-0.13, 0.37]
R-pos. HC + L-VTA	0.147	0.839	[-0.11, 0.39]
R-pos. HC + R-VTA	-0.151	0.999	[-0.37, 0.08]
L-ant. HC + L-NAcc	0.221	0.561	[-0.07, 0.49]
L-ant. HC + R-NAcc	0.029	0.994	[-0.28, 0.33]
L-ant. HC + L-VTA	-0.111	0.999	[-0.38, 0.16]
L-ant. HC + R-VTA	-0.140	0.999	[-0.40, 0.17]
R-ant. HC + L-NAcc	0.028	0.994	[-0.29, 0.32]
R-ant. HC + R-NAcc	-0.092	0.999	[-0.36, 0.20]
R-ant. HC + L-VTA	0.093	0.949	[-0.13, 0.28]
R-ant. HC + R-VTA	0.113	0.917	[-0.13, 0.34]
L-NAcc + L-VTA	0.336	0.127	[0.10, 0.54]
L-NAcc + R-VTA	0.155	0.820	[-0.08, 0.37]
R-NAcc + L-VTA	0.052	0.983	[-0.21, 0.30]
R-NAcc + R-VTA	0.109	0.923	[-0.14, 0.35]

EC, *Epistemic Curiosity*; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

12B. RSFC-behaviour correlations are based on 49 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Deprivation EC.

ROI-to-ROI functional connectivity	Deprivation EC		
	r(47)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.083	0.956	[-0.18, 0.34]
L-pos. HC + R-NAcc	0.060	0.978	[-0.21, 0.32]
L-pos. HC + L-VTA	-0.042	0.999	[-0.33, 0.24]
L-pos. HC + R-VTA	0.021	0.991	[-0.32, 0.33]
R-pos. HC + L-NAcc	-0.052	0.999	[-0.34, 0.20]
R-pos. HC + R-NAcc	0.152	0.819	[-0.15, 0.43]
R-pos. HC + L-VTA	0.051	0.983	[-0.26, 0.32]
R-pos. HC + R-VTA	-0.132	0.999	[-0.40, 0.16]
L-ant. HC + L-NAcc	0.086	0.954	[-0.16, 0.35]
L-ant. HC + R-NAcc	-0.013	0.998	[-0.29, 0.27]
L-ant. HC + L-VTA	0.003	0.995	[-0.24, 0.25]
L-ant. HC + R-VTA	0.004	0.995	[-0.30, 0.32]
R-ant. HC + L-NAcc	0.075	0.966	[-0.17, 0.35]
R-ant. HC + R-NAcc	0.031	0.989	[-0.29, 0.35]
R-ant. HC + L-VTA	0.035	0.987	[-0.28, 0.32]
R-ant. HC + R-VTA	-0.047	0.999	[-0.32, 0.22]
L-NAcc + L-VTA	0.044	0.985	[-0.18, 0.30]
L-NAcc + R-VTA	0.006	0.995	[-0.27, 0.24]
R-NAcc + L-VTA	0.097	0.940	[-0.17, 0.33]
R-NAcc + R-VTA	0.072	0.970	[-0.24, 0.35]

EC, *Epistemic Curiosity*; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

12C. RSFC-behaviour correlations are based on 49 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Specific PC.

ROI-to-ROI functional connectivity	Specific PC		
	r(47)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.110	0.927	[-0.19, 0.44]
L-pos. HC + R-NAcc	0.139	0.863	[-0.17, 0.42]
L-pos. HC + L-VTA	-0.052	0.999	[-0.33, 0.22]
L-pos. HC + R-VTA	-0.038	0.999	[-0.30, 0.25]
R-pos. HC + L-NAcc	-0.169	0.999	[-0.43, 0.14]
R-pos. HC + R-NAcc	-0.014	0.999	[-0.28, 0.25]
R-pos. HC + L-VTA	0.008	0.997	[-0.29, 0.31]
R-pos. HC + R-VTA	-0.007	0.998	[-0.26, 0.25]
L-ant. HC + L-NAcc	0.230	0.526	[-0.02, 0.48]
L-ant. HC + R-NAcc	-0.051	0.999	[-0.32, 0.25]
L-ant. HC + L-VTA	0.034	0.991	[-0.29, 0.33]
L-ant. HC + R-VTA	0.078	0.967	[-0.19, 0.38]
R-ant. HC + L-NAcc	0.069	0.974	[-0.24, 0.38]
R-ant. HC + R-NAcc	0.192	0.688	[-0.10, 0.47]
R-ant. HC + L-VTA	-0.122	0.999	[-0.42, 0.17]
R-ant. HC + R-VTA	-0.106	0.999	[-0.39, 0.17]
L-NAcc + L-VTA	0.217	0.582	[-0.06, 0.48]
L-NAcc + R-VTA	0.339	0.124	[-0.02, 0.60]
R-NAcc + L-VTA	-0.039	0.999	[-0.32, 0.27]
R-NAcc + R-VTA	0.254	0.431	[-0.05, 0.51]

PC, *Perceptual Curiosity*; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

Appendix 13

Chapter 3, Experiment 2: Resting state functional connectivity (RSFC) results

Second level analysis (one sample t-test) across 53 subjects during rest. All source ROIs show high connectivity to respective target ROIs.

Source ROI	Connection to target ROI	L/R	Fisher-transformed correlation coefficient	T(52)
Left posterior HC				
	NAcc	L	0.09	7.45
		R	0.11	8.29
	VTA	L	0.11	9.40
		R	0.10	8.11
Right posterior HC				
	NAcc	L	0.08	7.01
		R	0.11	9.58
	VTA	L	0.09	7.03
		R	0.10	7.32
Left anterior HC				
	NAcc	L	0.11	6.97
		R	0.13	8.28
	VTA	L	0.09	4.61
		R	0.09	5.14
Right anterior HC				
	NAcc	L	0.10	7.20
		R	0.16	9.36
	VTA	L	0.12	6.60
		R	0.11	5.51
Left NAcc				
	VTA	L	0.12	7.80
		R	0.14	8.27
Right NAcc				
	VTA	L	0.14	7.74
		R	0.13	9.08

ROI-to-ROI functional connectivity reported at p-FDR<0.001, one sided, positive contrasts. All source ROIs had a high connectivity to respective target ROIs. VTA, *ventral tegmental area*; NAcc, *nucleus accumbens*; HC, *hippocampus*; L, *left*; R, *right*.

Appendix 14

Chapter 3, Experiment 2: Relationship between ROI-to-ROI functional connectivity coefficients and Interest EC, Deprivation EC, Diversive PC, Specific PC, Joyous Exploration, Deprivation Sensitivity, Stress Tolerance, Social Curiosity, and Thrill Seeking

14A. RSFC-behaviour correlations are based on 53 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Interest EC.

ROI-to-ROI functional connectivity	Interest EC		
	$r(51)$	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.048	0.988	[-0.18, 0.29]
L-pos. HC + R-NAcc	0.102	0.938	[-0.14, 0.34]
L-pos. HC + L-VTA	-0.318	0.999	[-0.53, -0.08]
L-pos. HC + R-VTA	-0.061	0.999	[-0.16, 0.36]
R-pos. HC + L-NAcc	0.112	0.921	[-0.16, 0.36]
R-pos. HC + R-NAcc	0.258	0.369	[0.05, 0.45]
R-pos. HC + L-VTA	-0.145	0.999	[-0.39, 0.12]
R-pos. HC + R-VTA	0.121	0.902	[-0.14, 0.35]
L-ant. HC + L-NAcc	0.052	0.986	[-0.22, 0.28]
L-ant. HC + R-NAcc	-0.027	0.999	[-0.28, 0.21]
L-ant. HC + L-VTA	0.021	0.995	[-0.21, 0.25]
L-ant. HC + R-VTA	0.097	0.947	[-0.15, 0.31]
R-ant. HC + L-NAcc	-0.101	0.999	[-0.31, 0.10]
R-ant. HC + R-NAcc	-0.151	0.999	[-0.37, 0.09]
R-ant. HC + L-VTA	-0.175	0.999	[-0.41, 0.09]
R-ant. HC + R-VTA	0.074	0.972	[-0.17, 0.30]
L-NAcc + L-VTA	-0.013	0.999	[-0.32, 0.32]
L-NAcc + R-VTA	0.153	0.819	[-0.12, 0.39]
R-NAcc + L-VTA	0.069	0.976	[-0.20, 0.38]
R-NAcc + R-VTA	0.090	0.955	[-0.16, 0.36]

EC, *Epistemic Curiosity*; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

14B. RSFC-behaviour correlations are based on 53 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Deprivation EC.

ROI-to-ROI functional connectivity	Deprivation EC		
	$r(51)$	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	-0.076	0.999	[-0.29, 0.17]
L-pos. HC + R-NAcc	-0.008	0.998	[-0.21, 0.25]
L-pos. HC + L-VTA	-0.283	0.999	[-0.52, -0.01]
L-pos. HC + R-VTA	-0.177	0.999	[-0.40, 0.06]
R-pos. HC + L-NAcc	-0.001	0.998	[-0.28, 0.28]
R-pos. HC + R-NAcc	0.049	0.986	[-0.23, 0.35]
R-pos. HC + L-VTA	-0.358	0.999	[-0.56, -0.16]
R-pos. HC + R-VTA	-0.167	0.999	[-0.40, 0.06]
L-ant. HC + L-NAcc	0.058	0.981	[-0.20, 0.29]
L-ant. HC + R-NAcc	-0.123	0.999	[-0.39, 0.19]
L-ant. HC + L-VTA	-0.050	0.999	[-0.30, 0.18]
L-ant. HC + R-VTA	-0.064	0.999	[-0.34, 0.20]
R-ant. HC + L-NAcc	-0.107	0.999	[-0.34, 0.16]
R-ant. HC + R-NAcc	-0.247	0.999	[-0.45, 0.02]
R-ant. HC + L-VTA	-0.114	0.999	[-0.39, 0.16]
R-ant. HC + R-VTA	-0.074	0.999	[-0.32, 0.20]
L-NAcc + L-VTA	-0.043	0.999	[-0.33, 0.24]
L-NAcc + R-VTA	-0.056	0.999	[-0.32, 0.20]
R-NAcc + L-VTA	-0.016	0.999	[-0.25, 0.21]
R-NAcc + R-VTA	0.187	0.687	[-0.07, 0.43]

EC, *Epistemic Curiosity*; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

14C. RSFC-behaviour correlations are based on 53 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Diversive PC.

ROI-to-ROI functional connectivity	Diversive PC		
	r(51)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	-0.076	0.999	[-0.34, 0.20]
L-pos. HC + R-NAcc	0.078	0.970	[-0.16, 0.33]
L-pos. HC + L-VTA	-0.210	0.999	[-0.48, 0.07]
L-pos. HC + R-VTA	-0.091	0.999	[-0.33, 0.16]
R-pos. HC + L-NAcc	0.097	0.952	[-0.14, 0.32]
R-pos. HC + R-NAcc	0.238	0.461	[-0.11, 0.51]
R-pos. HC + L-VTA	-0.106	0.999	[-0.34, 0.14]
R-pos. HC + R-VTA	-0.041	0.999	[-0.29, 0.21]
L-ant. HC + L-NAcc	0.045	0.989	[-0.25, 0.30]
L-ant. HC + R-NAcc	-0.162	0.999	[-0.40, 0.06]
L-ant. HC + L-VTA	0.059	0.983	[-0.21, 0.32]
L-ant. HC + R-VTA	-0.031	0.999	[-0.26, 0.21]
R-ant. HC + L-NAcc	-0.072	0.999	[-0.35, 0.23]
R-ant. HC + R-NAcc	-0.207	0.999	[-0.42, 0.01]
R-ant. HC + L-VTA	-0.124	0.999	[-0.35, 0.10]
R-ant. HC + R-VTA	-0.099	0.999	[-0.31, 0.13]
L-NAcc + L-VTA	0.007	0.998	[-0.23, 0.27]
L-NAcc + R-VTA	-0.019	0.999	[-0.29, 0.26]
R-NAcc + L-VTA	0.266	0.335	[-0.002, 0.51]
R-NAcc + R-VTA	0.118	0.918	[-0.13, 0.38]

PC, *Perceptual Curiosity*; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

14D. RSFC-behaviour correlations are based on 53 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Specific PC.

ROI-to-ROI functional connectivity	Specific PC		
	r(51)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	-0.221	0.999	[-0.46, 0.07]
L-pos. HC + R-NAcc	-0.081	0.999	[-0.33, 0.19]
L-pos. HC + L-VTA	-0.159	0.999	[-0.41, 0.09]
L-pos. HC + R-VTA	-0.084	0.999	[-0.34, 0.16]
R-pos. HC + L-NAcc	-0.102	0.999	[-0.35, 0.16]
R-pos. HC + R-NAcc	-0.220	0.999	[-0.44, 0.03]
R-pos. HC + L-VTA	-0.069	0.999	[-0.33, 0.23]
R-pos. HC + R-VTA	-0.052	0.999	[-0.33, 0.25]
L-ant. HC + L-NAcc	-0.159	0.999	[-0.38, 0.06]
L-ant. HC + R-NAcc	-0.120	0.999	[-0.34, 0.09]
L-ant. HC + L-VTA	0.012	0.997	[-0.24, 0.26]
L-ant. HC + R-VTA	-0.071	0.999	[-0.30, 0.16]
R-ant. HC + L-NAcc	-0.101	0.999	[-0.34, 0.19]
R-ant. HC + R-NAcc	-0.091	0.999	[-0.34, 0.13]
R-ant. HC + L-VTA	-0.070	0.999	[-0.28, 0.15]
R-ant. HC + R-VTA	0.023	0.995	[-0.22, 0.26]
L-NAcc + L-VTA	0.087	0.960	[-0.18, 0.37]
L-NAcc + R-VTA	0.060	0.984	[-0.24, 0.31]
R-NAcc + L-VTA	0.187	0.695	[-0.10, 0.45]
R-NAcc + R-VTA	0.212	0.581	[-0.07, 0.44]

PC, *Perceptual Curiosity*; L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

14E. RSFC-behaviour correlations are based on 52 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Joyous Exploration.

ROI-to-ROI functional connectivity	Joyous Exploration		
	r(50)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.165	0.777	[-0.10, 0.39]
L-pos. HC + R-NAcc	-0.127	0.999	[-0.39, 0.12]
L-pos. HC + L-VTA	-0.203	0.999	[-0.47, 0.05]
L-pos. HC + R-VTA	-0.078	0.999	[-0.31, 0.16]
R-pos. HC + L-NAcc	0.099	0.939	[-0.16, 0.31]
R-pos. HC + R-NAcc	0.040	0.988	[-0.27, 0.35]
R-pos. HC + L-VTA	-0.135	0.999	[-0.38, 0.12]
R-pos. HC + R-VTA	-0.012	0.999	[-0.25, 0.20]
L-ant. HC + L-NAcc	0.080	0.961	[-0.15, 0.29]
L-ant. HC + R-NAcc	-0.115	0.999	[-0.39, 0.16]
L-ant. HC + L-VTA	0.013	0.996	[-0.25, 0.25]
L-ant. HC + R-VTA	0.036	0.990	[-0.26, 0.29]
R-ant. HC + L-NAcc	0.069	0.972	[-0.18, 0.30]
R-ant. HC + R-NAcc	-0.298	0.999	[-0.52, -0.05]
R-ant. HC + L-VTA	-0.160	0.999	[-0.44, 0.13]
R-ant. HC + R-VTA	-0.042	0.999	[-0.31, 0.21]
L-NAcc + L-VTA	0.153	0.813	[-0.17, 0.45]
L-NAcc + R-VTA	0.202	0.625	[-0.05, 0.43]
R-NAcc + L-VTA	0.112	0.917	[-0.20, 0.39]
R-NAcc + R-VTA	0.012	0.997	[-0.25, 0.28]

L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

14F. RSFC-behaviour correlations are based on 53 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Deprivation Sensitivity.

ROI-to-ROI functional connectivity	Deprivation Sensitivity		
	r(51)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.116	0.918	[-0.11, 0.37]
L-pos. HC + R-NAcc	-0.015	0.998	[-0.23, 0.21]
L-pos. HC + L-VTA	-0.060	0.999	[-0.33, 0.25]
L-pos. HC + R-VTA	0.079	0.970	[-0.21, 0.35]
R-pos. HC + L-NAcc	0.052	0.988	[-0.19, 0.34]
R-pos. HC + R-NAcc	0.037	0.992	[-0.21, 0.28]
R-pos. HC + L-VTA	-0.127	0.999	[-0.36, 0.10]
R-pos. HC + R-VTA	-0.049	0.999	[-0.25, 0.16]
L-ant. HC + L-NAcc	-0.017	0.998	[-0.28, 0.26]
L-ant. HC + R-NAcc	-0.048	0.999	[-0.32, 0.25]
L-ant. HC + L-VTA	-0.193	0.999	[-0.43, 0.01]
L-ant. HC + R-VTA	-0.089	0.999	[-0.33, 0.16]
R-ant. HC + L-NAcc	-0.024	0.999	[-0.39, 0.29]
R-ant. HC + R-NAcc	-0.289	0.999	[-0.48, -0.07]
R-ant. HC + L-VTA	-0.162	0.999	[-0.45, 0.12]
R-ant. HC + R-VTA	-0.070	0.999	[-0.34, 0.23]
L-NAcc + L-VTA	0.091	0.957	[-0.15, 0.31]
L-NAcc + R-VTA	0.100	0.944	[-0.17, 0.36]
R-NAcc + L-VTA	-0.029	0.999	[-0.29, 0.22]
R-NAcc + R-VTA	0.158	0.805	[-0.11, 0.38]

L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

14G. RSFC-behaviour correlations are based on 52 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Social Curiosity.

ROI-to-ROI functional connectivity	Social Curiosity		
	r(50)	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.056	0.981	[-0.18, 0.29]
L-pos. HC + R-NAcc	0.049	0.985	[-0.22, 0.31]
L-pos. HC + L-VTA	-0.280	0.999	[-0.48, -0.05]
L-pos. HC + R-VTA	-0.177	0.999	[-0.38, 0.06]
R-pos. HC + L-NAcc	0.114	0.919	[-0.13, 0.37]
R-pos. HC + R-NAcc	0.041	0.988	[-0.24, 0.36]
R-pos. HC + L-VTA	0.149	0.835	[-0.12, 0.40]
R-pos. HC + R-VTA	0.00002	0.997	[-0.24, 0.22]
L-ant. HC + L-NAcc	0.063	0.977	[-0.15, 0.27]
L-ant. HC + R-NAcc	0.064	0.976	[-0.21, 0.33]
L-ant. HC + L-VTA	0.120	0.907	[-0.17, 0.39]
L-ant. HC + R-VTA	0.149	0.835	[-0.12, 0.41]
R-ant. HC + L-NAcc	0.043	0.987	[-0.18, 0.34]
R-ant. HC + R-NAcc	0.003	0.996	[-0.26, 0.27]
R-ant. HC + L-VTA	-0.031	0.999	[-0.27, 0.26]
R-ant. HC + R-VTA	0.036	0.990	[-0.17, 0.26]
L-NAcc + L-VTA	0.254	0.398	[-0.08, 0.53]
L-NAcc + R-VTA	0.135	0.875	[-0.16, 0.40]
R-NAcc + L-VTA	-0.063	0.999	[-0.34, 0.23]
R-NAcc + R-VTA	0.035	0.991	[-0.27, 0.34]

L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

14H. RSFC-behaviour correlations are based on 53 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 20 pairs of ROIs when correlated with Thrill Seeking.

ROI-to-ROI functional connectivity	Thrill Seeking		
	$r(51)$	p_{corr}	CI [LL, UL]
L-pos. HC + L-NAcc	0.080	0.968	[-0.15, 0.29]
L-pos. HC + R-NAcc	0.158	0.806	[-0.07, 0.39]
L-pos. HC + L-VTA	-0.011	0.998	[-0.31, 0.25]
L-pos. HC + R-VTA	0.010	0.995	[-0.26, 0.25]
R-pos. HC + L-NAcc	0.172	0.753	[-0.06, 0.40]
R-pos. HC + R-NAcc	0.183	0.712	[-0.20, 0.52]
R-pos. HC + L-VTA	0.074	0.972	[-0.14, 0.27]
R-pos. HC + R-VTA	-0.021	0.999	[-0.27, 0.22]
L-ant. HC + L-NAcc	0.024	0.993	[-0.26, 0.28]
L-ant. HC + R-NAcc	-0.132	0.999	[-0.37, 0.12]
L-ant. HC + L-VTA	-0.082	0.999	[-0.32, 0.14]
L-ant. HC + R-VTA	0.013	0.995	[-0.23, 0.23]
R-ant. HC + L-NAcc	0.011	0.995	[-0.26, 0.28]
R-ant. HC + R-NAcc	-0.196	0.999	[-0.40, 0.03]
R-ant. HC + L-VTA	-0.101	0.999	[-0.36, 0.10]
R-ant. HC + R-VTA	-0.048	0.999	[-0.29, 0.15]
L-NAcc + L-VTA	0.033	0.991	[-0.22, 0.28]
L-NAcc + R-VTA	0.172	0.753	[-0.09, 0.42]
R-NAcc + L-VTA	0.223	0.529	[-0.05, 0.48]
R-NAcc + R-VTA	0.072	0.973	[-0.19, 0.35]

L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; ant., *anterior*; pos., *posterior*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

Appendix 15

Chapter 4, Experiment 2: Cronbach's alpha

The mean (SD) total score across participants (N=55) and Cronbach's alpha (α) coefficients for each curiosity self-report measure.

Self-report measure	Mean (SD)	**α**
Epistemic Curiosity (EC) subscales		
Interest EC	13.96 (2.64)	0.80
Deprivation EC	10.24 (2.76)	0.82
Perceptual Curiosity (PC) subscales		
Diversive PC	18.09 (3.37)	0.73
Specific PC	14.44 (3.71)	0.75
Subscales of interest from the 5-Dimensional Curiosity scale		
Joyous Exploration	25.00 (4.60)	0.78
Deprivation Sensitivity	21.44 (5.61)	0.83
Stress Tolerance	22.25 (6.52)	0.89

α, *Cronbach's alpha coefficient*

Appendix 16

Chapter 5: Resting state functional connectivity (RSFC) results

Second level analysis (one sample t-test) across 53 subjects during rest. All source ROIs show high connectivity to respective target ROIs.

Source ROI	Connection to target ROI	L/R	Fisher-transformed correlation coefficient	T(52)
Left hippocampus				
	NAcc	L	0.15	9.20
		R	0.18	11.21
	VTA	L	0.15	9.19
		R	0.15	8.08
Right hippocampus				
	NAcc	L	0.13	8.75
		R	0.19	12.22
	VTA	L	0.15	8.91
		R	0.15	7.87
Left NAcc				
	VTA	L	0.12	7.80
		R	0.14	8.27
Right NAcc				
	VTA	L	0.14	7.74
		R	0.13	9.08

ROI-to-ROI functional connectivity reported at p-FDR<0.001, one sided, positive contrasts. VTA, *ventral tegmental area*; NAcc, *nucleus accumbens*; L, *left*; R, *right*.

Appendix 17

Chapter 5: Relationship between ROI-to-ROI functional connectivity coefficients and curiosity-related answer memory benefit.

RSFC-behaviour correlations are based on 49 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 12 pairs of ROIs when correlated with curiosity-related answer memory benefit.

ROI-to-ROI functional connectivity	Curiosity answer memory benefit		
	$r(47)$	p_{corr}	CI [LL, UL]
L-NAcc + L-HC	-0.314	0.999	[-0.52, -0.08]
L-NAcc + R-HC	0.033	0.969	[-0.28, 0.31]
R-NAcc + L-HC	0.100	0.866	[-0.20, 0.38]
R-NAcc + R-HC	0.170	0.639	[-0.10, 0.42]
L-VTA + L-HC	-0.013	0.991	[-0.25, 0.23]
L-VTA + R-HC	-0.020	0.993	[-0.30, 0.22]
L-VTA + L-NAcc	0.143	0.741	[-0.21, 0.46]
L-VTA + R-NAcc	**0.382**	**0.030**	[0.13, 0.58]
R-VTA + L-HC	0.049	0.956	[-0.20, 0.34]
R-VTA + R-HC	-0.117	0.999	[-0.42, 0.16]
R-VTA + L-NAcc	-0.037	0.996	[-0.35, 0.25]
R-VTA + R-NAcc	0.302	0.144	[0.03, 0.51]

p<0.05 (one-tailed), L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

Appendix 18

Chapter 5: Relationship between DTI metrics and overall answer memory, curiosity-related face memory benefit, overall face memory, high curiosity IPE-related answer memory benefit and finally low curiosity IPE-related answer memory benefit.

18A. DTI-behaviour correlations are based on 42 participants. Separate non-parametric permutation tests were carried out for each DTI metric correlated with overall answer memory. One-tailed Pearson correlation coefficients, p-values and 95% confidence intervals are reported for each diffusion metric (i.e., FA and MD) of the fornix when correlated with overall answer memory.

		Overall answer memory		
		r(40)	p_{corr}	CI [LL, UL]
Fornix	FA	0.048	0.376	[-0.21, 0.32]
	MD	-0.002	0.494	[-0.24, 0.27]

FA, *fractional anisotropy*; MD, *mean diffusivity*; CI, *confidence interval*; LL, *lower limit*; UL, *upper limit*

18B. DTI-behaviour correlations are based on 41 participants. Separate non-parametric permutation tests were carried out for each DTI metric correlated with curiosity-related face memory benefit. One-tailed Pearson correlation coefficients, p-values and 95% confidence intervals are reported for each diffusion metric (i.e., FA and MD) of the fornix when correlated with curiosity-related face memory benefit.

		Curiosity face memory benefit		
		r(39)	p_{corr}	CI [LL, UL]
Fornix	FA	0.221	0.082	[-0.04, 0.49]
	MD	-0.236	0.077	[-0.52, 0.09]

FA, *fractional anisotropy*; MD, *mean diffusivity*; CI, *confidence interval*; LL, *lower limit*; UL, *upper limit*

18C. DTI-behaviour correlations are based on 41 participants. Separate non-parametric permutation tests were carried out for each DTI metric correlated with overall face memory. One-tailed Pearson correlation coefficients, p-values and 95% confidence intervals are reported for each diffusion metric (i.e., FA and MD) of the fornix when correlated with overall face memory.

		Overall face memory		
		r(39)	p_{corr}	CI [LL, UL]
Fornix	FA	0.028	0.571	[-0.23, 0.30]
	MD	-0.072	0.322	[-0.37, 0.23]

FA, *fractional anisotropy*; MD, *mean diffusivity*; CI, *confidence interval*; LL, *lower limit*; UL, *upper limit*

18D. DTI-behaviour correlations are based on 42 participants. Separate non-parametric permutation tests were carried out for each DTI metric correlated with high curiosity IPE-related answer memory benefit. One-tailed Pearson correlation coefficients, p-values and 95% confidence intervals are reported for each diffusion metric (i.e., FA and MD) of the fornix when correlated with high curiosity IPE-related answer memory benefit.

		High curiosity IPE-related answer memory benefit		
		r(40)	p_{corr}	CI [LL, UL]
Fornix	FA	-0.025	0.440	[-0.26, 0.23]
	MD	0.143	0.818	[-0.08, 0.34]

IPE, *information prediction error;* FA, *fractional anisotropy*; MD, *mean diffusivity*; CI, *confidence interval*; LL, *lower limit*; UL, *upper limit*

Appendix 19

Chapter 5: Relationship between ROI-to-ROI functional connectivity coefficients and overall answer memory, curiosity-related face memory benefit, overall face memory, high curiosity IPE-related answer memory benefit, and finally low curiosity IPE-related answer memory benefit.

19A. RSFC-behaviour correlations are based on 49 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 12 pairs of ROIs when correlated with overall answer memory.

ROI-to-ROI functional connectivity	Overall answer memory		
	r(47)	p_{corr}	CI [LL, UL]
L-NAcc + L-HC	0.122	0.796	[-0.18, 0.44]
L-NAcc + R-HC	0.021	0.973	[-0.23, 0.30]
R-NAcc + L-HC	-0.034	0.996	[-0.29, 0.25]
R-NAcc + R-HC	0.099	0.856	[-0.14, 0.38]
L-VTA + L-HC	0.047	0.947	[-0.22, 0.31]
L-VTA + R-HC	0.042	0.952	[-0.24, 0.30]
L-VTA + L-NAcc	-0.171	0.999	[-0.42, 0.16]
L-VTA + R-NAcc	-0.179	0.999	[-0.39, 0.06]
R-VTA + L-HC	0.084	0.888	[-0.21, 0.37]
R-VTA + R-HC	0.183	0.584	[-0.11, 0.46]
R-VTA + L-NAcc	0.062	0.927	[-0.22, 0.30]
R-VTA + R-NAcc	-0.138	0.999	[-0.47, 0.23]

L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

19B. RSFC-behaviour correlations are based on 48 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 12 pairs of ROIs when correlated with curiosity-related face memory benefit.

ROI-to-ROI functional connectivity	Curiosity face memory benefit		
	r(46)	p_{corr}	CI [LL, UL]
L-NAcc + L-HC	-0.093	0.999	[-0.31, 0.16]
L-NAcc + R-HC	0.096	0.865	[-0.15, 0.34]
R-NAcc + L-HC	-0.017	0.989	[-0.28, 0.27]
R-NAcc + R-HC	-0.029	0.992	[-0.27, 0.22]
L-VTA + L-HC	0.003	0.982	[-0.25, 0.24]
L-VTA + R-HC	0.058	0.935	[-0.15, 0.29]
L-VTA + L-NAcc	-0.067	0.998	[-0.28, 0.17]
L-VTA + R-NAcc	0.035	0.962	[-0.29, 0.34]
R-VTA + L-HC	-0.054	0.997	[-0.25, 0.12]
R-VTA + R-HC	-0.080	0.999	[-0.25, 0.09]
R-VTA + L-NAcc	-0.089	0.999	[-0.38, 0.20]
R-VTA + R-NAcc	-0.112	0.999	[-0.40, 0.19]

L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

19C. RSFC-behaviour correlations are based on 48 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 12 pairs of ROIs when correlated with overall face memory.

ROI-to-ROI functional connectivity	Overall face memory		
	r(46)	p_{corr}	CI [LL, UL]
L-NAcc + L-HC	-0.060	0.998	[-0.29, 0.18]
L-NAcc + R-HC	0.040	0.959	[-0.21, 0.27]
R-NAcc + L-HC	-0.039	0.996	[-0.27, 0.21]
R-NAcc + R-HC	0.238	0.366	[-0.03, 0.46]
L-VTA + L-HC	-0.062	0.998	[-0.39, 0.23]
L-VTA + R-HC	-0.078	0.999	[-0.37, 0.22]
L-VTA + L-NAcc	0.059	0.938	[-0.20, 0.30]
L-VTA + R-NAcc	-0.053	0.997	[-0.30, 0.22]
R-VTA + L-HC	-0.120	0.999	[-0.49, 0.21]
R-VTA + R-HC	0.017	0.977	[-0.30, 0.31]
R-VTA + L-NAcc	-0.115	0.999	[-0.37, 0.19]
R-VTA + R-NAcc	0.060	0.936	[-0.15, 0.29]

L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

19D. RSFC-behaviour correlations are based on 49 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 12 pairs of ROIs when correlated with high curiosity IPE-related answer memory benefit.

ROI-to-ROI functional connectivity	High curiosity IPE-related answer memory benefit		
	$r(47)$	p_{corr}	CI [LL, UL]
L-NAcc + L-HC	0.029	0.967	[-0.21, 0.25]
L-NAcc + R-HC	0.060	0.937	[-0.21, 0.31]
R-NAcc + L-HC	-0.185	0.999	[-0.42, 0.06]
R-NAcc + R-HC	-0.037	0.997	[-0.33, 0.29]
L-VTA + L-HC	-0.272	0.999	[-0.47, -0.05]
L-VTA + R-HC	-0.248	0.999	[-0.47, -0.02]
L-VTA + L-NAcc	-0.044	0.998	[-0.24, 0.20]
L-VTA + R-NAcc	-0.072	0.999	[-0.41, 0.30]
R-VTA + L-HC	-0.071	0.999	[-0.31, 0.23]
R-VTA + R-HC	0.002	0.983	[-0.26, 0.27]
R-VTA + L-NAcc	-0.009	0.988	[-0.27, 0.24]
R-VTA + R-NAcc	-0.129	0.999	[-0.40, 0.15]

IPE, *information prediction error;* L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

19E. RSFC-behaviour correlations are based on 48 participants. These results were obtained from a non-parametric permutation test (one-tailed) correcting for multiple comparisons across the 12 pairs of ROIs when correlated with low curiosity IPE-related answer memory benefit.

ROI-to-ROI functional connectivity	Low curiosity IPE-related answer memory benefit		
	r(46)	p_{corr}	CI [LL, UL]
L-NAcc + L-HC	**0.401**	**0.021**	[0.10, 0.63]
L-NAcc + R-HC	0.215	0.458	[-0.10, 0.48]
R-NAcc + L-HC	0.021	0.977	[-0.10, 0.43]
R-NAcc + R-HC	0.184	0.589	[-0.09, 0.42]
L-VTA + L-HC	0.254	0.300	[-0.03, 0.52]
L-VTA + R-HC	0.143	0.737	[-0.15, 0.43]
L-VTA + L-NAcc	0.131	0.775	[-0.18, 0.46]
L-VTA + R-NAcc	0.155	0.691	[-0.15, 0.41]
R-VTA + L-HC	0.055	0.943	[-0.22, 0.37]
R-VTA + R-HC	0.155	0.694	[-0.15, 0.44]
R-VTA + L-NAcc	-0.076	0.999	[-0.35, 0.23]
R-VTA + R-NAcc	0.054	0.945	[-0.24, 0.32]

p<0.05 (one-tailed), IPE, *information prediction error;* L, *left*; R, *right*; HC, *hippocampus*; NAcc, *nucleus accumbens*; VTA, *ventral tegmental area*; CI, *confidence interval*; LL, *lower level*; UL, *upper level.*

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