Window into the Wandering Mind:
Investigating the Neural and Pupillometric Correlates of Mind Wandering with a Dual Task Paradigm

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Abstract

Mind wandering (MW) is a heterogeneous and private phenomenon, which is nonetheless omnipresent in people's lives. Research on this phenomenon has grown considerably during the past decade, thanks also to the development of neuroimaging techniques which have given us a window into the brain's activity while we are lost in our thoughts. However, there are still two important issues for researchers in this field. The first, is the need to evoke in an experimental setting what is, by definition, a spontaneous phenomenon. This can be solved by developing an experimental task that creates certain conditions in which MW is more or less likely to arise. The second issue is the reliance on individuals' self-reports, which are inherently subjective, to understand the emergence, and content, of MW. This issue is harder to tackle, but one possibility is to develop a physiological, objective marker of MW. Recently, two candidates have emerged as potential markers of MW: one is the default mode network (DMN), a set of brain areas that show coordinated activity when people drift off to their inner thoughts; the second candidate is baseline pupil size, which has showed sensitivity to changes in external and internal attention, such as during episodes of MW. This thesis describes the development of a novel paradigm for the study of mind wandering, and its use to understand the potential that the DMN and baseline pupil size have as markers of this phenomenon. In three empirical studies, this paradigm successfully modulates individuals' performance, MW, and on-task focus. Further, evidence from these studies indicates that DMN activity and baseline pupil size don't provide sufficient precision to be used in isolation as markers of MW: in particular, it is suggested that their predictive power strongly depends on taking into account the content of the MW experience, and the context in which it occurs.

Table of Contents

List of Tables

List of Figures

perceived stimulus (is the square on the left or the right?); the NTs are thus irrelevant to the task, allowing for long periods in the 0-back condition when attention is unconstrained by the task. Conversely, in the 1-back condition the target decision is based on the previously attended NT (was the square on the left or the right?). Under these conditions, participants must maintain external attention on the task in order to perform accurately. ..41

Acknowledgements

Author's Declaration

This thesis is a presentation of original work completed by the author, Mahiko Konishi, under the supervision of Dr. Jonathan Smallwood. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Each of the studies presented was conducted in accordance with the ethical standards of the Ministry of Defence Research Ethics Committee and the University of York's Department of Psychology and York NeuroImaging Centre.

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Chapter 1.   Introduction

Human cognition has the tendency to seamlessly switch its focus between the external environment and its inner, self-generated thoughts. One phenomenon that captures this unique aspect is mind wandering (MW), in which attention flows from an ongoing task to unrelated thoughts (Smallwood & Schooler, 2006, 2015), such as finding ourselves thinking about what to cook for dinner while driving home from work. Mind wandering is a very common experience; studies estimate that individuals spend a quarter to half of their waking lives engaged in MW (Kane et al., 2007; Klinger & Cox, 1987; Killingsworth & Gilbert, 2010). In spite of the ubiquitous nature of MW in our conscious lives, this phenomenon was neglected in psychological research for a long time, for a handful of reasons, the chief of which being the general skepticism towards internal experience and introspection inherited from the behaviourist era (Callard, Smallwood, & Margulies, 2012; Smallwood & Schooler, 2015). However, in recent years there has been renewed interest in the study of internal experiences from both fields of Experimental Psychology and Neuroscience; this is in large part due to the fast development of new methodologies, allowing researchers to acquire neurocognitive measures and not solely rely on self-reports and behavioural measures like in the past. Figure 1.1 shows the number of papers published on the subject of mind wandering in the past century. The same phenomenon, i.e. attention diverging from an external task to internal thoughts, has received several different scientific terms throughout the years: "daydreaming", "mind wandering", "stimulus-independent thought", "task-unrelated thought" are some of the main terms used in the literature. From the figure it is possible to see research in the daydreaming phenomenon starting in the mid 1960's with the seminal work of Antrobus, Singer, & Greenberg, (1966), and subsequently the spike in interest in MW research in the past decade, together with this latter term's general acceptance in the scientific community, which in turn can be retraced to Smallwood & Schooler 2006's article "The Restless Mind".
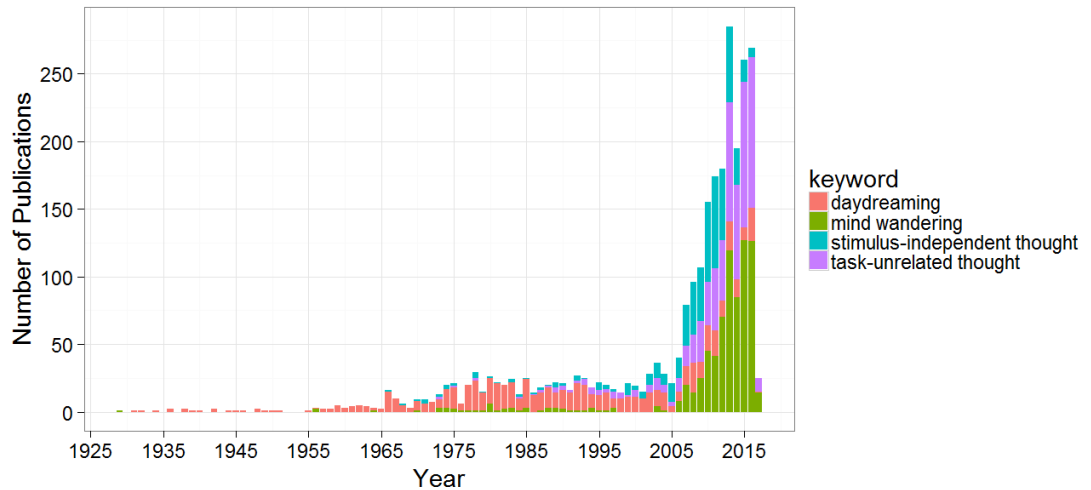
Figure 1.1 - The number of papers for the different keywords in each year was calculated through a bibliography search using the software Publish or Perish (Harzing, 2007). The rapid growth in interest in the topic starts around 2006.

Despite these advances, mind wandering research still largely relies on self-reports, and does not have a standard experimental paradigm used for its study. The research presented in this thesis aimed to build on the literature in order to find a solution to these two problems: developing an experimental paradigm for the study of MW, and investigating the neural and pupillary correlates of this phenomenon, to understand their potential as objective markers.

While the field of mind wandering research is young relative to other psychological topics, there already are a number of findings that have been reproduced by different research groups and are thus widely accepted in the community. Mind wandering is known to be a frequent and permeating phenomenon in individuals' waking lives; it is more often than not oriented towards future thoughts, although past-oriented MW has been linked to negative mood effects; it arises more commonly whenever the individual is engaged in an easy, well-practiced task; however, if MW does arise during a demanding task, it often leads to costs in performance; the content of an individual's mind wandering is not trivial in determining the benefits or costs that it will produce; finally, states of MW have been paired to a number of neural correlates, using fMRI, pupillometry, and electroencephalography (EEG).

1.1 Mind Wandering Is a Frequent and Ubiquitous Phenomenon

It is a common experience to find oneself mind wandering multiple times every day; at least six studies tried to estimate exactly how often this happens, using real-life paradigms (Michael J Kane et al., 2007; Killingsworth & Gilbert, 2010; Klinger & Cox, 1987; McVay, Kane, & Kwapil, 2009; Poerio, Totterdell, & Miles, 2013; Song & Wang, 2012). All studies used slight variations of experience sampling (ES; Kahneman, Krueger, Schkade, Schwarz, & Stone, 2004) methodology, which involves probing participants at different moments of the day using a beeper or a phone app, and asking them a series of questions regarding the occurrence, and quality, of the thoughts they were having just before they were prompted (probe-caught ES). Klinger & Cox (1987), Kane et al. (2007), McVay et al., (2009), and Poerio et al., (2013) all found that for ~30% of the samples, participants reported experiences of MW just before being probed; Killingsworth & Gilbert (2010) found that number to be slightly higher, with their participants reporting MW on ~47% of the thought samples; Song & Wang (2012), who conducted their study in China, found a MW rate of ~24%. Interestingly, all studies showed a wide inter-individual range in MW rates, ranging from < 10% to > 90%. In brief, both everyday experience and real-world studies point to MW being a very common mental phenomenon, with individuals being decoupled from the external environment for large parts of their waking lives.

1.2 Mind Wandering Has Both Costs and Benefits

The fact that human minds wander this frequently suggests that there could be benefits to the otherwise potentially dangerous state of being decoupled from the external environment. Already in the mid '60s, Antrobus et al. (1966) noted: "The presence of this non-perceptual cognitive activity on such a large scale is perhaps the strongest argument that daydreaming and imagining serve a useful purpose for the individual". At the same time, if the mind wanders towards one's inner thoughts whenever the external environment demands attention, it can come at a cost. Two lines of research have been researching how the context and the content of mind wandering episodes relate to its potential costs and benefits.

1.2.1 Benefits of Mind Wandering

One of the most consistent findings in the field is that individuals engaged in mind wandering tend to think more about future than past events. This has been found in a range of different MW paradigms, and in different cultures (Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Baird, Smallwood, & Schooler, 2011; Smallwood et al., 2011; Song & Wang, 2012; Stawarczyk, Cassol, & D'Argembeau, 2013; Stawarczyk, Majerus, Maj, Van der Linden, & D'Argembeau, 2011); these results are summarised in Figure 1.2. This prospective bias, together with the findings that MW is often directed towards an individual's personal goals (Medea et al., 2016; Smallwood & Schooler, 2006; Stawarczyk, Majerus, Maj, et al., 2011) and that MW is linked with improvements in creative problem solving (Baird et al., 2012), has led some researchers to argue that one of the main benefits and functions of MW is to prepare and plan for the future (Baird et al., 2011; Smallwood & Schooler, 2015; Stawarczyk, Majerus, Maj, et al., 2011); indeed, the idea that mental time travel, such as conscious simulations of future events, is a major benefit for the organism, has been also theorised in the field of self-regulation and emotional coping (Taylor, Pham, Rivkin, & Armor, 1998; Taylor & Schneider, 1989), and even as one the evolutionary basis for conscious thought (Baumeister & Masicampo, 2010; Baumeister, Masicampo, & Vohs, 2011) and the human mind (Suddendorf & Corballis, 1997).
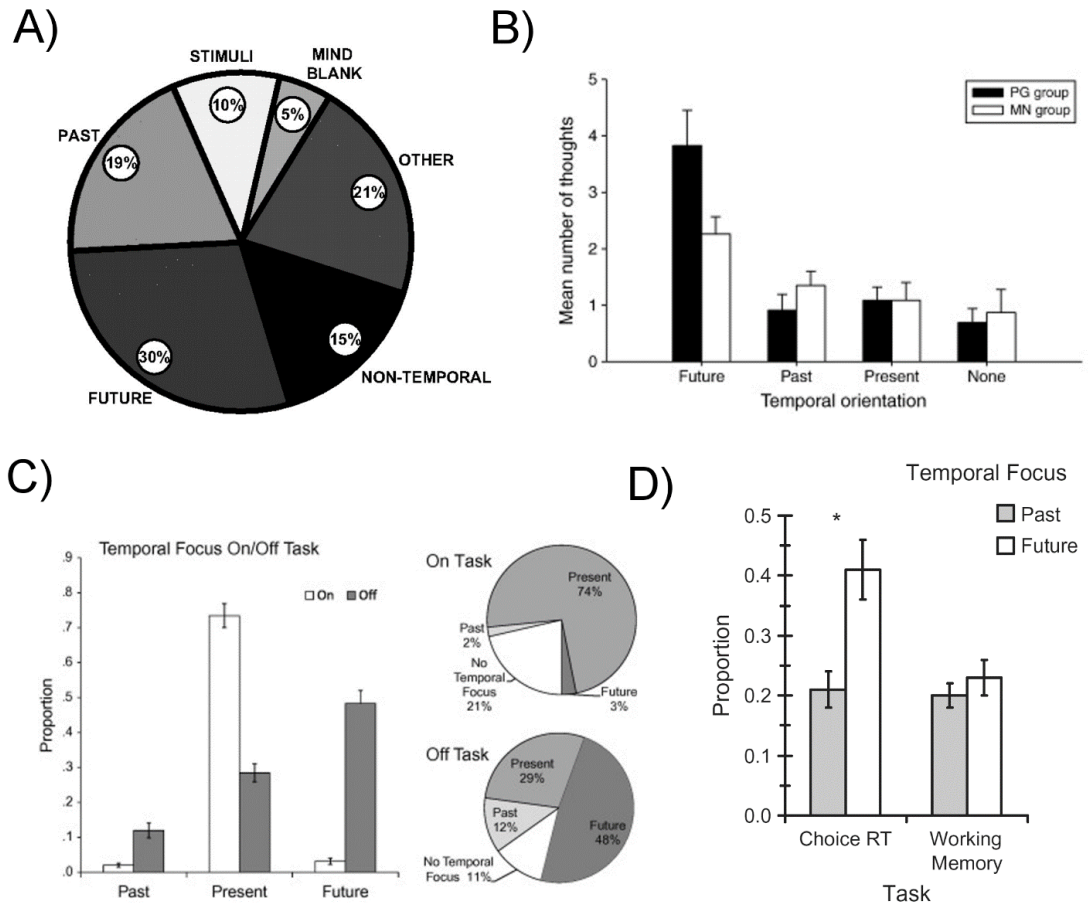
Figure 1.2 - Four different studies showing the propensity of individuals of thinking more about the future than of the past. A) Adapted from Andrews-Hanna et al. (2010). B) From Stawarczyk et al. (2011); PG and MN refer to two experimental conditions in their study. Regardless of condition, participants show the prospective bias. C) From Baird et al. (2011); off task thought shows a clear prospective bias, while on task thought is predictably directed to the present. D) Adapted from Smallwood et al. (2011); participants show a prospective bias in an easy task that allows mind wandering.

1.2.2 Costs of Mind Wandering

Mind wandering has traditionally been researched by Psychologists as unrelated thoughts emerging during an ongoing task, so that its study has often focused on the performance costs that occur in this scenario. One such important line of research regards the effects of MW on reading comprehension (Franklin, Broadway, Mrazek, Smallwood, & Schooler, 2013; Franklin, Smallwood, & Schooler, 2011; McVay & Kane, 2012b; Reichle, Reineberg, & Schooler, 2010; Sanders, Wang, Schooler, & Smallwood, 2016; Smallwood, McSpadden, & Schooler, 2008; Smilek, Carriere, & Cheyne, 2010; Unsworth & McMillan, 2012; Uzzaman & Joordens, 2011). The classic paradigm involves giving participants a text to read, and assessing their reading comprehension by means of a questionnaire; importantly their MW is

monitored throughout the reading task, either by probing them at certain intervals with questions regarding their experiences (probe-caught ES), letting the participants spontaneously provide reports of whenever they catch themselves drifting off (self-caught ES), or by gathering information at the end of the task by means of a questionnaire (retrospective ES). These studies routinely found that MW rates are negatively correlated with reading comprehension; some studies also found that this comprehension cost is related to differences in eye movements (Franklin et al., 2011; Reichle et al., 2010; Uzzaman & Joordens, 2011), working memory capacity (McVay & Kane, 2012b; Unsworth & McMillan, 2012), and might be caused by disrupting the building of propositional models of the text (Smallwood, McSpadden, et al., 2008).

Another classic line of research investigates the effects of MW on the performance of tasks that require a constant attentional engagement, such as the Sustained Attention to Response Task (SART; Robertson, Manly, Andrade, Baddeley, & Yiend, 1997). It is widely accepted that in such tasks, MW occurrence is related to poor performance such as slower reaction times (Cheyne, Carriere, & Smilek, 2006; Cheyne, Solman, Carriere, & Smilek, 2009; Geden & Feng, 2015; Helton, Kern, & Walker, 2009; Mcvay & Kane, 2009; McVay & Kane, 2012a; Smallwood et al., 2004; Thomson, Seli, Besner, & Smilek, 2014; Unsworth & Robison, 2016; Yanko & Spalek, 2014), omissions and errors (Allen et al., 2013; Cheyne et al., 2006, 2009; Helton et al., 2009; Mcvay & Kane, 2009; McVay & Kane, 2012a; Smallwood et al., 2004; Thomson et al., 2014), impaired working memory performance (McVay & Kane, 2012a; Mrazek et al., 2012; Teasdale et al., 1995), and higher RTs variability (Cheyne et al., 2009; Seli, Cheyne, & Smilek, 2013); a summary of these results is shown in Figure 1.3. The strong relation between off-task thought and poor performance in demanding tasks is an important one, as it allows the use of behavioural performance as a potential objective index of MW in the right experimental paradigm.
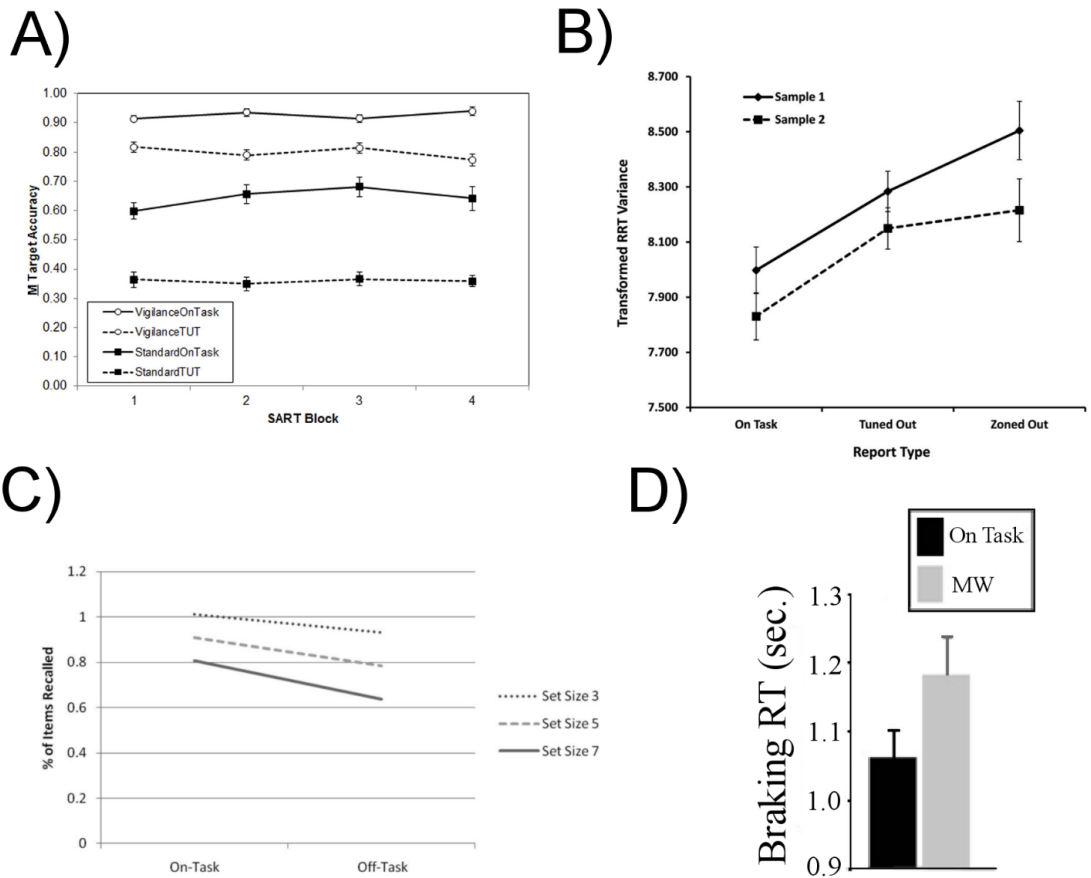
Figure 1.3 – Four studies showing the disruptive effects of MW on tasks that require executive resources. A) From McVay & Kane (2012a); participants show lower accuracy when engaged in task-unrelated thought (TUT; dotted lines) in two different engaging tasks (white and black lines). B) From Seli et al. (2013); RT variance on a metronome response task increases when participants mind wander, regardless if they are aware ("Tuned Out") of it, or not ("Zoned Out"). C) From Mrazek et al. (2012); participants recall fewer items in a working memory task (OSPAN task; Turner & Engle, (1989)) if they were mind wandering; the disruptive effect of mind wandering increases with task difficulty (increasing the number of items to maintain in working memory). D) Adapted from Yanko & Spalek (2014); participants RTs are slower while braking in a high-fidelity driving simulator if they were mind wandering compared to being on task.

Finally, another important aspect of MW is its relation to negative mood. There is substantial evidence that unhappiness is a correlate of MW (Killingsworth & Gilbert, 2010; Smallwood, Fitzgerald, Miles, & Phillips, 2009; Smallwood & O'Connor, 2011; Smallwood, O'Connor, Sudbery, & Obonsawin, 2007; Song & Wang, 2012), especially when the latter is directed towards past events (Poerio et al., 2013; Ruby, Smallwood, Engen, & Singer, 2013; Smallwood & O'Connor, 2011; Stawarczyk, Majerus, & D'Argembeau, 2013); however, the directionality of this relation is still not clear, as studies have suggested both a causal effect of induced negative mood on the subsequent frequency of MW (Poerio et al., 2013; Smallwood,

Fitzgerald, et al., 2009; Smallwood & O'Connor, 2011; Song & Wang, 2012; Stawarczyk, Majerus, et al., 2013), and the opposite (Killingsworth & Gilbert, 2010; Ruby, Smallwood, Engen, et al., 2013). It is likely that the two are so closely intertwined, both functionally and structurally, that they can't be temporally disentangled. Although MW has been related to negative mood by most studies, it is important to note that at least two studies have also found a relation to positive mood in certain cases, specifically when MW is directed towards the future instead of the past (Ruby, Smallwood, Engen, et al., 2013), and when its content is of high interest for the individual (Franklin, Mrazek, et al., 2013). As with any other complex and heterogenous phenomenon, analysing the content of MW, and the context in which it occurs, is key in understanding the consequences that it will have on the individual and his/her performance.

1.3   Mind Wandering Occurrence Depends on Context

Mind wandering arises more commonly when we are not involved in a demanding task, or in a task at all (Antrobus et al., 1966; Konishi, McLaren, Engen, & Smallwood, 2015; Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007; McKiernan, D'Angelo, Kaufman, & Binder, 2006; Smallwood & Schooler, 2015; Teasdale et al., 1995); for example, it is more likely that a car passenger would drift off in his/her own thoughts than it would be for the driver of the car. This is optimal, as MW can interfere with a concurring task and affect its performance. The idea that an adaptive cognitive system has the capacity to regulate the occurrence of MW to minimise its costs on task performance has been summarised as the *context-regulation hypothesis* (Smallwood & Andrews-Hanna, 2013). This hypothesis predicts that individuals who are able to limit their MW to non-demanding situations will reap the greater benefits, and experience the fewer costs related to this experience. In support of this hypothesis, it has been found that when faced with demanding activities, individuals with high working memory capacity (WMC) are able to maintain on-task focus, limit their MW, and perform better (better accuracy/lower RTs) than individuals with low WMC (Michael J. Kane et al., 2007; Mcvay & Kane, 2009); furthermore, it has been shown that, during a low demand task, participants with higher WMC also experience more MW episodes than participants with lower WMC (Levinson, Smallwood, & Davidson, 2012), suggesting that an adaptive system does not reduce the overall amount of MW episodes, but regulates their occurrence to times in which they are not disruptive.

The frequency of MW thus seems to generally increase linearly as task difficulty decreases (Antrobus, 1968; McKiernan et al., 2006; Teasdale et al., 1995), but is also known to increase as a task becomes well practiced (Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007; Teasdale et al., 1995): this is due to the effects of practice in lowering the executive demands of the task, as the cognitive system automatizes the processes needed to perform the task optimally, so that fewer decisions have to be made consciously (Newell & Rosenbloom, 1981; Shiffrin & Schneider, 1977; Teasdale et al., 1995). This is the reason for which, relative to a beginner driver, an experienced driver experiences more episodes of MW while driving, especially on a well-practiced route (e.g. from home to the office). The fact that MW frequency can be modulated by the task demands is important, because it allows some control on a phenomenon that is largely spontaneous. The relation between MW frequency, task demands and task practice is illustrated in Figure 1.4.
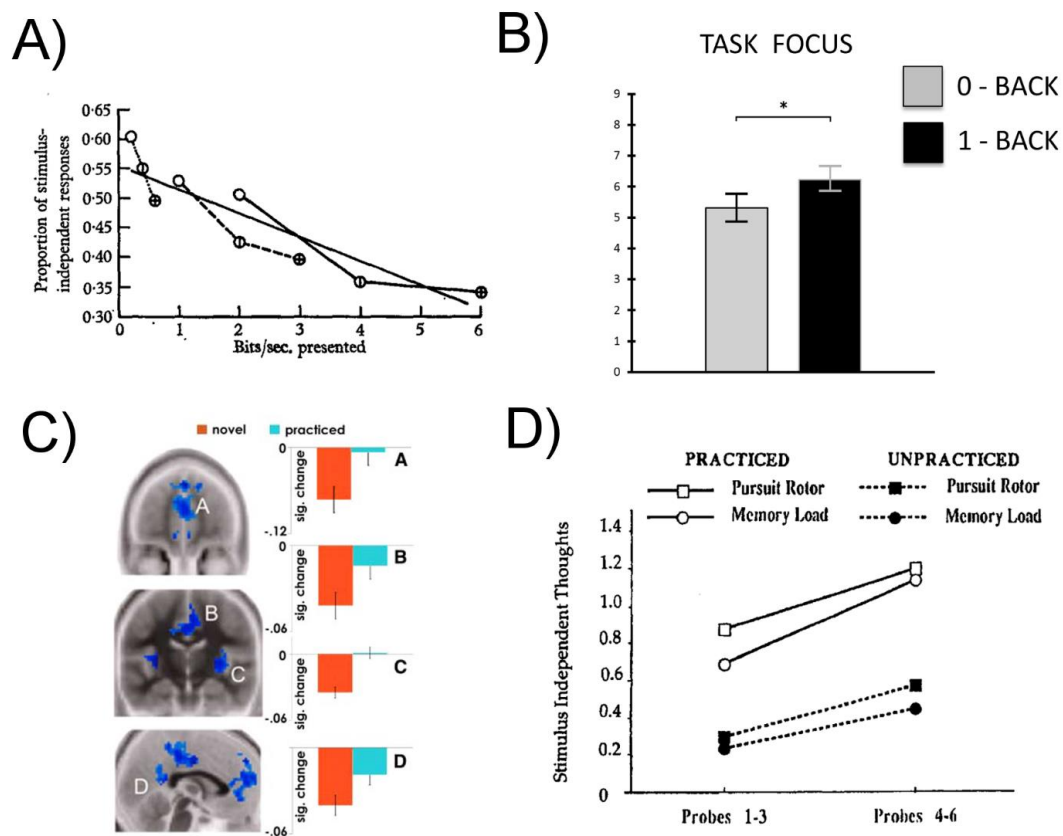
Figure 1.4 – Four studies showing the effect of task demands and task practice on mind wandering frequency. A) From Antrobus, (1968): stimulus-independent thoughts (y-axis) are less frequent as more information is presented to the participants in an auditory detection task. B) Adapted from Konishi et al., (2015): thoughts are reported as more off-task in an easier task (0-back) relative to a harder, 1-back working memory task. C) Adapted from Mason, Norton, Horn, et al., (2007): areas of the Default Mode Network (DMN), which are active during mind wandering episodes, increase activity during task blocks that had been practiced before, relative

to novel ones. D) From Teasdale et al., (1995): stimulus-independent thoughts are reported more frequently in two different tasks when these had been practiced (white lines) compared to the same unpracticed tasks (black lines).

1.4 Mind Wandering Is Heterogenous in Content

The mere presence (or absence) of MW episodes can often tell very little to the researcher; instead, the content of those episodes is equally or more important in determining the costs or benefits that they will have on the individual that experiences them. Our minds can travel back in time, somehow bypassing the otherwise unbreakable unidirectionality of time (Tulving, 2002) and accessing memories of minutes or decades past, can plan events that will happen in the future, or imagine fantasies that will never do so. Our brains recombine the sensory information that we have perceived in our lives in infinite new ways, rendering our mental life unrivaled in richness. Several recent studies have experimentally investigated the content of MW episodes and the differential effects that these have on individuals' well-being. As described in section 1.2, it is known that MW can be related to lower mood when oriented towards past events (Smallwood & O'Connor, 2011) but have benefits, and is generally more common, when oriented towards the future (Baird et al., 2011). Similarly, repetitive and recurrent thoughts, normally associated with negative outcomes, have been shown to have constructive consequences depending on the content, valence and context in which they arise (Watkins, 2008). Furthermore future thoughts are generally rated as more positive (D'Argembeau & Van der Linden, 2006), providing support to the idea that individuals have an optimistic bias towards the future (Taylor & Brown, 1988); on the other hand, thoughts about the past have been described as containing more sensory information, being more detailed and coherent (D'Argembeau & Van der Linden, 2006), although this can vary depending on the temporal distance of the event remembered or imagined (D'Argembeau & Van Der Linden, 2004). Although having differences, future and past thoughts also show remarkable similarities (D'Argembeau & Van der Linden, 2006; D'Argembeau & Van Der Linden, 2004) and have been hypothesized to be intimately related (Atance & O'Neill, 2001; D'Argembeau & Van der Linden, 2006; Suddendorf & Corballis, 1997) to the point of sharing the same neural substrate (Schacter, Addis, & Buckner, 2007). The idea that the costs and benefits of mind wandering strongly depend on the content of these episodes has been described as a *content-regulation hypothesis* (Smallwood & Andrews-Hanna, 2013; Smallwood & Schooler, 2015).

As the content of MW is basically unlimited, researchers have to investigate this variety while somehow constraining it in order to measure it. One potential solution to this problem is to ask participants a set number of questions to see if they fit their experience (e.g. "where you thinking about the past?", "where your thoughts positive or negative?", etc.); this methodology, dubbed as experience sampling (Csíkszentmihályi & Larson, 1987; Larson & Csikszentmihalyi, 1983), is most commonly done either by briefly interrupting participants during their daily lives in ecological studies, while they are performing a concurrent task (probe-caught ES), or by giving a longer questionnaire at the end of the task (retrospective ES). An additional step that can then be taken, is to apply a decomposition technique such as principal component analysis (PCA) to check for patterns of covariance in the responses: for example, whenever participants report more thoughts about the past it could be that they also systematically rate them as more negative. Klinger & Cox (1987) pioneered this method, also dubbed multi-dimensional experience sampling (MDES; Konishi & Smallwood, 2016; Smallwood & Schooler, 2015) which was then applied by several other researchers to investigate a number of different questions, such as: the phenomenology of future-oriented MW (Stawarczyk, Cassol, et al., 2013); the relation between the content of MW and the brain's functional architecture (Gorgolewski et al., 2014; Medea et al., 2016; Smallwood et al., 2016a); the relation between MW and mood (Ruby, Smallwood, Engen, et al., 2013), between MW and social problem solving (Ruby, Smallwood, Sackur, & Singer, 2013); the role of future-directed thought in the processing of personal goals (Medea et al., 2016). An example of the MDES approach is shown in Figure 1.5.

A)

Dimension	Question	Left	Right
Task	My thoughts were focused on the task I was performing	Not at all	Completely
Future	My thoughts involved future events	Not at all	Completely
Past	My thoughts involved past events	Not at all	Completely
Self	My thoughts involved myself	Not at all	Completely
Other	My thoughts involved other people	Not at all	Completely
Emotion	The content of my thoughts was	Negative	Positive
Images	My thoughts were in the form of images	Not at all	Completely
Words	My thoughts were in the form of words	Not at all	Completely
Intrusive	My thoughts were intrusive	Not at all	Completely
Detail	My thoughts were vague and non-specific	Not at all	Completely
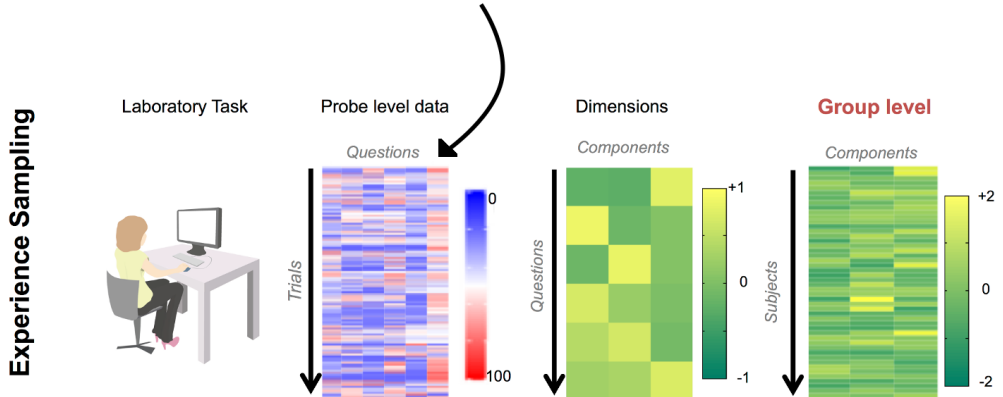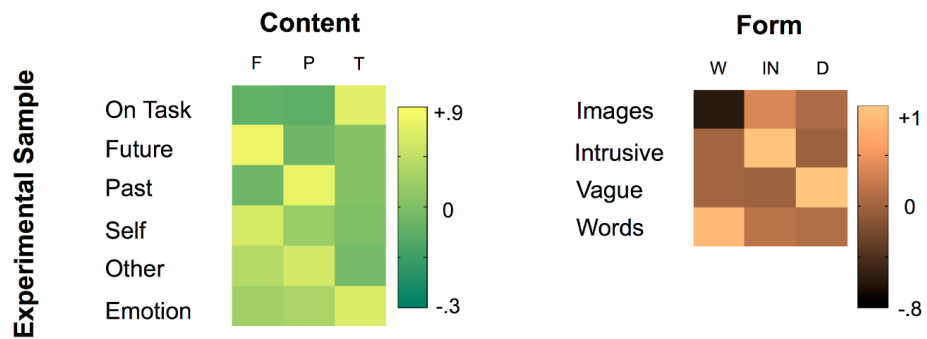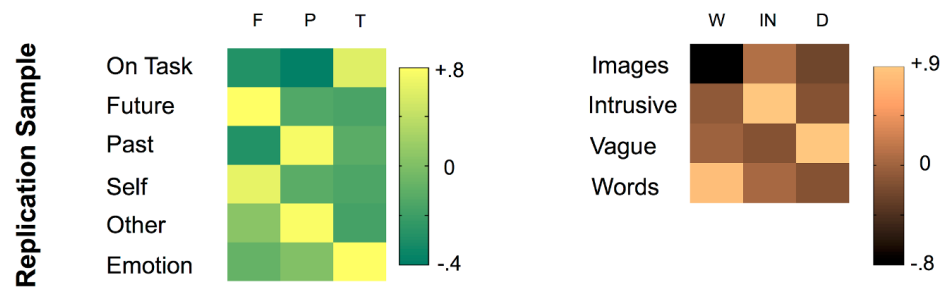
Figure 1.5 – Adapted from Smallwood et al., (2016b) The figure illustrates the various steps of multi-dimensional experience sampling. A) Participants are asked questions regarding multiple dimensions of their mind wandering experience, through probe-caught ES. B) Principal component analysis is applied in order to investigate the possible correlations in the data. C) Visualization of the orthogonal factors in an experimental sample, derived from the PCA: six components are derived, three describing the content of thoughts and three describing the form of thoughts. D) A replication sample showing principal components largely overlapping with the ones in the experimental sample.

1.5 Neural and Physiological Correlates of Mind Wandering

Technological advances in the past decades, such as the development of functional magnetic resonance imaging (fMRI; Kwong et al., 1992; Ogawa, Lee, Kay, & Tank, 1990), have allowed researchers to look at the relation between cognitive processes and activations in areas of the brain, and indeed, to develop the field of cognitive neuroscience all together. In the past twenty years, cognitive neuroscience has grown increasingly interested in mind wandering after the discovery of the default mode network (DMN; Buckner, Andrews-Hanna, & Schacter, 2008; Gusnard & Raichle, 2001; McGuire, Paulesu, Frackowiak, & Frith, 1996; Raichle et al., 2001; Raichle & Snyder, 2007); the term DMN refers to a series of brain areas including medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC) and inferior parietal lobule (IPL) (Buckner et al., 2008). These often show activation in the absence of a specific task such as during waking rest, which is also when we are more likely to engage in MW (Smallwood, Nind, & O'Connor, 2009). Techniques such as fMRI can be especially beneficial when looking at private phenomena such as MW, as they allow the pairing of an objective measure (e.g. the change in blood oxygenation levels in certain areas of the brain) to a subjective experience (e.g. remembering a childhood memory). Similarly, another line of research has used electroencephalography (EEG) to investigate the effects of MW on external processing; Smallwood, Beach, Schooler, & Handy (2008) found evidence of reduced amplitude of the P3, an event related potential linked to cortical analysis of external stimuli, during episodes of MW, a finding replicated by other studies (Barron, Riby, Greer, & Smallwood, 2011; Macdonald, Mathan, & Yeung, 2011); similarly, Braboszcz & Delorme (2011) found mind wandering episodes to be linked to increases in EEG delta power and to elicit a larger P2 component, both phenomena related to decreases in alertness and disengagement of participants' attention to external stimuli (De Gennaro, Ferrara, & Bertini, 2001; Näätänen & Picton, 1987).

Indeed, the covert nature of MW is one of the major obstacles in its scientific investigation (Konishi & Smallwood, 2016; Smallwood & Schooler, 2015), and one solution is to combine subjective measures, such as ES, with objective measures; the core idea of this approach, dubbed as *triangulation*, is to obtain several concurring, but different, measures of the same phenomenon in order to pinpoint the variance common to all of them and link it with the phenomenological experience of the participant (Smallwood & Schooler, 2015).

1.5.1 fMRI Correlates of Mind Wandering

Following this approach, several researchers have shown evidence that directly link activation of the DMN with participants' reports of mind wandering episodes in different contexts (Andrews-Hanna, Smallwood, & Spreng, 2014; K. C. R. Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015), such as drifting off from a demanding task (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Greicius & Menon, 2004; Mckiernan, Kaufman, Kucera-thompson, & Binder, 2003; Stawarczyk, Majerus, Maquet, & D'Argembeau, 2011), or experiencing mind wandering thoughts during periods of waking rest (Andrews-Hanna, Reidler, Huang, et al., 2010) and while performing a well-practiced task (Mason, Norton, Van Horn, Wegner, Grafton, Macrae, et al., 2007). In addition to the afore mentioned hubs of the DMN (mPFC, PCC and bilateral IPL), a recent neuroimaging meta-analysis (K. C. R. Fox et al., 2015) has highlighted the contribution of several other areas in the mind wandering phenomenon, such as the dorsal anterior cingulate cortex (dACC), dorsolateral prefrontal cortex (dlPFC), medial temporal lobe (MTL), and insula. Recent studies (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Andrews-Hanna et al., 2014) have shown that the DMN can be divided into two subsystems, a *medial temporal subsystem*, active during mental time travel, and a *dorsal medial* subsystem, active during social thinking, such as mentalizing; the two subsystems appear to be coordinated by the two major hubs of the DMN, namely the mPFC and PCC. Given that the term mind wandering refers to a large variety of self-generated thought constructs, it is unsurprising that several brain areas are differentially involved in the phenomenon.

The DMN has been implicated in stimulus-independent thought and MW since its discovery (Gusnard & Raichle, 2001; McGuire et al., 1996; Raichle et al., 2001), so much so as to become known as the task negative network (Spreng, 2012), but recent studies have shown that the DMN can be activated, and interact with "task-positive" networks such as the executive network (Seeley et al., 2007), during demanding, working memory (Spreng et al., 2014; Vatansever, Menon, Manktelow, Sahakian, & Stamatakis, 2015) and creativity tasks (Beaty, Benedek, Silvia, & Schacter, 2016). Furthermore, the main hubs of the DMN, and especially the mPFC, have also consistently been implicated in simple reaction time tasks (Burgess, Dumontheil, & Gilbert, 2007; Gilbert, Frith, & Burgess, 2005; Gilbert, Simons, Frith, & Burgess, 2006). The observed activity of the DMN during both MW and several different tasks engaging attention to external stimuli is important, because it hints to the idea that activation in these areas is necessary but not sufficient to describe a MW episode in terms

of its neural correlates, as a covert marker should do. The relation between DMN activity, mind wandering, and task performance will thus be one of the focuses of this thesis.

1.5.2   Pupillometric Correlates of Mind Wandering

A further physiological measure that has shown promise as a covert marker of mind wandering is pupil dilation. Pupil dilation has been traditionally used in Psychological research as a measure of cognitive effort and working memory load, as early studies (Beatty & Kahneman, 1966; Hess & Polt, 1964; Kahneman & Beatty, 1966) indicated that pupils' dilation linearly increases with mental effort: for example, individuals' pupils dilate more if they have to remember more items in a short-term memory task, if they have to process read or heard complex grammatical sentences, or if they engage in mental arithmetic (Beatty, 1982).

Recently, interest in pupillometric measures has newly risen, thanks also to the development of a theoretical framework which links the dilation of pupils to arousal, via activity of the locus coeruleus (LC), with large pupils indicating a highly aroused, distractible state, and small pupils linked to drowsiness (Aston-Jones & Cohen, 2005; Aston-Jones, Rajkowski, & Cohen, 1999; Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014). Arousal has also been classically related to behavioral performance through an U-shaped curve (Yerkes-Dodson law) with optimal performance found in moderate levels of arousal, and extreme levels linked to disrupted performance (Aston-Jones & Cohen, 2005; Yerkes & Dodson, 1908); it is important to note that while this relationship has thus been reported and cited in the past century, the original study theorized an U-shaped relationship between arousal and performance only for difficult tasks, while suggesting a linear relationship for easy tasks, with increasing arousal linked to better performance (Diamond, Campbell, Park, Halonen, & Zoladz, 2007; Yerkes & Dodson, 1908). Furthermore, this U-shaped relationship is thought to arise from an LC-mediated switch from an exploitation to an exploration mode, with moderate levels of arousal encouraging task-directed behavior (Aston-Jones & Cohen, 2005; Hauser, Fiore, Moutoussis, & Dolan, 2016; Jepma & Nieuwenhuis, 2011). As mind wandering is also both related to task performance and task-disengagement, several researchers have tried to bridge the theoretical gap between MW, performance, and pupil dilation (Mittner, Hawkins, Boekel, & Forstmann, 2016a; Smallwood, Brown, et al., 2011; Unsworth & Robison, 2016).

Following this theoretical account, prior studies have found that performance is lower when pupils are very small or very large (Gilzenrat et al., 2010; Smallwood, Brown, et al., 2011; Van Den Brink, Murphy, & Nieuwenhuis, 2016; Van Orden, Jung, & Makeig, 2000); similarly, a few other studies have linked episodes of MW either to large (Franklin, Broadway, et al., 2013), or small pupils (Grandchamp, Braboszcz, & Delorme, 2014; Unsworth & Robison, 2016). Thus, while pupil dynamics seem to track lapses of attention and episodes of mind wandering to a certain level, and although some of these results are consistent with the pupil-arousal-performance framework, it is clear that there are several important inconsistencies in the literature that need to be addressed. Figure 1.6 provides an illustrated summary of the links between pupil dilation, brain activity, and mind wandering.
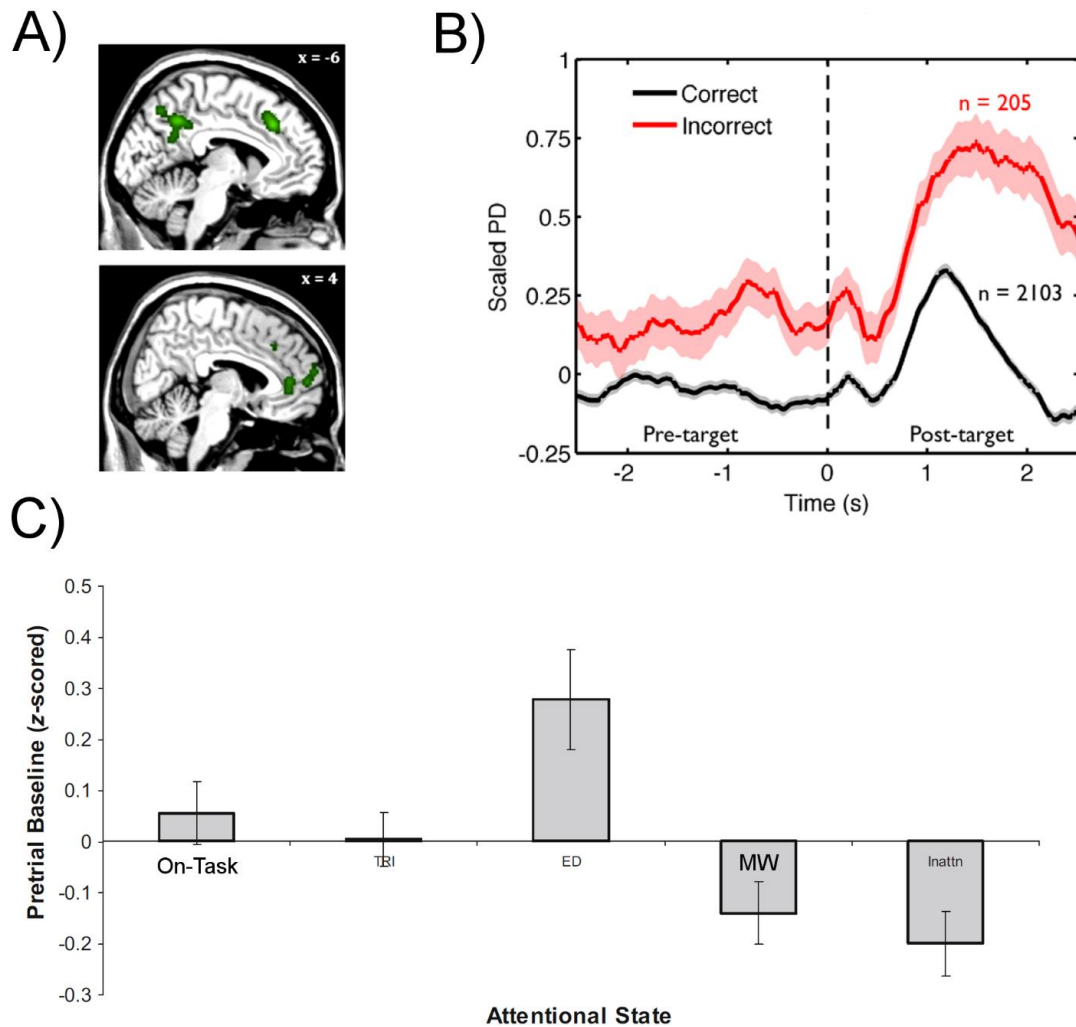
Figure 1.6 - Three studies showing the links between brain activity, pupil dilation and mind wandering. A) Adapted from (K. C. R. Fox et al., 2015): a meta-analysis of fMRI studies of MW shows clusters of activation in the PCC/precuneus and the dorsal ACC (top sub-panel), and mPFC (bottom sub-panel), associated with mind wandering and spontaneous thought processes. Subpanel C of Figure 1.4 also shows activity in PCC and mPFC during episodes of MW. B) Adapted from (Smallwood, Brown, et al., 2011): baseline pupil is higher prior to incorrect target responses in a working memory task. Targets were presented at the 0-time mark on the x-axis. C) Adapted from (Unsworth & Robison, 2016): baseline pupil is smaller during MW relative to being on-task or to being distracted by external stimuli (ED).

1.6 Thesis Outline and Aims

As discussed so far, applying the scientific method to investigate mind wandering presents specific hurdles, also shared by many fields of consciousness research, and the research presented in this thesis attempts to solve two of them. The first hurdle is the need to consistently elicit a spontaneous phenomenon in an experimental setting: while other

cognitive states can be induced with relative ease, such as mood induction through the use of music or films (Westermann, Spies, Stahl, & Hesse, 1996), MW is defined as spontaneous thoughts unrelated to the main task at hand, and as such it needs a tailored experimental paradigm for its emergence. Albeit spontaneous, MW is known to arise more frequently under certain circumstances, such as during boring, or easy contexts. In the lab, this corresponds to having a context of low task demands: by systematically varying the difficulty of a task, it should then be possible to modulate the frequency of MW episodes. The second issue regards the ability to objectively measure this heterogenous, intimate conscious phenomenon: the field still largely relies on individuals' self-reports in order to assess their MW experiences, but these reports are inherently subjective. However, it should also be possible to track these subjective experiences through their physiological correlates and their consequences on performance.

The research conducted in this PhD project sought to develop a paradigm to study mind wandering, from the ideation and validation of an experimental task that could entice this fleeting phenomenon, to its capture, by combining behavioral, physiological, and subjective measures. This paradigm is then used in three empirical studies to understand the neural and pupillometric correlates of mind wandering and their potential in the development of a covert marker of this phenomenon.

A full outline of the contribution of each chapter to the thesis' aims is outlined below:

Chapter 2. The paradigm. This chapter discusses the development of the 0-back/1-back paradigm used in the studies presented in this thesis.

Chapter 3. How understanding the mind wandering state can inform our appreciation of conscious experience. This review chapter illustrates the two main experimental issues that mind wandering and consciousness researchers face, along with suggestions on how to overcome them.

Chapter 4. The default mode network supports cognition that is independent of immediate perceptual input. This empirical chapter explores a novel hypothesis of default mode network function, namely that the DMN's main function is to support cognition independent of stimuli that are presently available to the senses.

Chapter 5. *Pupillometric signatures of fluctuations in external attention*. This empirical chapter investigates the pupillometric correlates of mind wandering and of external attention. In particular, it explores how these can be modulated by task context and mind wandering content.

Chapter 6. *The role of practice in task-positive and task-negative default mode network activity*. This empirical chapter replicates the study presented in Chapter 4 and extends it to understand the effect of task practice on goal-directed, and stimulus-independent, DMN activity.

Chapter 7. *General discussion*. This chapter synthetizes the results from the previous chapters to discuss how these studies can contribute to the development of a marker of mind wandering. Moreover, this chapter provides directions for future research in this field.

Chapter 2.   The Paradigm

The first step in this PhD project involved the development of a task that could manipulate the occurrence of MW. This would allow for a certain degree of experimental control on a spontaneous phenomenon. Previous studies tried to solve this issue by implicitly relying on time: given enough of it, participants' minds, engaged in some sort of demanding task, would inevitably start to wander. The use of these attentionally demanding tasks was also due to the fact that, for a long time, mind wandering was almost exclusively defined as "task-irrelevant, "task-unrelated", or "stimulus-independent": it existed only in juxtaposition to the classic experimental tasks of cognitive psychology as an undesirable side effect. The very first studies typically used auditory or visual signal-detection tasks (Antrobus, 1968; Antrobus, Coleman, & Singer, 1967; Antrobus et al., 1966), with long experimental sessions of about 3 hours per participant. More recently, studies began to shift towards the use of working memory tasks (Teasdale et al., 1995; Teasdale, Proctor, Lloyd, & Baddeley, 1993), sustained attention tasks (Robertson et al., 1997), or vigilance tasks (Giambra, 1989, 1995); the latter ones being particularly successful at eliciting MW, given the rare need for a participant's response, thus lowering the task's demands.

As illustrated in Chapter 1.3, mind wandering is more likely to emerge during low demand tasks; on the other hand, MW is infrequent, but has more tangible behavioural costs, when arising during demanding tasks, as described in Chapter 1.2.2. A mind wandering paradigm should encourage the frequent occurrence of the phenomenon, while at the same time providing a challenge to participants: indeed, if they were to perform near ceiling levels, it would be impossible to use behavioural performance as an additional marker of MW occurrence. One possible solution is to alternate an easy, low-demand task, to a more demanding attentional or working memory task.

2.1   The Choice Reaction Time/Working Memory Task

Smallwood, Nind, & O'Connor (2009) first pioneered this idea by making participants perform a Choice Reaction Time (CRT), and a Working Memory task (WM), which present similar stimuli but vary in the cognitive processes that must be applied to them. The CRT task is essentially a vigilance task; participants are shown a stream of single-digit numbers and

have to make a decision (is the number odd or even, by pressing one of two keys) whenever a rare target digit, differently coloured, is presented. The WM task is a variation of a 1-back task; participants again are presented with a stream of digits, but must decide whether the stimulus preceding the infrequent target (a coloured "?") was odd or even, again pressing one of two keys. Thus, in the CRT task participants are, for the most part, shown stimuli that are irrelevant to the task (the non-targets), and are able to drift off to their self-generated thoughts without this affecting their performance; on the other hand, participants in the WM task have to be constantly focused on the non-targets because they don't know when a target will appear, probing them to make a decision based on the previously shown stimulus. Although the stimuli presented to the participants are essentially the same (streams of numbers), the different instructions in the two tasks effectively induce different experiences. This paradigm has then been used for several other MW studies (Baird et al., 2012; Smallwood, Schooler, et al., 2011; Smallwood, Ruby, & Singer, 2013), including fMRI (Smallwood, Tipper, et al., 2013) and pupillometry (Smallwood, Brown, et al., 2011) studies: these show consistent results, with the CRT task notably eliciting more frequent mind wandering, especially related to the future, relative to the WM task. The CRT/WM paradigm is illustrated in Figure 2.1.
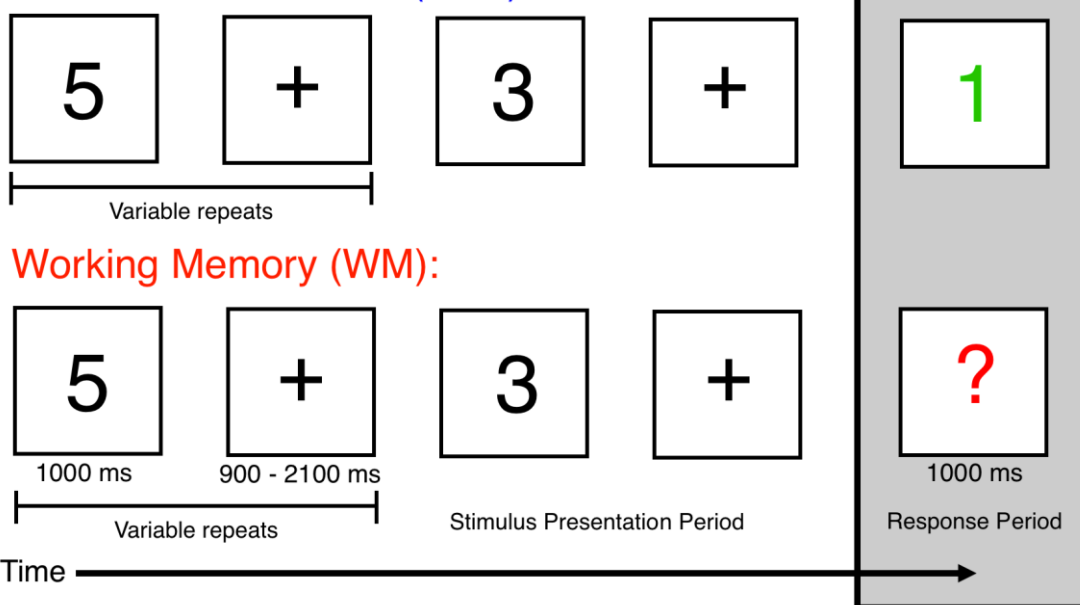
Figure 2.1 – Adapted from (Smallwood, Brown, et al., 2011): the CRT and WM tasks show the same stimuli, interspersed with fixation crosses, to participants, but the instructions for each task produce different experiences in the individuals. In the CRT, participants press one of two keys depending if the green target number (the '1' in the figure) is odd or even. In the WM, if a red question mark is presented, participants press one of two keys

depending if the previous shown stimulus (the '3' in the figure) was odd or even. In the CRT, participants' attention can drift off during the black non-targets (NTs), without this affecting their capacity to decide if the green target is an odd or even digit; in the WM, participants need to constantly monitor and encode the NTs, as a red question mark will probe them about the previously shown NT.

This paradigm is well suited for the study of mind wandering, providing two task conditions that can be compared and analysed in terms of executive demands, frequency of MW, and behavioural performances; additionally, it is easy to couple physiological measures to the tasks, such as fMRI and pupillometry. Nevertheless, it suffers from some minor issues, which can potentially change participants' experiences in ways not foreseen by the experimenter. Importantly, the key, intended manipulation of the task, is to make participants constantly focused and coupled with the external stimuli (the NTs) in the WM task, while allowing freedom of thought and cognition for the same NTs in the CRT, as they are not needed to perform the task correctly. However, in the WM task a sly participant could choose to rest his finger on the "correct" key after being presented a NT, and then updating this for every newly presented NT, e.g. a '5' is presented, the sly participant rests his finger on the "odd" response key; if a target question mark is then presented, the participant would just need to press the key on which his finger is resting, thus not having to encode and maintain the digits throughout, effectively lowering the task demands. Secondly, RT analyses of these two task in previous studies, either showed no difference in the two tasks (Smallwood, Schooler, et al., 2011), or faster RTs in the demanding task (Baird et al., 2012; Ruby, Smallwood, Sackur, et al., 2013); furthermore, target accuracy was found higher in the CRT relative to the WM task in a study (Smallwood, Schooler, et al., 2011) while the opposite was found in another study (Ruby, Smallwood, Sackur, et al., 2013), with a third study finding no significant accuracy differences in the two tasks (Baird et al., 2012). The lack of consistent behavioural performance is an issue if these are to be used as mind wandering indexes in a paradigm; moreover, the more demanding WM task should elicit lower accuracy rates and slower reaction times, a pattern not found in the afore mentioned studies. For the purpose of this project, the original CRT/WM paradigm was modified in a way that would maximise the difference in attentional demands of the two tasks, and also prevent participants to use any work arounds.

2.2   The 0-back/1-back Task

One solution was found by using pairs of shapes instead of a stream of single digit numbers as the main stimuli used in the two tasks: in the new version of the CRT task, participants see two black geometric shapes divided by a blue vertical line. These black pairs are the non-targets (NTs), and the shapes can either be a circle, triangle, or a square, but never two of the same type together; after several NTs, the number of which can be decided on a random or semi-random manner, to minimise the effects of anticipation by participants, a pair of blue shapes is presented (the target stimulus), divided by a vertical line in the middle of which is another small shape, representing one of the two shapes on the sides. When a target is presented, the participant needs to make a response by pressing either the left or right arrow key, depending on which side the shape shown in the middle is. For example, a target is presented with a blue triangle on the left, a blue circle on the right, and a small blue triangle in the middle: in this case, the participant would have to press the 'left' arrow key, as the triangle is on the left. This can be considered a 0-back task, and similarly to the CRT, the response depends on the stimuli presented on screen at the moment. In the new WM version, again pairs of black shapes are presented as NTs, divided by a red line. The difference is that the target stimulus is, in this case, two red question marks, with a small shape in the middle: the small shape refers to one of the two presented in the NT just previously shown. The participant needs to remember where the shape was, and respond accordingly with the right/left arrow keys. This is effectively a 1-back working memory task, in which participants need to continuously encode the NTs until a target is presented. The two tasks continuously switch between each other after a certain number of target events, and the colour coding (red lines for the 1-back, blue lines for the 0-back, which can be counterbalanced) helps participants remember in which condition they are. A diagram of the new 0-back/1-back task is shown in Figure 2.2.
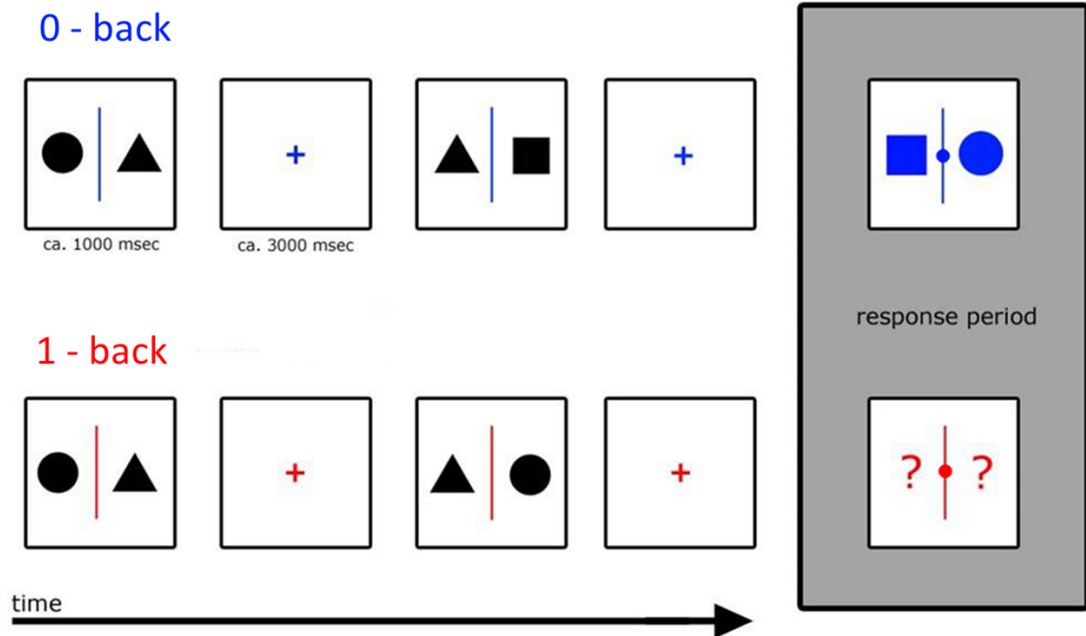
Figure 2.2 – In the 0-back/1-back paradigm, participants alternate between the two conditions: in both conditions, after a certain number of non-targets (NTs), participants are faced with a target decision. In the 0-back condition, the decision is based on the presently perceived stimulus (is the square on the left or the right?); the NTs are thus irrelevant to the task, allowing for long periods in the 0-back condition when attention is unconstrained by the task. Conversely, in the 1-back condition the target decision is based on the previously attended NT (was the square on the left or the right?). Under these conditions, participants must maintain external attention on the task in order to perform accurately.

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In this new version, participants' attention must be constantly coupled to the NT stimuli in the 1-back task; on the other hand, the 0-back task largely allows participants' attention to fluctuate between the task and internal thoughts, without affecting their performance. Furthermore, different types of stimuli in the two task conditions can shift the locus of attention between internal and external cognition: for example, to respond correctly to the targets in the 0-back task, it is necessary to be focused on the presented external stimulus, as it is to encode the NTs in the 1-back task. On the other hand, to respond to targets in the 1-back task, internal cognition is needed to recall the position of the previously encoded NT; internal cognition also likely plays a part during presentation of the 0-back NTs, in which participants are free to drift off to their own thoughts, without consequences.

The use of this type of paradigm not only fixes the issues that the previous CRT/WM task had, but it leaves the door open to further variations: depending on the researcher's interest, the basic, geometrical shapes can be substituted by more complex stimuli, such as written

41

words or pictures (faces, landscapes, objects etc.): at least one recent fMRI study has taken this approach, modifying the 0-back/1-back by using pictures of objects instead of shapes (Murphy et al., *in review*). Moreover, like the CRT/WM, the 0-back/1-back paradigm can be easily coupled with several physiological measures, as it is easy to run in an MRI scanner or with an eye-tracker camera, and importantly, this paradigm is well suited to be paired with experience sampling (ES) techniques, such as multi-dimensional experience sampling (MDES; referenced in chapter 1.4).

2.3   Multi-Dimensional Experience Sampling

One way to sample participants' inner experiences, is to present a retrospective questionnaire at the end of the experimental session, asking them to self-report their levels of focus and engagement throughout the task; several such questionnaires exist and have been successfully used in MW studies (Barron et al., 2011; Gorgolewski et al., 2014; Smallwood, Brown, Baird, Mrazek, et al., 2012), such as the Dundee Stress State Questionnaire (DSSQ; Matthews et al., 1999), Amsterdam Resting-State Questionnaire (ARSQ, Diaz et al., 2013), and New York Cognition Questionnaire (NYCQ; Gorgolewski et al., 2014). These have the advantage of being administered after completion of the task, so that participants are not disturbed or interrupted, which can be important for certain covert measures such as fMRI; on the other hand, such retrospective measures require participants to average and rate their experiences over the course of several minutes, which can lead to a loss of specificity and be prone to cognitive biases (e.g. recency/primacy biases).

Another possibility is to use probe-caught ES, in which participants are intermittently interrupted during a concurrent task, and probed regarding the contents of their experience (Smallwood & Schooler, 2006). The probes are usually administered on a random or semi-random basis, and have the advantage of potentially capturing individual instances of mind wandering episodes: this is important if the researcher is interested in online measurements (e.g. was the report of a specific MW episode preceded by a certain pattern of brain activity?) and not just overall MW rates, in which case a retrospective questionnaire can be satisfactory. Furthermore, participants can describe their experiences as they just happened, so that these reports are less likely to be affected by temporal degradation or other cognitive biases, as it can happen with retrospective reports. On the other hand, probe-caught ES can be disruptive to the normal flow of the concurrent task, and the rate of probes has been shown to affect the

rate of MW reports, (Seli, Carriere, Levene, & Smilek, 2013), with MW reports decreasing as the number of probes in a session increase.

In probe-caught ES, as in retrospective ES, participants are typically asked several questions (also called thought-probes) regarding their experience: examples of typical questions are the task-focus of thoughts (on-task VS. off-task/MW), the temporal direction of thoughts (past VS. future), the form of thoughts, such as thinking in images, words, or the level of detail of thoughts. In the case of probe-caught ES, many such probes can be administered in a single session to one participant, so that the final dataset results in a large number of thought probes, each of which contains several individual questions (task focus, temporal direction, etc.). One issue with this method is that mind wandering episodes are often varied in content and form, and individual questions can only capture separate aspects of an episode; moreover, there is a chance that some questions could be highly correlated between each other (e.g. most thoughts about the past are also very detailed), and this relation would also not be captured by analysing the individual scales. As mentioned in Chapter 1.4, one way to process such a dataset is to reduce its dimensions by work of a factor analysis, such as principal component analysis (PCA); PCA is a statistical method that reduces multi-dimensional data to a set of fewer, orthogonal (and thus uncorrelated) dimensions, called principal components. Applying PCA to a set of thought probes controls for the possible correlations between the different scales, and the principal components thus obtained can then be projected back onto the probe-level dataset, so that each thought probe is described not only by the individual questions, but also by the principal components, each of which is weighted based on how much it is described by that specific probe. For example, the PCA might result in a principal component describing detailed thoughts about the past, which would be heavily weighted on the "past" and "detailed" questions, but not on other questions. When this component is then projected back at the probe-level, its weight depends on the specific thought probe: it would have a high value if, for a specific probe, the participant had responded highly on the individual scales of "past" and "detailed" thoughts, and vice versa. These resulting principal components, which attempt to capture the relation between multiple dimensions of thought in a reduced number of measures, can then be analysed without potential correlational confounds. This methodology, also known as multi-dimensional experience sampling (MDES; Konishi & Smallwood, 2016; Smallwood & Schooler, 2015), is summarised in Figure 1.5.

The 0-back/1-back task here presented can be paired with either ES method. Retrospective questionnaires can always be administered at the end of a task session, the length of which can

be manipulated if concerns arise regarding the ability of participants to report on their overall rates of MW throughout the task: shorter sessions should help in this sense. In the same way, thought probes can be easily inserted in the task if a probe-caught ES is preferred, such as presenting a thought probe in place of a target. If such probe-caught ES is then paired with a physiological measure (fMRI, EEG, pupillometry, etc.), this would allow several analyses of interest to be conducted. For example, it would be possible to compare what brain activity (or pupil dynamic) is common (or different) when participants report being off-task and when they respond incorrectly or slow to a target, by analysing the time windows preceding a target or a thought probe. The rate of presentation of such probes in place of targets can in turn be manipulated, so as to have enough reports without excessively disrupting the natural flow of the task.

By combining a dual task with experience sampling and physiological measures, the paradigm presented in this chapter attempts to solve two important issues in mind wandering research: eliciting this spontaneous phenomenon, and measuring it as objectively as possible. These are problems shared by other fields of consciousness research, and the next chapter discusses how the study of MW can help in finding a solution to these issues.

Chapter 3.   How Understanding the Mind Wandering State Can Inform Our Appreciation of Conscious Experience

The following chapter has been adapted from:

3.1   Abstract

The mind wandering state illustrates two fundamental aspects of consciousness: its generative nature, which is reflected by the stimulus-independent content of thought that occurs when our minds wander; and metacognition, the unique capacity of the mind to reflect and understand itself. Self-generated thought, which allows us to consider people and events that are not present in the immediate environment, and metacognition, allowing us to introspect and report our inner experiences, are both essential to the scientific study of mind wandering. Nevertheless, they also inevitably lead to specific issues that mirror more general problems in the field of consciousness research. The generative nature of consciousness makes it difficult to have direct control on the phenomenon, and the act of introspecting on inner experience has the potential to influence the state itself. We illustrate how the field of mind wandering research can overcome these problems. Its generative nature can be understood by triangulating the objective measures (such as neural function) with subjective measures of experience and it can be manipulated indirectly by varying the demands of the external environment. Furthermore, we describe candidate covert markers for the mind wandering state, which allow the phenomenon to be observed without direct interference, minimizing the concern that instructions to introspect necessarily change conscious experience.

3.2 Introduction

Conscious experience is one of the most self-evident aspects of the human condition and yet its operation remains a mystery. There are at least two aspects of consciousness that are central to its status as a topic of scientific enquiry and that are also at the core of what makes it an empirically difficult line of investigation: its generative, stimulus-independent nature and its unique capacity to reflect and understand itself, also known as metacognition. The stimulus-independency of consciousness refers to the fact that its continuous stream of content is always active and can often be unrelated to the immediate environment (Antrobus et al., 1966; Giambra, 1993; Pope, 2013; Singer, 1966, 1993; Smallwood, 2013; Smallwood & Schooler, 2015; Wegner, 1997). Metacognition is the capacity of consciousness to introspect its own processing, allowing people to report their inner experiences (Flavell, 1979; Koriat, 2006; Metcalfe & Shimamura, 1994; Nelson, 1996; J. D. Smith, 2009). Both stimulus independence of conscious experience and its meta-cognitive access are exemplified in the experiences that arise during the mind wandering state.

Mind wandering refers to the experience that attention is not always tied to an external task being performed or to stimuli in the present environment, and that instead mental content can be experienced that is generated by the individual (Smallwood & Schooler, 2015). The mind wandering state makes up at least 25-50% of our waking lives (Michael J Kane et al., 2007; Killingsworth & Gilbert, 2010) and shows similar features across many different cultures (such as a focus on the future) (Giambra, 1982; Giambra & Stone, 1982; Singer & McCraven, 1961; Song & Wang, 2012). Mind wandering has broad implications for the human condition: for example, it has been linked to disruption of comprehension of material during reading (Dixon & Bortolussi, 2013; Smallwood, 2011; Smallwood, Fishman, & Schooler, 2007) and understanding of lectures in an educational context (Szpunar, Khan, & Schacter, 2013), issues in performance of executive control tasks (Mrazek et al., 2012), or being associated with unpleasant mood (Killingsworth & Gilbert, 2010; Poerio et al., 2013; Smallwood, Fitzgerald, et al., 2009; Smallwood & O'Connor, 2011). It has also been suggested to play a role in planning (Baird et al., 2011; Ruby, Smallwood, Sackur, et al., 2013; Smallwood, Schooler, et al., 2011) and creative insight (Baird et al., 2012).

Contemporary accounts suggest that at least two different component processes are engaged during the mind wandering state: a decoupling process, which allows inner experience to be independent from events in the external environment; and a representational process, which

provides mental content that is not directly attributable to the events in the here and now (Kam & Handy, 2013; Smallwood, 2013; Smallwood & Schooler, 2015). As the representations upon which we are focused during mind wandering are different from those related to the stimuli in the moment, these experiences are, by definition, stimulus independent. Moreover, the gold standard method to assess the mind wandering state is experience sampling, which in turn depends on our capacity to introspect on our own experiences. Our capacity for meta-cognition is therefore a key element to the mind wandering state since it is how participants share their experiences with the experimenter. The experience of mind wandering seems to have a parallel in night dreaming. Both are forms of self-generated thought that require decoupling from the external environment; both depend on mental content that is self-generated based on prior experience. The two phenomena also seem to rely on overlapping brain areas and networks, so that it has been suggested that dreaming is "an intensified version of mind wandering" (K. C. R. Fox, Nijeboer, Solomonova, Domhoff, & Christoff, 2013). Indeed, the term daydreaming might hold more scientific truth than previously assumed. Meta-cognition and stimulus independent representations are both important in other aspects of research into conscious experience and these are summarized in Figure 3.1, illustrating the paradigms of resting-state fMRI, continuous flash suppression (CFS), and binocular rivalry (explained in Box 1).

3.3 Challenges of Exploring the Wandering Mind - Stimulus Independence

Although stimulus independence is a hallmark of consciousness, it is also at the center of key methodological challenges in studying this aspect of the human condition. Since what we are aware of, is not always the same as the stimulus environment in which an experience occurs, the degree of mapping between the input into the system and the emergence of conscious experience can vary significantly across different situations. This is exemplified by the thoughts that occur during mind wandering, in which external stimuli are only minimally integrated into the content of our thoughts. This independence between the stimulus environment and experience means that controlling or manipulating perception-action contingencies alone cannot isolate the neurocognitive basis of consciousness. This dissociation between input and experience is obvious in the case of the thoughts that arise during the mind wandering state. It is an explicit assumption of researchers that the mental

content that arises during the mind wandering state is intrinsically driven and that this limits the capacity of the experimenter to directly manipulate the state (Smallwood & Schooler, 2015). Researchers can exploit the stimulus-independent nature of the thoughts that occur during the mind wandering state to understand this feature of conscious experience. In a similar fashion, a number of paradigms have been developed in other fields, especially in visual awareness research, which aim to zone in on a neural correlate of consciousness (NCC) (Chalmers, 2000) by exploiting its stimulus-independent nature. In Box 1 we briefly describe some of these paradigms, but see Axelrod, Bar, & Rees, (2015) and Kim & Blake, (2005) for more extensive reviews of this area of investigation.

BOX 1 – The Stimulus-Independent Nature of Consciousness in Different Experimental Paradigms

To study consciousness, paradigms are needed that capture its stimulus-independent nature. In the last decade, different paradigms have been developed that explore changes in psychological or neurocognitive processing that are minimally caused by external events.

• **Mind wandering** studies explore how conscious attention can be devoted to representations that are independent of stimuli in the environment. Typical paradigms involve asking participants to perform tasks of varying levels of external demands and to use combinations of different types of experience sampling to assess the conditions under which conscious experience has ceased to focus on events in the environment and instead has become directed to mental content that has been self-generated by the participant. By understanding the psychological and neural features of the representations that are not directly caused by environmental stimulation, studies of the mind wandering state can reveal the neural processes that are associated with stimulus independent conscious states.

• **Resting-state**. Advances in cognitive neuroscience have allowed investigation of neurocognitive processes that take place during wakeful rest. Studies of resting-state assess neurocognitive function when participants have no explicit task to do. Collecting measures of neural function under conditions with no salient environmental input allows the assessment of how the brain organizes itself.

• **Masking paradigms** provide a simple environment in which to study access to stimulus independent aspects of conscious experience. In a typical study, a target stimulus is

briefly flashed for a few milliseconds, and is preceded and/or followed by another stimulus, known as a mask. By varying the presentation time of the target, mask, or the inter-stimulus interval between the two, it is possible to create conditions in which the participant's ability to report the identity of the stimulus is at chance level. As the physical, objective features (presentation time, size, contrast, etc.) of the stimulus presented are unchanged between unseen and seen trials, it is hypothesized that the differences between the two reflect the neurocognitive basis of conscious experience of perceptual information (Dehaene, 2011; Kouider & Dehaene, 2007).

• **Perceptual rivalry paradigms** allow processes involved in shifts in conscious access to be determined. One such paradigm is binocular rivalry in which participants are presented with one image to each eye. Instead of perceiving two superimposed images, subjects usually perceive the images to alternate every few seconds. As with masking paradigms, the physical properties of the two images remain unchanged so neurocognitive changes that are correlated with changes in perception may reflect processes that are important for shifts in the content of consciousness.

• **Continuous Flash Suppression** (CFS; Tsuchiya & Koch, 2005) is a particular paradigm combining aspects of binocular rivalry and masking paradigms, in which images flashed into one eye reliably suppress visual awareness of an image presented to the other eye. CFS has gained incredible traction in consciousness research because it seems to allow participants to be exposed to stimuli that do not reach consciousness for much longer durations than with classical masking or binocular rivalry paradigms, thus improving the exploration of unconscious processes.

3.4 Challenges of Studying the Wandering Mind - Introspection

The stimulus independent aspects of consciousness can be explored by exploiting the second aspect of the experience: the capacity for introspective access to the contents of awareness. The use of self-report to understand the nature of conscious experience has a long history in psychology. It is widely accepted that Wilhelm Wundt was one of the first scientist to adopt the introspective method, which he used to explore the relationship between task stimuli and an individual's subsequent experience, although he was careful to point out that the method should only be used under carefully controlled conditions (Costall, 2006; Danziger, 1980;

Schultz & Schultz, 2007). This method was expanded and applied to experimental psychology by, among others, Alfred Binet in France, and Oswald Külpe and Karl Marbe in Germany, and Edward Titchener, who pioneered the use of introspection to understand other mental processes such as memory, thinking or attention (Schultz & Schultz, 2007). The application of introspection in experimental psychology was then heavily criticized by the Behaviourist movement led by John Watson, which rejected it as a truly scientific methodology in favour of the study of behaviour. It was not until the 1950s with the rise of the Cognitive Revolution that introspection became a tenable scientific approach again with the development of a variety of methodologies, such as experience sampling (ES; Csíkszentmihályi & Larson, 1987; Larson & Csikszentmihalyi, 1983) and the think-aloud protocol (van Someren, Barnard, & Sandberg, 1994), in which participants are asked to verbalize their every thought as they perform a particular task. The resulting verbal protocols are then analyzed to provide insight into how cognitive processes are organized to perform a particular task.
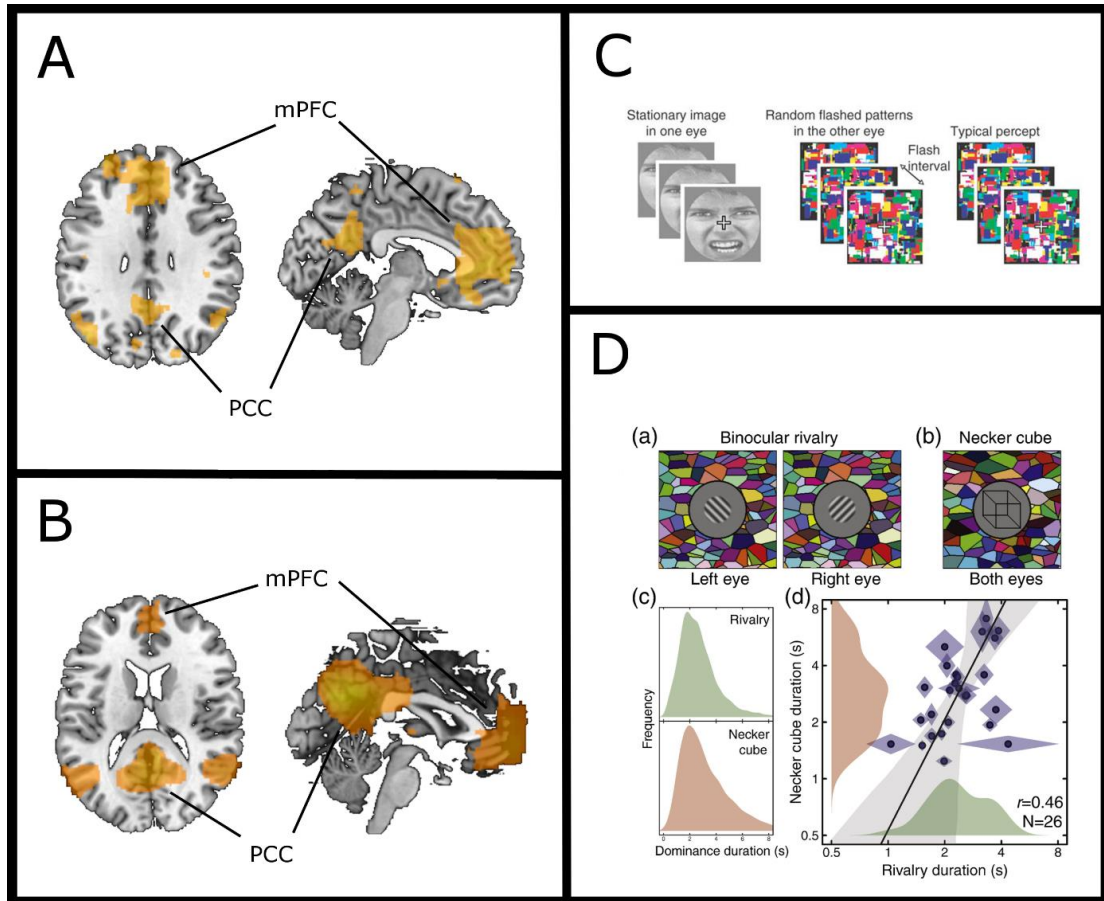
Figure 3.1 - The Stimulus-Independent Nature of Consciousness: A) Regions of the default mode network (DMN) activate during mind wandering. Data taken from (Allen et al., 2013). B) The same network shows co-ordinated activity during wakeful rest, in the absence of any particular task. Data taken from (Smith et al., 2009). C) In continuous flash suppression (CFS) paradigm (Tsuchiya & Koch, 2005) participants are consciously unaware of a stimulus presented to one eye as it becomes masked by another stimulus presented to the other eye. D) In binocular and perceptual rivalry paradigms (subpanels a) and b), respectively), what is consciously perceived changes even though the stimulus itself remains unchanged. The effects of the two paradigms correlate in individuals (subpanels c) and d)). Figure taken from (Baker, Karapanagiotidis, Coggan, Wailes-Newson, & Smallwood, 2015).

In mind wandering research introspection is especially important, as the experience is often entirely unrelated to events in the here and now or any particular task being performed. This independence of a participant's experience from any perception-action contingencies means that experience sampling is the only way to directly discern instances of spontaneous self-generated thought. The systematic investigation of the mind wandering state using the technique of experience sampling began in the 1960's with the pioneering work of Jerome Singer, John Antrobus and Eric Klinger and is still the gold standard in this field of research (Antrobus et al., 1966; Singer, 1966, 1993; Singer & McCraven, 1961). Experience sampling refers to the systematic collection of self-reports of a participant's ongoing experience

(Kahneman et al., 2004a; Smallwood & Schooler, 2015). Online probe-caught ES requires participants to answer random or quasi-random questions regarding their experience either in the lab or in daily life (Smallwood & Schooler, 2015). Retrospective ES involves the gathering of self-reports at the end of a task, either via questionnaires or open-ended questions. Descriptive Experience Sampling (DES; Hurlburt & Akhter, 2006) is a particular type of ES in which participants record their inner experiences throughout the day and then subsequently report them to the researcher in an expositional interview.

Although metacognition provides access to the stimulus independent features of conscious experience, it is not without limitations: for example, online ES is problematic because it disrupts the natural evolution of experience. By periodically interrupting participants during the course of a task, the natural dynamics of performance and of the phenomenon measured (in this case, mind wandering). Moreover, repeatedly probing participants about their experience is likely to alert them of the key dependent variable measured by the experiment and once more, to alter its natural occurrence (Seli, Carriere, et al., 2013). Some other fundamental issues of introspective evidence are its inherent subjectivity, confabulations, the interference between cognitive processes, and the privacy of mental content: unlike objective measures, such as response times, the veracity of subjective experiences cannot be (yet) verified with additional measures, as the participant is the only one to have direct access to his/her own mental content. It is also well known that in many cases people have little introspection access to a variety of cognitive processes; for example, participants can be unaware of the real reasons that influence a decision and at the same time confabulate that another reason is the cause (Johansson, Hall, Sikström, & Olsson, 2005; Nisbett & Wilson, 1977). Introspecting and reporting one's own mental content also involves performing two tasks at the same time. The act of introspection, therefore, might influence the mental content that is being experienced. This could either alter the likelihood that a particular form of experience will arise, or could change the qualities that the experience will have. Finally, there are cases in which participants might be unwilling to share certain private experiences, so that their reports could be systematically biased. Participants might purposely omit to report cultural/social taboo subjects, such as an embarrassing memory or a violent or erotic fantasy, and report a more "neutral" narrative.

Studies of mind wandering, therefore, highlight one of the fundamental paradoxes in studying conscious experience: without the capacity for metacognitive access to our experiences, studies of conscious experience would be almost impossible; however, our access to our own

experience means that the method of inquiry as part of an experiment may fundamentally alter the conscious experience itself. These issues between self-reports and the mind wandering state can be seen as arising from more general problems of a science of consciousness that relies simply on the introspective method.

3.5   Refining Methods of Measuring Mind Wandering

In the last decade, important strides in understanding conscious experience have been made through the refinement of the method through which self-reports are collected. In the domain of mind wandering one way that this has occurred is through the investigation of different types of mind wandering. Work on the functional outcomes of the mind wandering state has highlighted that it has both costs and benefits (Smallwood & Schooler, 2015): it affords creative and planning processes when external demands are low but can disrupt task performance when external task demands are elevated (McVay & Kane, 2012a; Mrazek et al., 2012; Stawarczyk, Majerus, Maj, et al., 2011). This is known as the context-regulation hypothesis (Smallwood & Andrews-Hanna, 2013). Other work has highlighted that the nature of the experience that emerges during mind wandering has implications for measures of well-being, with negative or past related experiences being linked to higher unhappiness (Poerio et al., 2013; Smallwood, Fitzgerald, et al., 2009; Smallwood & O'Connor, 2011). This is known as the content-regulation hypothesis (Smallwood & Andrews-Hanna, 2013).

One reason why this complex pattern of costs and benefits may arise is because there are several, different types of experience that emerge in the mind wandering state, each associated with unique functional outcomes, and initial ES methods were too crude to accurately differentiate between these distinctive states. For example, one fMRI investigation has directly tested the possibility that mind wandering depends on the interaction of two orthogonal dimensions, task-relatedness and stimulus-dependency, and has distinctive neural correlates when compared to external distractions or internal, task-related thoughts (Stawarczyk, Majerus, Maquet, et al., 2011). Other recent work has focused on patterns of co-variation between different aspects of the mind wandering state using the technique of Multidimensional Experience Sampling (MDES) (Gorgolewski et al., 2014; Ruby, Smallwood, Engen, et al., 2013; Ruby, Smallwood, Sackur, et al., 2013; Smallwood & Schooler, 2015): this refers to the investigation of mental content through questionnaires and/or thought probes acquiring a large amount of data with questions investigating different

aspects of experience, and then using dimension reduction techniques such as principal component analysis to reveal the dimensions that underlie these data. This methodology has shown to reliably reproduce certain dimensions of the content of mind wandering experience, for example patterns of temporal (future-past) thought (Gorgolewski et al., 2014; Ruby, Smallwood, Engen, et al., 2013; Ruby, Smallwood, Sackur, et al., 2013; Smallwood & Schooler, 2015). Using techniques that focus on co-variation between experiential features of the mind wandering state has made it possible to identify structural patterns in experience sampling reports. These are consistent across different samples of individuals and correspond in broad terms to patterns of thought (shown in Figure 3.2, sub-panel A). Importantly the different categories of thought explain unique variation associated functional outcomes: measures of emotional state, physiological arousal and ongoing task performance have all been shown to vary with differences in the content of experience that arises during the mind wandering state (Smallwood & Schooler, 2015).
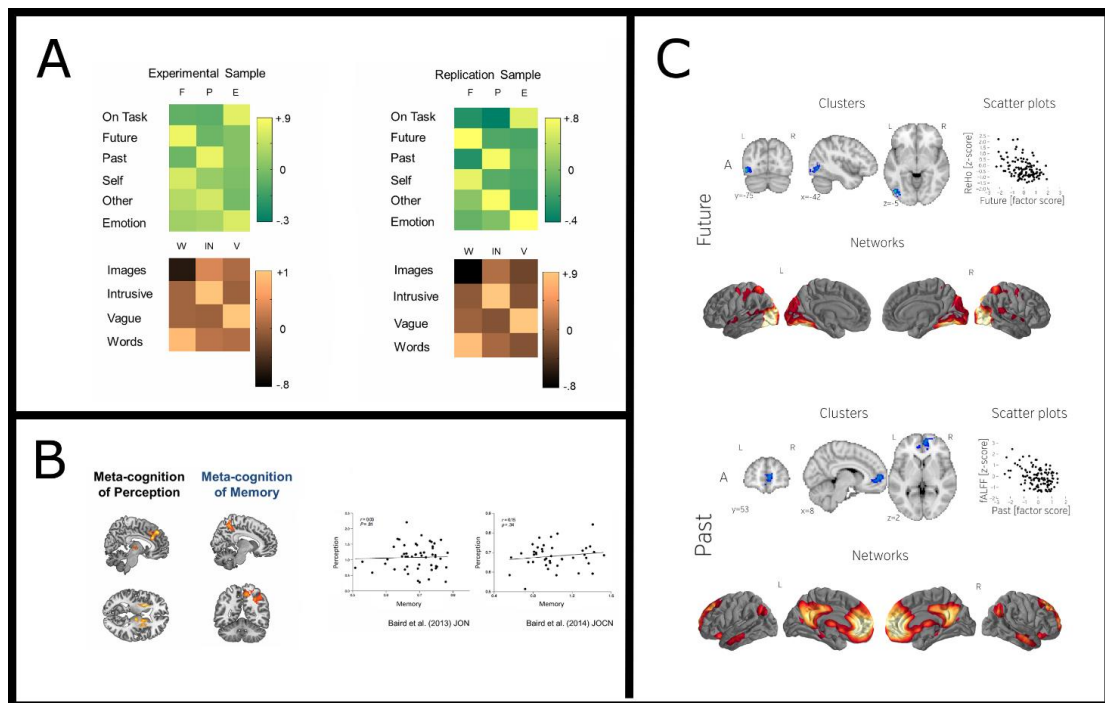
Figure 3.2 - Refining measures of introspection: A) Applying statistical methods such as principal component analysis to multidimensional experience sampling (MDES) data, shows that self-generated thought has a stable internal structure. Data taken from two different samples of healthy adults (n=87 & n= 64 respectively) see (Ruby, Smallwood, Engen, et al., 2013; Ruby, Smallwood, Sackur, et al., 2013) for details of the method. B) Metacognition for perception and memory depend on different neural substrates and are not correlated across individuals. Figure adapted from (Baird, Mrazek, Phillips, & Schooler, 2014; Baird, Smallwood, Gorgolewski, & Margulies, 2013). C) By combining MDES and neurocognitive measures, it is possible to investigate the neural substrates of different types of self-generated thought, such as future- and past-related thought. Figure adapted from (Gorgolewski et al., 2014).

One way that the utility of experience sampling could be improved is through an assessment of the accuracy of the reports. In this regard, important strides have been through the development of the meta-d' measure (Maniscalco & Lau, 2012), which objectively measures metacognitive sensitivity using signal detection theory (SDT). SDT was originally developed to measure stimulus discrimination accuracy independently of response bias (Macmillan & Creelman, 2005): in standard stimulus discrimination experiments, participants are involved in forced-choice tasks (known as the "type 1 task"), classifying a range of stimuli. On top of this, participants can be asked to classify their confidence level on the response they just made (type 2, or metacognitive task). SDT can be applied to both tasks to get a measure of participants' sensitivity in the stimulus discrimination (type I d-prime) or metacognitive task (type 2 d-prime): Maniscalco & Lau, (2012) extended this method by "characterizing the observed type 2 sensitivity as the value of d' that a metacognitively optimal observer would have required to produce the empirically observed type 2 data". In this sense, meta-d' is a measure of type 2 sensitivity expressed at the level of type 1 d', or in other words, a measure of the signal that is available to the subject to perform the type 2, metacognitive, task and is not influenced by either response bias or type 1 sensitivity.

The development of meta-d' has revolutionised the understanding of metacognition because through a process of triangulation with objective neurocognitive markers, it has revealed the complex and heterogeneous nature of the metacognitive state. Fleming and colleagues (Fleming & Dolan, 2014; Fleming, Huijgen, & Dolan, 2012; Fleming, Weil, Nagy, Dolan, & Rees, 2010) found evidence for a neural substrate of metacognitive ability for perceptual decision-making in a region of rostro-lateral prefrontal cortex. Building on these findings, it has been identified that metacognition for different aspects of experience depend on different neural substrates (see Figure 3.2, subpanel B, showing different neural substrates for meta-cognition of perception, and memory) (Baird, Mrazek, et al., 2014; Baird et al., 2013; McCurdy et al., 2013). Intriguingly, the integrity of key aspects of the default mode network (DMN, the medial pre-frontal cortex, precuneus and the inferior parietal lobule) determines an individual's metacognitive accuracy for information from memory (Baird et al., 2013), an observation that is important for understanding the role of the DMN in the mind wandering state (see Box 3: Open Questions).

3.6 Triangulation as a Method for Understanding Conscious Experience

Although it is possible to refine measures of ES, the inherent limitations of this approach mean that it will be necessary to develop measures that provide a proximal measure of conscious experience without requiring participants to actively report on the contents of their experience. Ultimately, it is only with this development that it is possible to address whether the act of introspection as part of the experimental procedure produces the effects that are measured by the paradigm. One way that this could be achieved is to explore the neural basis of the experiences that subjective reports are used to assess, the so-called neural correlate of consciousness. By pairing subjective reports with neurocognitive measures, it may be possible to develop techniques that infer inner mental states without relying on introspection.

The combination of objective and subjective information is referred to as the process of triangulation (Schooler & Schreiber, 2004; Smallwood & Schooler, 2015). Borrowing this term from the field of land surveying, triangulation refers to the pairing of subjective reports with behavioural and physiological measures, in order to minimize the weaknesses, and maximize the strengths of each type of measure. In mind-wandering research, triangulation can be achieved in different ways. For example, it is known that mind-wandering is more common in easy or practiced tasks (Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007; Teasdale et al., 1995) and behavioural performance is usually spared in these cases. This well documented situational modulation of the mind-wandering state allows researchers to explore objective neurocognitive measures in non-demanding conditions, or at rest, as a proximal measure of the mind-wandering state. In principle, these gross situational variations can be compared to online measures of ES to explore similarities in objective measures (such as the BOLD signal).

A second way to use triangulation in mind-wandering research is to exploit the capacity for these experiences to disrupt performance on a wide range of demanding tasks (Feng, D'Mello, & Graesser, 2013; Franklin et al., 2011; McVay & Kane, 2012a; Mrazek et al., 2012; Schooler, Reichle, & Halpern, 2004; Szpunar et al., 2013); even when performance is not completely disrupted, there is evidence that mind-wandering episodes alter behavioural performance in other ways, such as increasing response variability (Bixler & D'Mello, 2013; Seli, Cheyne, et al., 2013). Under demanding conditions, if a participant reports an episode of mind-wandering and her performance in that period was also impaired, this would provide supporting evidence that attention was decoupled from events in the here and now.

Reports of mind wandering episodes can be further corroborated by the use of different physiological or neurocognitive measures. Using fMRI, it is now well known that mind-wandering is linked to activity of the default mode network (DMN), a large scale network anchored by hubs on the anterior and posterior medial surface of the cortex (Allen et al., 2013; Andrews-Hanna, Reidler, Huang, et al., 2010; Konishi et al., 2015; Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007; McKiernan et al., 2006). Similarly, differences between periods of on task versus mind-wandering periods have been found using EEG (Baird, Smallwood, Lutz, & Schooler, 2014; Barron et al., 2011; Cunningham, Scerbo, & Freeman, 2000; Smallwood, Beach, et al., 2008), pupillometry (Franklin, Broadway, et al., 2013; Smallwood, Brown, Baird, Mrazek, et al., 2012; Smallwood, Brown, et al., 2011) and eye movements or blinks (Bixler & D'Mello, 2014; Reichle et al., 2010; Smilek et al., 2010). Following our example, if a participant's report of a mind-wandering episode in an MRI scanner was accompanied by poor task performance, heightened baseline pupil dilation and concurrent activation of the default mode network, this triangulation of physiology, behaviour, experience and neural processing would provide converging evidence that attention was decoupled from the events in the here and now. Figure 3.3 illustrates four examples on how different methods of ES, such as online probes vs. retrospective questionnaires, can be paired with different neurocognitive measures, such as Electroencephalography (EEG) and Pupillometry.

The process of triangulation is important in other paradigms that explore conscious awareness, as for example with the combination of the binocular rivalry paradigm with pupillometry and optokinetic nystagmus (OKN) measures in a study by Frässle and colleagues (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014). Using this technique, they showed that the OKN and pupil diameter were reliably tracking rival alternating percepts, as measured by participants' reports. Furthermore, they showed that the act of reporting modulated both the speed of rival percepts alternation and the activation of frontal brain areas, which could be dissociated by pure rivalry alternations and seemed to reflect only the act of introspection and reporting. Their conclusions focus on three key points: 1) they could track a subjective experience (the alternation of rival percepts) using only objective measures (OKN and pupillometry), 2) the act of reporting changed the experience itself, by accelerating the alternation of percepts, and 3) much of the frontal brain activation present in fMRI binocular rivalry studies could be explained simply by self-monitoring and the act of reporting, and not the phenomenon itself.
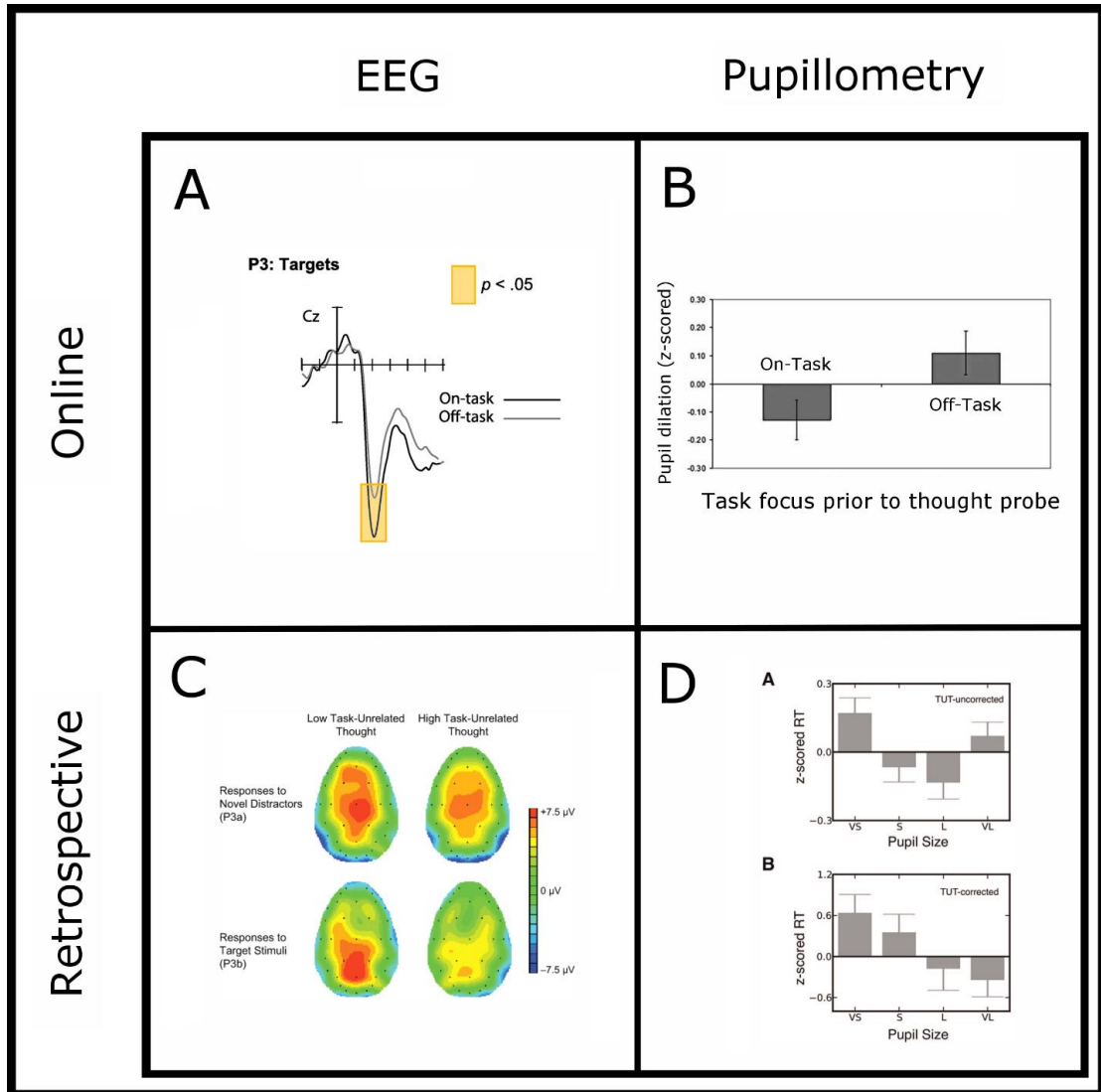
Figure 3.3 - Experience Sampling (ES) and Neurocognitive Measures: A) The amplitude of a positive event-related potential, the P3, as measured through EEG, is reduced during periods of off-task thought compared to on-task, as measured through online ES. Figure adapted from (Kam et al., 2010). B) Online ES can also be paired with pupillometry, showing larger pupil dilation in period of off-task thought compared to on-task. Figure adapted from (Franklin, Broadway, et al., 2013). C) Retrospective ES shows reduced evoked responses to target stimuli during off-task thought. Figure adapted from (Barron et al., 2011). D) Pairing of retrospective ES and pupillometry, showing a relation between mind-wandering, reaction times and pupil dilation. Figure taken from (Smallwood, Brown, Baird, Mrazek, et al., 2012).

The discussion on the advantages and disadvantages of using participants' reports in consciousness research has received a lot of attention in the last few decades (Tsuchiya, Frässle, Wilke, & Lamme, 2016), and while the development of an objective marker of conscious experience is necessary to advance the field, subjective reports remain the gold standard for accessing participants' inner experiences. Moving towards a covert marker of the

mind-wandering state requires that research focus on how accurately people can introspect on the contents of their experience. It is possible that incorporating techniques of hypnosis could help in maximizing participants' differences between their external vs. internal awareness, and shed light on the role of meta-awareness in self-generated thought, as was shown in a recent study (Demertzi, Vanhaudenhuyse, Noirhomme, Faymonville, & Laureys, 2014). Nevertheless, another recent study (Seli et al., 2015) suggests that participants have reasonable metacognitive access to their experience; the combination of this method with behavioral measures linked to the mind-wandering state can help to define an objective marker of conscious experience in the near future, in a way similar to Frässle and colleagues' study.

3.7 The Mind-Wandering State as a Paradigm for Assessing Conscious Experience

It is clear that canonical features of conscious experience (stimulus independency and metacognitive access) that are the core of its value as a topic of investigation are also central to the empirical challenges that it poses as an experimental phenomenon. It is equally apparent that the mind-wandering state embodies both features of conscious experience in a manner that can be readily accessed in the real world as well as under controlled laboratory conditions. This combination of the applicability of the mind-wandering state to consciousness research with the empirical tractability of its investigation means that it provides a powerful paradigm to understand the conscious state (Box 2).

BOX 2 – Capturing the wandering mind

The mind-wandering state is a common example of a conscious state that involves both stimulus-independence and metacognition that is common in daily life. There are at least three ways that mind-wandering can provide a useful paradigm to understand key aspects of conscious experience.

•   **Comparison of situational modulation and transient occurrence.** The thoughts and feelings that emerge in the mind wandering state are transient changes motivated by intrinsic processes and this spontaneous feature of the experience makes it hard to understand. Studies, however, have shown that the occurrence of unrelated thoughts wanes as the

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complexity of an external task increases (context-regulation hypothesis). The situational modulation of the mind-wandering state allows the researcher to exert indirect control over the occurrence of the mind-wandering state and so develop more causal accounts of the experience.

•   **Combining online and retrospective experience sampling**. Online and retrospective measures of ES both provide ways to access subjective aspects of experience; however, they both have different weaknesses. Online ES is disruptive of the natural dynamics of a task, whereas Retrospective ES is limited in temporal specificity since it relies on a person's memory. Complementary experimental findings from different ES techniques, however, cannot be the result of limitations in either approach and so provide a less biased method of exploring the mind-wandering state.

•   **Combination of objective and subjective markers.** Subjective measures of experience remain the gold standard measure of the mind-wandering state, however, in isolation these cannot be verified. Studies have shown that the mind-wandering state has objective behavioural and neural correlates (Smallwood, Brown, Baird, Mrazek, et al., 2012). Common neural markers associated with both experiential measures of mind-wandering and its associated behavioural consequences, allow researchers to identify verifiable accounts of this aspect of conscious experience.

We have developed a paradigm that takes advantage of how the mind-wandering state can be assessed in the laboratory (Konishi et al., 2015). In a recent version of this paradigm (illustrated in Figure 3.4) participants alternate between task blocks that require constant external attention (1-back) and blocks that only require rare, highlighted moments of external attention in order to be performed successfully (0-back). This manipulation allows the occurrence of mind-wandering to be manipulated indirectly. Performance failure on the 1-back condition reflects periods when explicit maintenance of the task fails allowing for objective indicators that attention is decoupled form the tasks. The task can be combined with different measures of neurocognitive functioning (such as functional magnetic resonance imaging, pupillometry) allowing objective information to be gained on the status of ongoing cognitive processing. Finally, in this paradigm experience can be measured using both online and retrospective ES. In combination with objective indicators this would allow the

identification of covert markers of the mind-wandering state that could not be determined by the act of introspection.

BOX 3 – Open Questions

Although recent work has identified important aspects of how the mind-wandering state can inform our understanding of conscious experience, there are several important questions that remain unanswered:

•   **What is the link between metacognition and mind-wandering?** A number of studies (K. C. R. Fox & Christoff, 2014; Schooler, 2002; Schooler et al., 2011; Seli et al., 2015) have shown that metacognitive awareness is implicated in the regulation of mind wandering and also in the capacity to report it effectively. It is also possible that the capacity to engage in self-generated thought in the first place is a metacognitive process. Experiencing thoughts about the future, for example, depends upon being aware of representations generated from stored knowledge and studies have shown that a similar network is implicated in this process as is involved in the effective meta cognition of information from memory (Baird, Mrazek, et al., 2014; Baird et al., 2013). This evidence suggests that the process of conscious attention to thoughts and feelings during the mind-wandering state may be inherently metacognitive in nature.

•   **Neural substrates of stimulus independent aspects of consciousness.** Is there a general neural substrate of stimulus-independency regardless of the content? The neural substrates for metacognition seem to be domain specific [58, 59]. Studies of brain organisation at rest suggest that most neural systems exhibit structured activity in the absence of an external task. These two lines of evidence suggest that stimulus independency may be a mode of cortical function rather than a property of a specific neural system.

•   **The functions of stimulus independent cognition**. Initial work exploring mind-wandering focused on its negative role in on-going tasks such as reading (Franklin et al., 2011; Reichle et al., 2010; Schooler et al., 2004). More recent work has demonstrated that there are beneficial aspects of the experience such as creativity and planning. Understanding the functional benefits that emerge from the mind-wandering state will be important in identifying the value that the stimulus independent aspect of conscious experience brings to the organism.
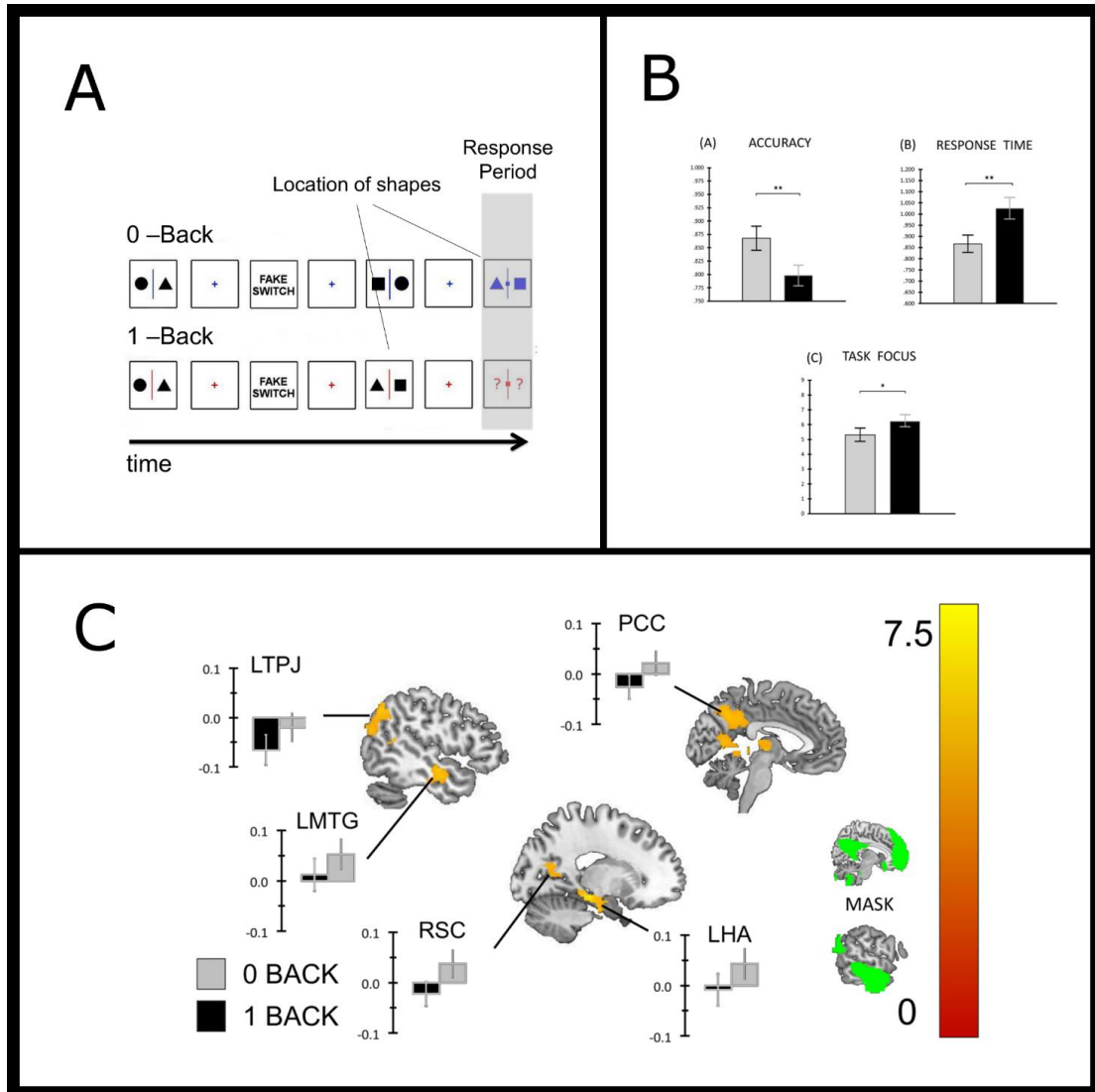
Figure 3.4 – Mind-Wandering Paradigm, Behavioral and fMRI Results: A) Participants alternate between a 0-back task, which allows and induces mind-wandering, and a 1-back task, which requires constant on-task focus. B) Participants performing the easier, 0-back task, have higher accuracy, lower RTs, and are less on task, as measured through online thought-probes. C) Key areas of the default mode network are active during periods of 0-back task. Figure taken from (Konishi et al., 2015).

3.8 Conclusions

The experiences that emerge in the mind-wandering state illustrate that the contents of conscious experience can be dissociated from the environment within which it is embedded (stimulus independence) as well as underlining that we have introspective access to this aspect of experience (metacognition). Since it can be studied easily in the laboratory and in daily life, the mind-wandering state provides a paradigm in which consciousness can be understood in

an ecologically valid manner. Advances in experience sampling techniques have confirmed the heterogeneity of the mind-wandering state in terms of its functional outcomes while advances in neuroimaging have revealed the underlying mechanisms that support these aspects of experience. Importantly, the technique of triangulating between experiential and neurocognitive measures holds the promise of identifying covert markers that describe the contents of consciousness without relying solely on the introspective process. Building on these advances, the continuing development of our understanding of the mind-wandering state will illuminate how we escape the constraints of our immediate environment, and will help understand the functional role that conscious experience plays in our lives.

Chapter 4. The Default Mode Network Supports Cognition that Is Independent of Immediate Perceptual Input

The following chapter has been adapted from:

4.1 Abstract

Although many different accounts of the functions of the default mode network (DMN) have been proposed, few can adequately account for the spectrum of different cognitive functions that utilize this network. The current study used functional magnetic resonance imaging (fMRI) to explore the hypothesis that the role of the DMN in higher order cognition is to allow cognition to be shaped by information from stored representations rather than information in the immediate environment. Using a novel task paradigm, we observed increased BOLD activity in regions of the medial prefrontal cortex and posterior cingulate cortex when individuals made decisions on the previous location of shapes (1-back), and decreased BOLD activity when individuals made decisions on the current location of shapes (0-back). These data are inconsistent with views of the DMN as a task-negative system or one that is sensitive only to stimuli with strong personal or emotional ties. Instead the involvement of the DMN when people make decisions about where a shape was, rather than where it is now, supports the hypothesis that the core hubs of the DMN allow cognition to be guided by information other than the immediate perceptual input. We propose that a variety of different forms of higher order thought (such as imagining the future or considering the perspective of another person) engage the DMN because these more complex introspective forms of higher order thought all depend on the capacity for cognition to be shaped by representations that are not present in the external environment.

4.2 Introduction

Understanding the function of the default mode network (DMN) has become an important question in cognitive neuroscience (Buckner et al., 2008). This core brain network, focused on hubs in both the medial prefrontal cortex (mPFC) and the posterior cingulate cortex (PCC), was initially identified via meta-analysis because of its tendency to deactivate during tasks that demand external focus (Raichle et al., 2001). Since then functional magnetic resonance imaging (fMRI) has shown that these regions show patterns of temporally correlated activity during the resting state (Greicius, Krasnow, Reiss, & Menon, 2003) and comparative studies have identified an analogue of the DMN in many species including rats (Lu et al., 2012), chimpanzees (Barks, Parr, & Rilling, 2013) and macaques (Mantini et al., 2011). Developmental studies have shown this network matures relatively late in life in humans (Fair et al., 2008) and degeneration within key structures of the DMN occurs with age and is particularly prevalent in dementias such as Alzheimer's Disease (Jones et al., 2011; Mevel et al., 2011).

Such evidence indicates that the DMN plays an important functional role in cognition (Buckner et al., 2008). Task based studies suggest the DMN is involved in a wide variety of cognitive functions including semantic processing (Binder & Desai, 2011), thinking about oneself (Kelley et al., 2002), imagining one's future (Gaesser, Spreng, Mclelland, Addis, & Schacter, 2013; Schacter et al., 2012; Schacter & Addis, 2007a, 2007b), encoding and retrieving episodic memories (Huijbers et al., 2013), retrieving autobiographical memories (H. Kim, 2010; Philippi, Tranel, Duff, & Rudrauf, 2014), considering the world from the perspective of another person (Mitchell, Banaji, & Macrae, 2005; Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008) and thinking creatively about a problem (Ellamil, Dobson, Beeman, & Christoff, 2012; Kuehn et al., 2014; Takeuchi et al., 2011) (for quantitative meta analyses see Andrews-Hanna, Smallwood, & Spreng, 2014; Spreng & Grady, 2009; Spreng & Mar, 2012; Spreng, Mar, & Kim, 2009).

The large number of functions utilizing the DMN has generated several hypotheses of this networks function. For example, the association between DMN and states of personally relevant processing has led to the suggestion that it supports information important for the

autobiographical (Qin & Northoff, 2011) or social aspects of the self (Schilbach et al., 2008). The DMN has also been identified as important in task-irrelevant states such as mind wandering or daydreaming (Allen et al., 2013; Christoff et al., 2009; K. C. R. Fox et al., 2015; Mason, Norton, Van Horn, Wegner, Grafton, Macrae, et al., 2007; McKiernan et al., 2006; Stawarczyk & D'Argembeau, 2015; Stawarczyk, Majerus, Maquet, et al., 2011) and has been shown to lead to errors on tasks demanding external perception (Eichele et al., 2008). This latter point, coupled with the DMNs tendency to deactivate when performing such tasks (Raichle et al., 2001), has led some authors to describe it as a task negative network (Bentley, Li, Snyder, Raichle, & Snyder, 2014; Fox et al., 2005; Landsiedel & Gilbert, 2014) (although see Spreng, 2012). Although the interpretations of the DMN as reflecting aspects of the self or as a task-negative system capture isolated aspects of the literature, they fail to provide an overarching account of the functions that this network performs. What is common, for example, to imaging the future or adopting another's perspective and to deactivations during demanding perceptual tasks?

One possibility is that the DMN allows cognition to process representations that are not presently available to the senses, an account we will refer to as the *mnemonic facilitation hypothesis*. Two recent studies support this basic premise. Smallwood and colleagues (Smallwood, Tipper, et al., 2013) used a paradigm in which individuals made decisions using information from past trials or from information available on that particular trial. They found that under conditions when individuals were asked to recollect details of the parity of numerical stimuli, regions of the medial pre-frontal cortex and the posterior cingulate cortex exhibited greater activity when this judgement was made rapidly rather than when it was made slowly. The opposite pattern was observed when decisions were made when the stimulus was available to perception. More recently, Spreng and colleagues (Spreng et al., 2014) explored the neural recruitment that occurs when participants perform a working memory task containing famous and non-famous faces. They found that the core aspects of the DMN show enhanced activity in a two-back task when the target to be retrieved was a famous face, thus involving a combination of working memory and episodic memory. Together these two studies suggest that the role of the DMN in cognition is neither task-negative nor related to personally significant information but may reflect a system that supports a wide range of psychological states that depend on representations that are not available to the senses.

If a primary function of the DMN was to allow representations unrelated to perceptual input to guide thought and behaviour this could also explain why it is implicated in states of imagination that rely on memorial input for their content (such as thinking about the past or the future). Guiding thoughts and actions based on memory is also unnecessary for tasks that rely on a continuous focus on perception, explaining why the DMN often deactivates in tasks as the Eriksen Flanker task or Go–No Go tasks and why, under these conditions, its activity can be a cause of error (Buckner et al., 2008; Christoff et al., 2009; Eichele et al., 2008; Li, Yan, Bergquist, & Sinha, 2007). The *mnemonic facilitation hypothesis* can also explain why aspects of the DMN are involved in semantic associative processes that depend on representations gained through experience (Binder & Desai, 2011) and why it exhibits activation when working memory targets are also encoded in long term memory (such as when they are a famous face; Spreng et al., 2014) . Importantly, it also explains the encoding-retrieval flip phenomenon where the DMN deactivates during encoding and activates during retrieval (Huijbers et al., 2013). Relative to both the task-negative and autobiographical/social hypothesis, the *mnemonic facilitation hypothesis* leads to a simple prediction: *regions of the DMN should be more engaged when a decision is made based on information represented in memory rather than immediate perceptual input*.

4.3   Current Study

We developed a paradigm to test of our account of DMN function that builds on both our prior work and that of Spreng and colleagues. Participants alternate between task blocks in which they either make decisions about the location of shapes as they are presented on screen (0-back) or with respect to their location on the prior trial (1-back, see Figure 4.1). Engaging working memory reduces the occurrence of task unrelated thought (Mason, Norton, Van Horn, Wegner, Grafton, Macrae, et al., 2007; Smallwood, Nind, et al., 2009; Smallwood, Ruby, et al., 2013; Teasdale et al., 1995). Based on prior studies, therefore, we expected to replicate an increase in off task thoughts in the 0-back task and to find greater sustained activity in the DMN during this period because of its documented role in cognition that is generated by the individual (Allen et al., 2013; Christoff et al., 2009; Mason, Norton, Van Horn, Wegner, Grafton, Macrae, et al., 2007; McKiernan et al., 2006; Stawarczyk, Majerus, Maquet, et al., 2011).
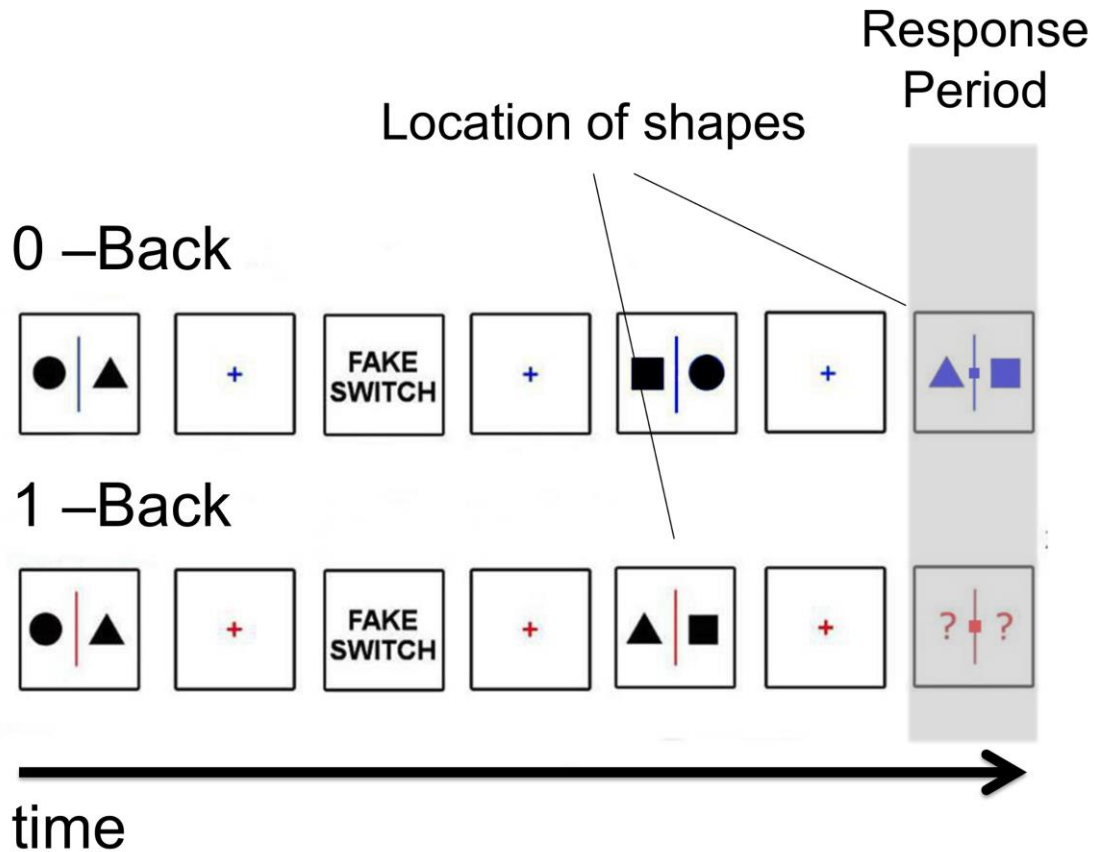
Figure 4.1 – Experimental Paradigm: Participants alternated between two tasks. One task involved observing non-coloured shapes presented at fixation waiting for the presentation of a coloured slide at which point they would indicate using a button press which side of the fixation cross a target shape was (0-back). In the other task participants had to encode the identity of shapes presented on screen and when prompted by a coloured slide to respond based on the position of a specific target shape on the prior trial (1-back). This paradigm requires participants to indicate the location of the same stimulus (for example the position of a square) which depends on whether the stimulus is immediately present or absent at the point at which the decision is made.

Critical to the current investigation, however, is whether the DMN allows operations to be performed on previously acquired representations rather than that which is available to the senses. If it does, it should exhibit greater activity when decisions are made on the position of the shapes in the 1-back task relative to the 0-back task. Importantly because the judgment is regarding the spatial location of triangles, circles or squares, activation of the DMN under these conditions could not be attributed to the personal or emotional significance of the stimulus. Moreover, because the 1-back task is more demanding than the 0-back task, greater DMN activity in this context could not be accounted for by the task-negative hypothesis. Finally, because we manipulate whether the same stimulus is available to perception or not, we can rule out differences in the role of long-term memory (such as familiarity with a

famous face). To understand these questions, we conducted a behavioural experiment to confirm that our modulation of working memory reduced off task thought and an fMRI experiment to explore the mnemonic facilitation hypothesis of DMN function.

4.4 Methods

4.4.1 Participants

4.4.1.1 Behavioral

Twenty-nine healthy participants (9 males, age = 21.7±2 years) completed the behavioural study. Participants were recruited using the Psychology Electronic Experiment Booking System (PEEBS) of the University of York.

4.4.1.2 Task-based fMRI

Twenty healthy, right-handed participants (9 males, age = 23.8±3 years) completed the fMRI study. Participants were recruited using both PEEBS and the York Neuroimaging Center (YNiC) participants' pool.

Both studies were approved by the Ethics Committee of the Psychology Department of the University of York. All investigation was conducted according to the principles expressed in the Declaration of Helsinki and for both studies participants provided written informed consent.

4.4.2 Task Paradigm

4.4.2.1 Behavioural

The task used in this experiment was programmed using PsychoPy (Peirce, 2007). The task featured a 0-back and a 1-back condition that continuously switched from one another throughout the experimental session (see Figure 4.1). Our paradigm is broadly similar to the paradigm used by Smallwood and colleagues (Smallwood, Tipper, et al., 2013) and was modified with the specific aim of maximising the differences between the 0-back and the 1-back conditions. In both conditions participants saw different pairs of shapes (Non-Targets, NT) appearing on the screen divided by a vertical line; the pairs could be: a circle and a

square, a circle and a triangle, or a square and a triangle for a total of 6 possible pairs (two different left/right configurations for each). The pairs never had shapes of the same kind (e.g. a square and a square). In both tasks, a block of NT was followed by target requiring participants to make a manual response. The target was a small stimulus presented in either blue or red and the colour was counterbalanced across participants. In the 0-back condition the target was flanked by one of two shapes and participants had to indicate by pressing the appropriate button which shape matched the target shape. In the 1-back condition, the target was flanked by two question marks and participants had to respond depending on which side the target shape was on the prior trial. For the behavioural study responses were made using the left and right arrow keys, for the neuroimaging study responses were made using a button box. Importantly, unlike the paradigm employed by Smallwood and colleagues (Smallwood, Tipper, et al., 2013) this design ensures that the participants cannot know what response to make when presented with the to be encoded stimulus.

Each block lasted between 40 to 120 seconds before switching to the other condition; the change of condition was signalled by a message ("SWITCH") that remained on screen for 5 seconds. On each trial the number of NTs preceding the Targets varied between 2 and 6, the number of trials per block varied between 2 and 5 and the total number of blocks was 8 for each condition. The order of conditions was counterbalanced across participants and the whole task lasted ~35 minutes. The total number of targets was 15 to 20 per condition (0-back and 1-back). Also, in every block the word "STAY" was presented at the end of a trial indicating that participants were to remain in that condition. In order to sample the participants' ongoing experiences we used a probe-caught, experience sampling method (Kahneman, Krueger, Schkade, Schwarz, & Stone, 2004b; Smallwood & Schooler, 2006).The task was built so that there was a 50% chance of a thought probe being presented in place of a Target in a condition block and a maximum of one probe per condition block was allowed. The thought probe consisted in a screen prompting the participants to rate their focus level ("Where you focused on the task or were you thinking about something else?") on a scale from 0 (completely off task) to 9 (completely on task).

Presentation rate of the stimuli was jittered in the following way. Fixation crosses ranged from 2–4 seconds in steps of 0.1s, Non-targets were varied from 1–3 seconds in steps of 0.1s. Targets always lasted a maximum of 4 seconds and a response from participants immediately ended the target presentation.

4.4.2.2   Task-based fMRI data acquisition

The paradigm used for the fMRI study was essentially the same with the following changes: there were no thought probes presented, fixation crosses were jittered between 2–3 seconds in steps of 0.1s, non-targets were jittered between 1–2 seconds in steps of 0.1s, targets stayed on the screen for 2.5 seconds regardless of a response being made by participants, switches and stay screens lasted 4 seconds, responses were made using an MRI compatible button box. The total number of blocks was 6 per condition in each run and the total number of targets was 8 to 12 per condition (0-back and 1-back) in each run, making it 12 blocks and 16 to 24 targets per condition in total.

Imaging was performed at the York Neuroimaging Centre (YNiC) using a GE 3.0 Tesla HDx Excite MRI scanner using an 8-channel head coil. Functional data were acquired using a T2*-weighted gradient echo planar imaging sequence with the following parameters: 32 interleaved axial slices, repetition time = 2000ms, echo time = 30ms, flip angle = 90°, slice thickness = 3mm, field of view = 192x192, matrix 64x64). The first 10 time points were removed to allow magnetization equilibrium. T1-weighted scans were acquired to confirm no participants had brain abnormalities and for normalization with the following parameters: repetition time = 7.8ms, echo time = 3ms, flip angle = 20°, slice thickness = 1.13 x 1.13 x 1.0 mm, field of view = 290 x 290 x 176, matrix = 256 x 256 x 176. The scanning session involved a 7 minute resting state scan (eyes open, fixating on a black cross on grey background) followed by two task runs each lasting approximately 15 minutes. Between the two sessions participants were given a short break. Finally, we recorded a 7 minute structural scan.

4.4.3   Pre-processing

4.4.3.1   Task-based fMRI

Pre-processing of the task based fMRI data was performed using Statistical Parametric Mapping (SPM8; Penny, Friston, Ashburner, Kiebel, & Nichols, 2011; available at: http://www.fil.ion.ucl.ac.uk/spm/software/spm8) implemented in Matlab R 2013a (The Mathworks Inc.; available at: http://www.mathworks.com). Data underwent the following processing steps: (1) slice-time correction, (2) motion correction, (3) co-registration of the T1-weighted image to the mean EPI scans, (4) normalized to MNI space using the T1-weighted normalization parameters computed during unified segmentation, (5) resampled to 2mm isotropic voxels, and (6) smoothed using a 6mm FWHM Gaussian kernel.

4.4.3.2   Resting state fMRI

Pre-processing of the resting state data used the DPARSF v2.3 toolbox (Chao-Gan & Yu-Feng, 2010) implemented in Matlab R 2013a. Data underwent the following processing steps: (1) slice-time correction, (2) motion correction, (3) co-registered the T1-weighted image to the mean functional image, (4) normalized to MNI space using the T1-weighted normalization parameters computed during New Segment and DARTEL, (5) resampled to 2mm isotropic voxels, and (6) smoothed using a 6mm FWHM Gaussian kernel, (7) nuisance regression using the six movement parameters, the signal from the the white matter and the signal from the CSF, and (8) band-pass filtered .008 to .01Hz.

4.4.4   First Level Analysis

4.4.4.1   Task-based fMRI

To analyse our mixed block-event related design (see Figure 4.2) (Fair et al., 2007; Petersen & Dubis, 2012), we employed a GLM to model each event type. The transient events in each task (targets, switches and stays) were modelled as single events with the relevant duration in seconds (2, 4 and 4 respectively). The sustained activity in each task was modelled by creating a block that began at the first NT in each block and lasted until the participant switched to the other task. Each of these events was convolved with the canonical hemodynamic response function as implemented in SPM 8. The GLMs included a constant term per run, a high frequency signal filtering (cut off = 128 s), an AR(1) filter and the motion parameters. For each individual we computed two contrast images: (1) 1-back greater than 0-back sustained responses and (2) 1-back greater than 0-back target transient responses.
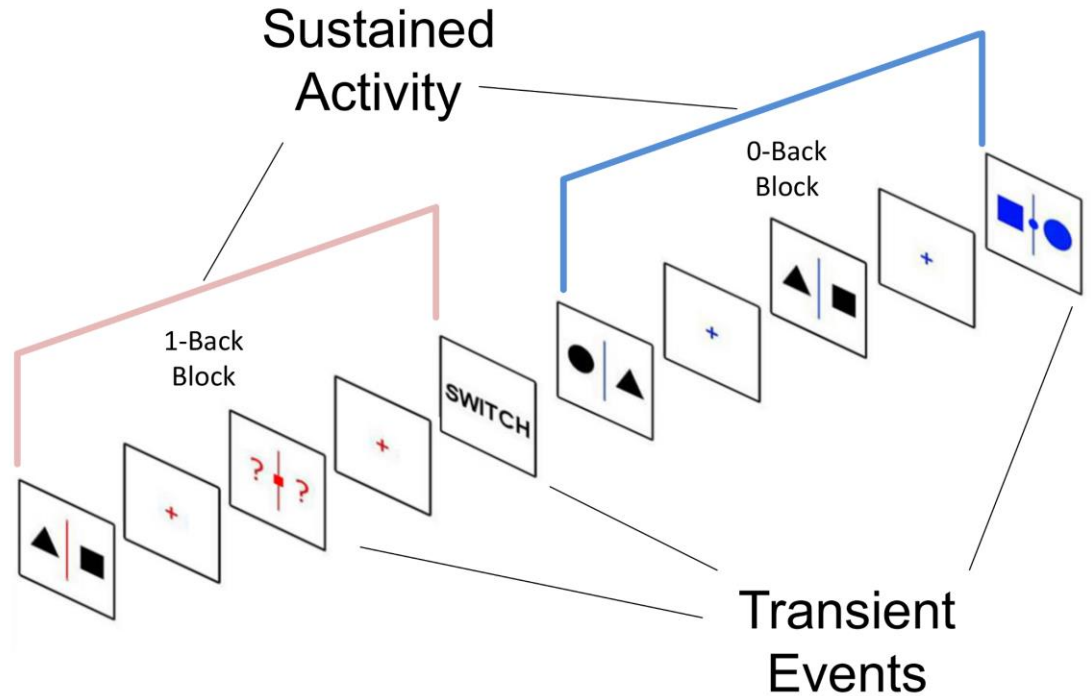
Figure 4.2 – Analytic strategy: The task-based data was analysed using a mixed block / event design. We modelled transient events in both tasks as single event with a length equivalent to the stimulus duration. To model the sustained changes that occur during each task block we created a box-car that began at the beginning of the task block and lasted until the participant received the instruction to switch to the other task.

4.4.4.2   Resting state fMRI

To provide a quantitative description of the spatial extent of the DMN we calculated the functional connectivity of the PCC region using the resting state scans acquired as part of this study. We calculated the time series of two 6mm diameter spheres centred on the co-ordinates of the PCC [–8, –52, 26] in each hemisphere reported by Andrews-Hanna et al. (Andrews-Hanna, Reidler, Sepulcre, et al., 2010) and used these as regressors in a standard functional connectivity analysis implemented using the DPARSF toolbox for SPM. Correlation coefficients were then transformed to Z-scores using Fisher's r-to-Z transformation for group level analyses.

4.4.5   Group Level Analysis

4.4.5.1   Task-based fMRI

One-sample t-tests were used to evaluate the differences in 1-back and 0-back BOLD responses for transient and sustained events separately. Results were masked with the grey

matter mask provided by DPARSF. We used a voxel wise threshold of $p < 0.01$ and topological False Discovery Rate with a p-value of $p < 0.05$ as implemented in SPM to control for multiple comparisons.

4.4.5.2 <u>Resting state fMRI</u>

A one-sample t-test was used to determine the extent of the DMN. The subsequent images were thresholded with a T of 7 and binarised. This was used as a mask for analysis of the task based data.

4.4.5.3 <u>Conjunction analysis</u>

One-sample t-tests were used for the transient and sustained events on the 1-back and 0-back conditions using a cluster-forming threshold of $p < 0.05$. We then calculated the overlap between the resulting maps and masked them with the DMN mask obtained from the resting-state analysis.

4.5 Results

4.5.1 Behavioural

We analysed accuracy and response time data for both the behavioural and neuroimaging samples using paired sample t-tests. These demonstrated that participants were both slower and less accurate in the 1-back than in the 0-back task in both experiments (behavioural RTs: $t (25) = 3.75$, $p < 0.001$; behavioural accuracy: $t (25) = -4.92$, $p < 0.001$; fMRI RTs: $t (19) = 6.70$, $p < 0.001$; fMRI accuracy: $t (19) = 2.38$, $p = 0.03$; see Figure 4.3 A and Figure 4.3 B). In addition analysis of the experience sampling reports collected in the behavioural study indicated that participants rated their experience as reflecting greater off task thought in the 0-back than the 1-back task ($t (25) = 2.45$, $p = 0.02$; Figure 4.3 C).
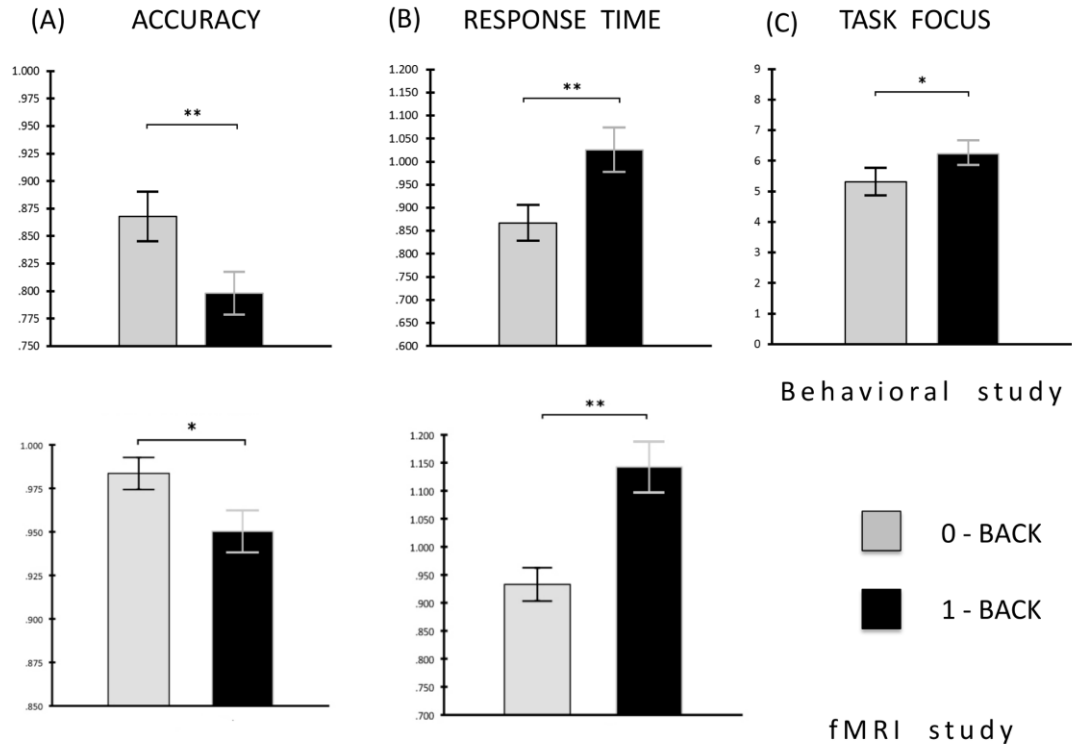
Figure 4.3 - Behavioral results: Analysis of the behavioural data collected during both the behavioural (top three graphs) and fMRI (bottom two graphs) experiment indicated that participants were both faster (shown in ms) and more accurate when they were asked to make decisions about the location of a shape based on the present trial relative to where it was on the previous trial. In addition, analysis of the experience sampling data recorded in the behavioural experiment (top right graph), demonstrated that participants engaged in more off task thought during the 0-back than the 1-back task: participants rated their task focus on a scale from 0 (completely off task) to 9 (completely on task). The mean of participants' responses to the probes in each condition is shown. ** $p < 0.001$, * $p < 0.05$.

4.5.2 Functional Magnetic Resonance Imaging (fMRI)

4.5.2.1 Whole brain analysis–Transient activity

We identified a large set of regions that were significantly more activated for correct responses to the targets in the 1-back task than the 0-back task (see Table 4.1 and Figure 4.4). These included regions traditionally associated with working memory including the anterior cingulate cortex, the anterior insula (bilaterally), inferior parietal sulcus (IPS) and regions of the lateral pre-frontal cortex (bilaterally). To ascertain whether this pattern of activity is consistently observed in working memory tasks we explored the overlap between our findings and those observed in a meta-analysis of studies involving the term working memory using Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). We saw overlaps in

regions of mid cingulate cortex as well as dorsal regions of lateral pre-frontal and parietal cortex. This information is presented as a sub panel in Figure 4.4.
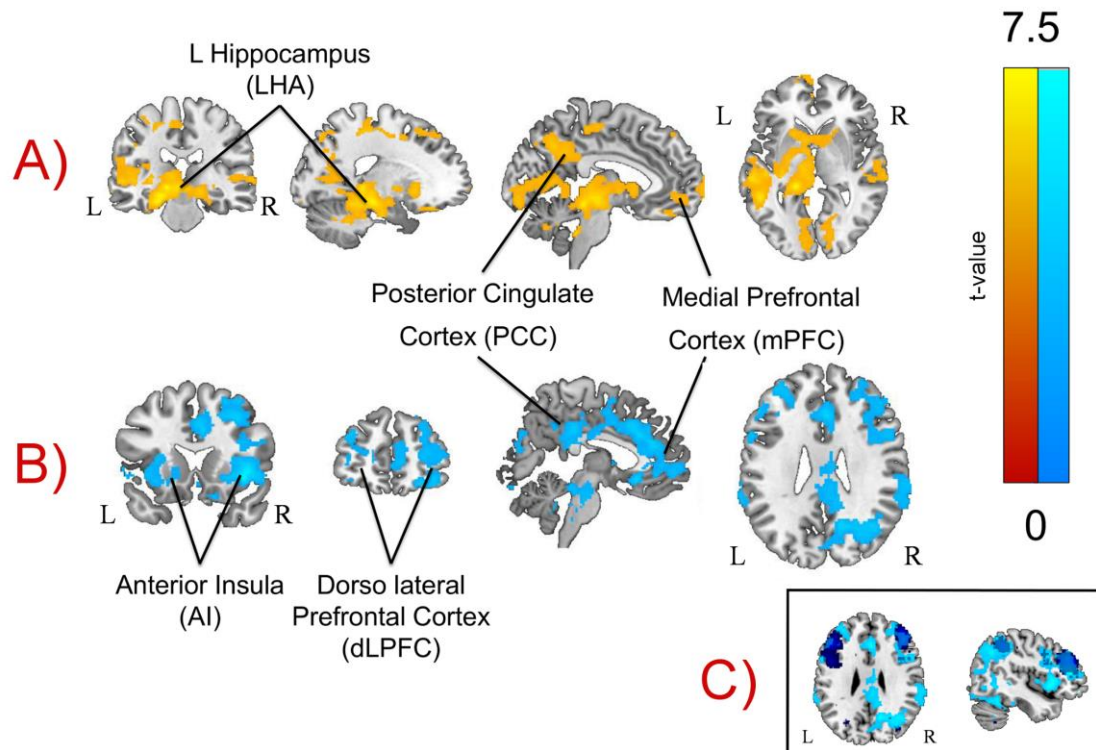
Figure 4.4 – Whole brain analyses: We conducted a whole brain analysis of the observed transient and sustained changes in the BOLD signal. Row A): Yellow areas show sustained activation for the 0-back task. Row B): Blue areas show transient activation for the 1-back task. Importantly regions of both the medial prefrontal cortex and the posterior cingulate cortex exhibited greater activity during target retrieval in the 1-back task (B) and increased sustained activity in the 0-back condition (A). These images were created using a cluster forming threshold of p < .01 and multiple comparisons were controlled for using topological FDR (p < .05). Subpanel C) on the bottom-right shows the overlap in frontal and posterior dorsal regions between the transient activation for the 1-back task (light blue) and a meta-analysis using the term "working memory" using Neurosynth (dark blue).

Region	Peak T	Peak equivZ	Peak p(unc)	x,y,z (mm)
Precuneus	5.27	3.85	0.001	14–64 30
	4.65	3.56	0.001	18–52 16
	4.62	3.54	0.001	10–46 0
Right Dorsolateral Prefrontal Cortex	5.05	3.75	0.001	32 14 42
	4.47	3.46	0.001	22 42 40
	4.22	3.33	0.001	28 20 46
Medial Prefrontal Cortex	4.98	3.72	0.001	0 36 22
	4.83	3.64	0.001	16 64 0
	4.72	3.59	0.001	28 56 8
Right Inferior Parietal Lobule	4.8	3.63	0.001	44–58 36
	4.6	3.53	0.001	36–62 26
	4.33	3.39	0.001	40–68 44
Posterior Cingulate Cortex	4.54	3.5	0.001	2–32 36
	4.01	3.22	0.001	10–46 34
	3.79	3.09	0.001	8–16 30

Table 4.1 – Transient activity: Regions showing increased transient BOLD activity during correct responding in the 1-Back > 0 Back task.

More relevant to the current investigation was the enhanced activity for targets in the 1-back task that extended into regions of the core DMN including the PCC and mPFC (Figure 4.4). We found no region exhibiting activity surpassing the cluster-forming threshold for the opposite contrast (0-back > 1-back).

4.5.2.2   Whole brain analysis–Sustained activity

The easier 0-back task activated areas of the DMN to a greater extent than in the harder 1-back task (see Table 4.2 and Figure 4.4). These included anterior and posterior regions of the mPFC and the PCC, as well as regions in the temporal parietal junction and the lateral temporal lobes. Activity was also enhanced in the several sub-cortical structures including the caudate / putamen, thalamus, hippocampus. We found no region exhibiting activity surpassing the cluster-forming threshold for the opposite contrast (1-back > 0-back).

Region	PeakT	Peak Z	Peakp(unc)	x,y,z (mm)
Left Hippocampus	7.7	4.74	0.001	-24–20–18
	5.76	4.06	0.001	-22–34–8
	5.63	4	0.001	-16–34 2
Left Middle Temporal Gyrus	5.2	3.82	0.001	-54–8–18
	4.06	3.24	0.001	-62–18–10
	4.03	3.23	0.001	-52–16–22
Left Inferior Parietal Lobule	4.65	3.56	0.001	-38–72 36
	4.29	3.37	0.001	-48–62 42
	4.24	3.34	0.001	-38–74 28
Posterior Cingulate Cortex	4.59	3.53	0.001	-8–60 38
	4.02	3.23	0.001	-10–38 28
	4	3.21	0.001	-2–48 34
Retrosplenial Cortex	3.86	3.13	0.001	-6–66 6
	3.49	2.91	0.002	-18–66 18
	3.32	2.81	0.003	-18–64 8

Table 4.2 - Sustained activity: Areas showing greater sustained BOLD activity in the O-Back than 1-Back blocks.

4.5.2.3   DMN Region of interest analysis

We repeated the one-sample t-tests reported above using our mask of the DMN (see Figure 4.5). We found that regions of the precuneus (Prec), the PCC, the mPFC and regions of the right dorsomedial prefrontal cortex (dmPFC) exhibited greater transient activity for correct responses to the 1-back than the 0-back targets (see Figure 4.5). Similarly, regions of the PCC, the inferior parietal lobule (IPL), the left middle temporal gyrus (L. MTG) and the hippocampus (Hipp.) exhibited greater sustained activity in the 0-back than the 1-back task (see Fig 6). To demonstrate that these transient and sustained changes constitute increases in the BOLD signal we extracted beta weights from each cluster using the rfxplot toolbox for SPM (Figure 4.5 and Figure 4.6).
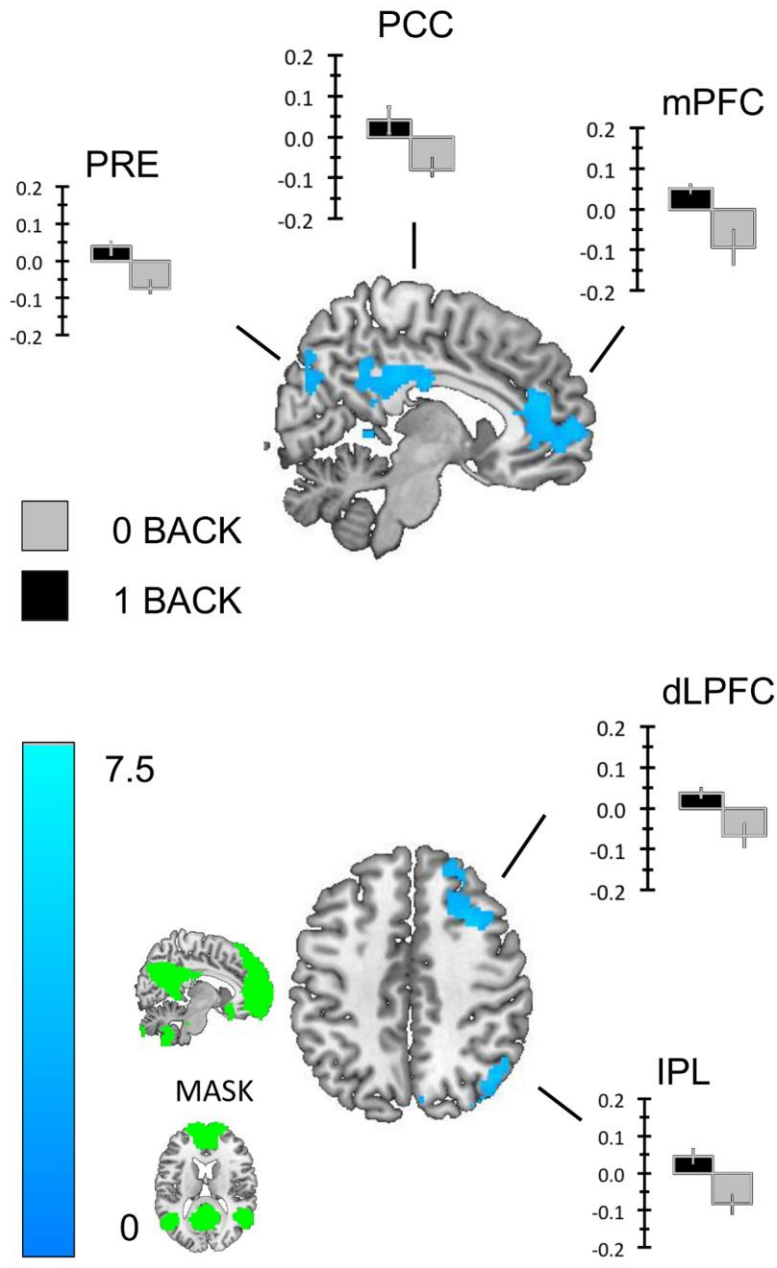
Figure 4.5 - Transient changes with the Default mode network: We repeated the analysis using a mask of the DMN created using functional connectivity from a sample of 39 healthy participants. This analysis revealed clusters in the posterior cingulate cortex, regions of the ventral and dorso-medial pre-frontal cortex and the right tempo parietal junction. To identify whether these clusters of activity constituted increases in activity in the 1-back task we extracted the beta weights for each and plotted the group averages. These images were created using a cluster forming threshold of p < .01 and multiple comparisons were controlled for using topological FDR (p < .05). The image used as a mask is presented in the sub-panel.
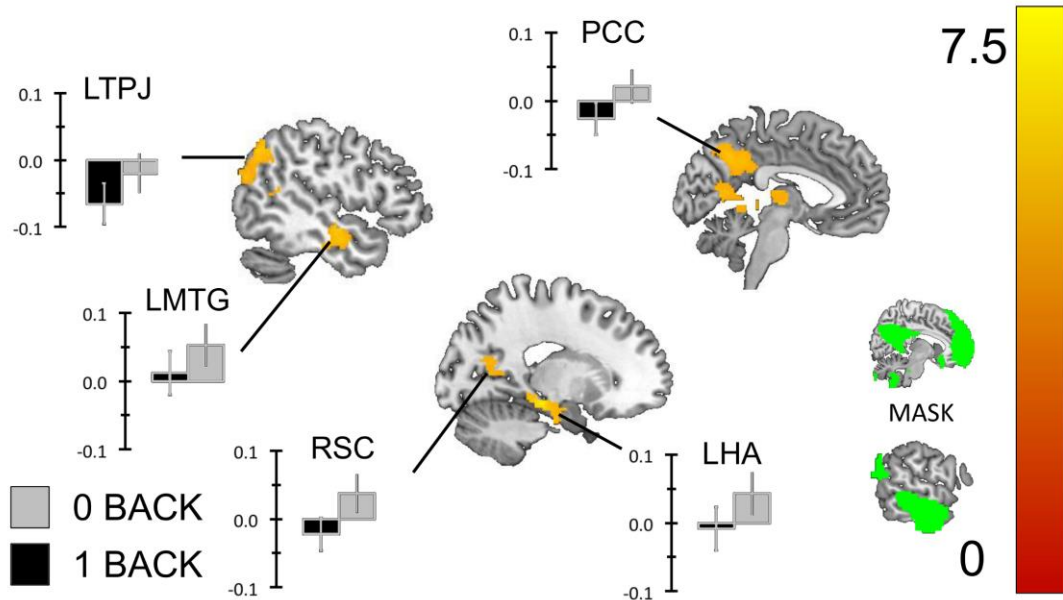
Figure 4.6 - Sustained changes within the Default mode network: To identify which patterns of increased sustained activity in the 0-back task observed in the whole brain analysis we repeated the analysis using a mask of the DMN created using functional connectivity from a sample of 39 healthy participants. This analysis revealed clusters in the posterior cingulate cortex, the left hippocampus, the left middle temporal gyrus and the right tempo parietal junction. To identify whether these clusters of activity constituted increases in sustained activity in the 0-back task we extracted the beta weights for each and plotted the group averages. These images were created using a cluster forming threshold of $p < .01$ and multiple comparisons were controlled for using topological FDR ($p < .05$). The images used as masks are presented in the sub-panel.

4.5.2.4   Conjunction analysis

Finally, we explored the spatial similarities in the sustained and transient changes in the DMN by examining their spatial conjunction. As the logic of conjunction of temporally different events is a relatively stringent statistical test we used a liberal cluster-forming threshold of $p < 0.05$ to rule out a Type II error. We calculated the overlap between the whole brain analysis of transient increases in the 1-Back task and the sustained increases in the 0-back condition using this liberal threshold. This image was masked by the DMN mask generated from the resting-state fMRI study. This analysis revealed patterns of cluster corrected sustained activity in the 0-back task and of target related activity in the 1-back task, which overlapped in a region of the PCC / retrosplenial cortex and in the mPFC (see Figure 4.7).
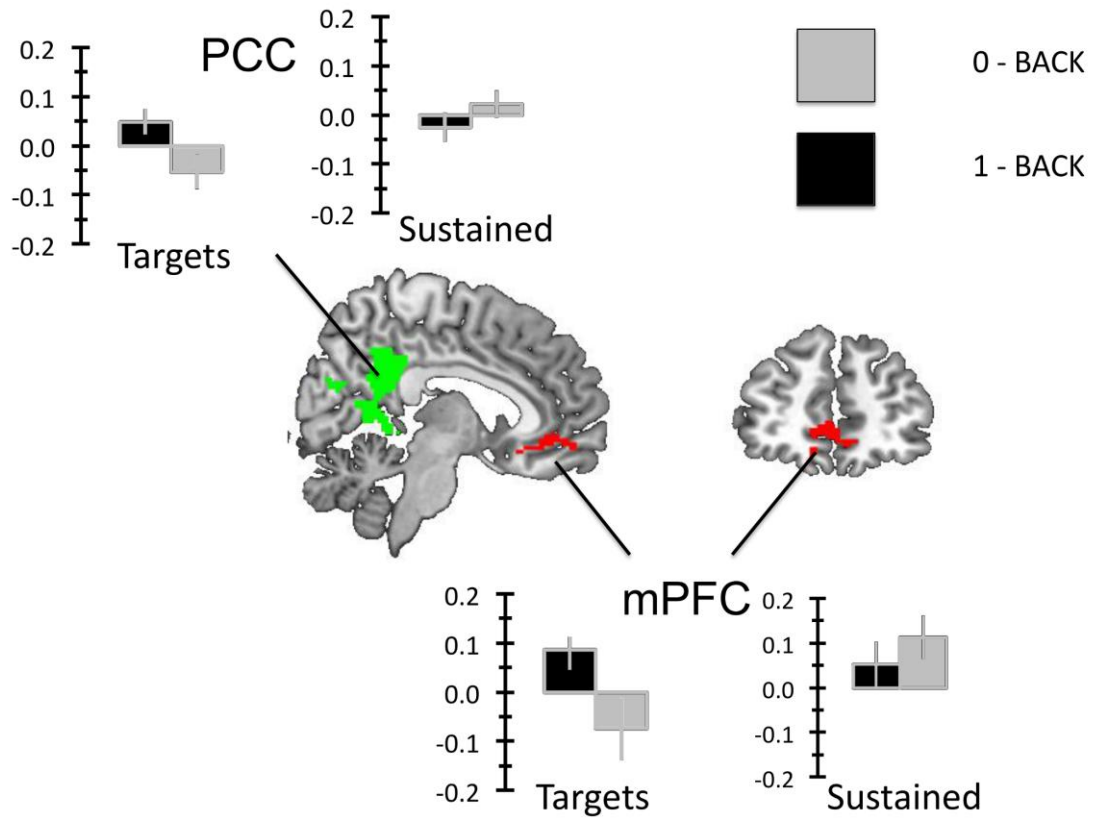
Figure 4.7 - Spatial conjunction analysis: To formally compare the activations arising from the sustained and transient increases in DMN activity observed in this experiment we created whole brain images for the Targets (1-back > 0-back) and the Blocks (0-back > 1-back). This analysis used a cluster forming threshold of p < .05 controlling for multiple comparisons using FDR (p < .05). These images were binarised and we calculated their overlap with each other as well as the DMN mask used in the prior analyses using ImCalc function of SPM.

4.6 Discussion

Using fMRI during performance of our working memory task, we found brain activity in working memory regions when participants performed a 1-back rather than a 0-back task, confirming previous findings. Importantly, however, these regions were accompanied by activity in regions within the mPFC and PCC corresponding to core hubs of the DMN. These results are inconsistent with at least two prevalent views of the functions of this network. Regions of mPFC and PCC increased activity when making a decision about a shapes position from memory and decreased activity when making the same decision using immediate perceptual input. As deciding where a shape was is more difficult than deciding where a shape is, the patterns of activation and deactivation of the mPFC and PCC in the more demanding 1-bask task indicates that this activity is not a task deactivation (M. D. Fox et al., 2005).

Furthermore, the relative activation of the mPFC and PCC by decisions regarding the position of a shape demonstrates that strong emotive or autobiographical ties with a stimulus are not necessary to activate these regions (Spreng & Grady, 2009). Nor must the stimulus be encoded in long-term memory (Spreng et al., 2014) as is the case for a famous face: our study shows that this capacity to guide cognition based on information from memory is not equivalent to long–term memory because the core of the DMN was activated when decisions were made based on representations of information that was presented a matter of seconds ago. Instead these data can simply be accounted for by the mnemonic facilitation hypothesis: that core regions of the DMN allow cognitive operations to be guided by information unrelated to immediate perceptual input.

Further support for our hypothesis comes from the observation that overlapping regions of the PCC and mPFC exhibited sustained activity in the 0-back task as well as transient target related activity in 1-back task. Our experience exampling study confirmed that the 0-back task was characterized by greater off task thought (see Figure 4.3) making it possible that the pattern of activity seen in both the PCC and mPFC may indicate a common role for these regions in allowing cognition the freedom to perform operations that are not constrained by immediate input whether it is to do with the momentary demands of a task or not. Without direct evidence linking DMN activity in the task to the experiences reported by the participants, this interpretation should be treated with caution; however, we hope to test this hypothesis in a larger sample of participants with online measures of self-generated thought in the future.

Our hypothesis that the DMN allows thought and behaviour to be guided by memory explains why this network is prominent in a range of higher order cognitive states such as future thinking, mentalizing or creativity, as well as task irrelevant activities such as daydreaming or mind wandering. All of these states depend on being able to consider information from memory, often to the extent that this can be detrimental to perceptual processing (as in the case of mind-wandering, (Baird, Smallwood, et al., 2014; Kam et al., 2010; Smallwood, Beach, et al., 2008). Our hypothesis that the DMN allows thought to be shaped by representations from memory also explains why this network has an analogue in a wide range of non-human species. While it is a matter of debate whether complex abilities like mental

time travel or language are unique to humans (Suddendorf & Busby, 2003), the capacity to guide behaviour using information from memory is a universal feature of mammalian cognition. As our data suggests that the DMN can support relatively mundane cognitive processes in humans ("Which side was the triangle on?") it seems that the presence of analogues for this network in different species may simply reflect the fact that they are also capable of guiding behaviour based on information other than immediate perceptual input.

Our hypothesis gains further support from work showing that perceptual input and DMN activity are often in opposition (Huijbers et al., 2013; Sperling et al., 2010; Vannini et al., 2012). For example, the recent work of Huijbers and colleagues (Huijbers et al., 2013) showing DMN increases in episodic memory retrieval and decreases during episodic memory encoding. This suppression of the DMN during encoding is consistent with the reduction in sustained activity we observe in the 1-back task because under these conditions participants must continually encode information from the environment. Our hypothesis also predicts that changes in the value of immediate input for a specific stimulus or task will be associated with increased activity in the DMN. This prediction is supported by a recent study of repetition suppression, which observed decreases in DMN deactivations during encoding as participants viewed the same items, suggest that the DMN deactivates less as participants form a stronger memory trace of a stimulus (Vannini et al., 2012).

When participants made decisions in the 1-back task we also observed increased activity in cortical regions outside of the DMN. For example, we found increased activity in the DLPFC and IPS: both elements of the fronto-parietal network (FPN (Coull, Frith, Frackowiak, & Grasby, 1996; Duncan, 2010)). BOLD increases during 1-back decisions were also observed in the anterior insula and anterior cingulate, regions which are important in the cingular-opercular, or saliency network (Seeley et al., 2007). Variations on this pattern of network activity has been observed when participants make plans for their future (Gerlach, Spreng, Gilmore, & Schacter, 2011; Gerlach, Spreng, Madore, & Schacter, 2013; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010), engage in creative thought (Ellamil et al., 2012), resist future rewards in the service of greater long term return (Benoit, Gilbert, & Burgess, 2011), and when maintaining social information in memory (Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012). Most recently, Spreng and colleagues demonstrated that the DMN and

the FPN co-operate to perform a working memory task with famous faces as the target (Spreng et al., 2014). Our study, therefore, adds to a growing body of research that demonstrates that many complex higher order tasks cannot be attributed to a single neural network and instead depend on the coordinated activity of multiple networks in a flexible fashion (for further discussion see (McLaren, Ries, Xu, & Johnson, 2012; Schacter, 2012; Smallwood, Brown, Baird, & Schooler, 2012; Spreng, 2012).

Our data demonstrate that core regions of the DMN are activated when participants are asked where a shape was rather than where it is right now. A simple account of these data is that it reflects the role of the DMN in allowing cognition to be shaped by representations that are distinct from those provided by immediate perceptual input. We propose this process is necessary for a range of different functions including task judgements that depend on recollections based on memory but also daydreams about a holiday or ruminations about a personal problem, thus accounting in a parsimonious manner for many of the functions that utilize the DMN. While this hypothesis is important because it offers an account for why the DMN is common to seemingly disparate functions, it offers no explanation for how these functions are differentiated within the DMN, nor the precise mechanisms that allow behaviour to be guided by information that is represented internally rather in the external environment. Moving forward it is likely we will need more sophisticated models of the cognitive functions that the DMN supports, as well as more comprehensive accounts of the functions that different regions perform, in order to truly understand the complex role this network plays in human cognition.

Chapter 5.   Pupillometric Signatures of Fluctuations in External Attention

The following chapter has been adapted from:

5.1   Abstract

Attention is not always directed to events in the external environment. On occasion our thoughts wander to people and places distant from the here and now. Sometimes, this lack of external attention can compromise ongoing task performance. In the current study we set out to understand the extent to which states of internal and external attention can be determined using pupillometry as an index of ongoing cognition. In two experiments we found that periods of slow responding were associated with elevations in the baseline pupil signal over three and a half seconds prior to a behavioural response. In the second experiment we found that unlike behavioural lapses, states of off-task thought, particularly those associated with a focus on the past and with an intrusive quality, were associated with reductions in the size of the pupil over the same window prior to the probe. These data show that both states of large and small baseline pupil size are linked to states when attention is not effectively focused on the external environment, although these states have different qualities. More generally, these findings illustrate that subjective and objective markers of task performance may not be equivalent and underscore the importance of developing objective indicators that can allow these different states to be understood.

5.2 Introduction

Attention is not always focused on the external environment; experiences like mind-wandering and daydreaming illustrate situations when cognition is generated based on our factual knowledge of the world, and episodic memories about the people we know and the places we have visited over the course of our lives (Smallwood, 2013; Smallwood et al., 2016a; Smallwood & Schooler, 2015). Although we now know that these experiences make contributions to our well-being (Killingsworth & Gilbert, 2010; Poerio et al., 2013), can arise either intentionally or spontaneously (Seli et al., 2016), and can compromise ongoing performance (Mcvay & Kane, 2009; Smallwood et al., 2008), the intrinsic nature of these experiences has hindered our capacity to understand their contributions to the human condition.

One barrier to the investigation of self-generated states is a reliance on measures of self-report. Introspective evidence allows the internal landscape of personal experience to be described, and participants have been shown to be reliable assessors of their task focus (Mittner et al., 2016; Seli et al., 2015). Nonetheless, the requirement that participants must explicitly reflect on the contents of their experience makes it possible that results that are generated in this fashion may alter the nature of the experiences that are being investigated (Konishi & Smallwood, 2016). One way to understand, and ultimately overcome, these issues, is through the development of indirect markers that could be used as a proximal measure for the occurrence of self-generated thoughts. The current study attempts to address this issue using pupillometry as a covert marker for ongoing cognitive processing.

Prior studies have found that when the baseline diameter of pupils is unusually small or large, attention is not always effectively focused on the external environment. For example, momentary lapses in attention, as indexed by slow response times or errors in performance, are preceded by periods of both large and small baseline pupil size (Gilzenrat et al., 2010; Van Den Brink, Murphy, & Nieuwenhuis, 2016; Smallwood et al., 2011, 2012; Van Orden et al., 2000). A similar pattern has been observed across studies of mind-wandering, with some finding increased pupil diameter co-occurring with self-reports of off task/mind-wandering episodes (Franklin, Broadway, et al., 2013), while others have found the reverse (Grandchamp et al., 2014). A more recent study (Unsworth & Robison, 2016), which differentiated between types of off task states, found increased baseline pupil size before reports of external distraction and reduced pupil size before both reports of mind wandering episodes and

inattentiveness. It is widely accepted that pupillometry provides an indirect measure of arousal and of locus coeruleus (LC) activity (Aston-Jones & Cohen, 2005; Morad et al., 2000; Murphy et al., 2011; Stanners et al., 1979; Wilhelm et al., 1998; Yoss et al., 1970), and that arousal/LC activity have a known relation to performance and attention (Aston-Jones et al., 1999; Yerkes & Dodson, 1908), with extreme levels of arousal linked to drowsiness or high distractibility. Moreover, catecholamines such as noradrenaline, which are linked to the LC, are thought to adjust the gain on neural processing across the cortex, and at moderate levels help gate sensory processing in a goal related manner and thus ensuring cognitive and behavioural stability (Hauser et al., 2016). It thus seems plausible that states of optimal focus may be indicated by moderate levels of arousal, with extremely large or small pupils indicating situations when attention is not engaged with the external environment to the same degree (Aston-Jones & Cohen, 2005; Smallwood, Brown, et al., 2011). Moreover, the pupil signal may provide important descriptive information on how the mind shifts between these states (Hauser et al., 2016; Mittner et al., 2016a).

It has been suggested that understanding the relationship between self-generated thought and other aspects of neurocognitive functioning can depend on the *content* of individuals' experiences (Smallwood & Andrews-Hanna, 2013). For example, studies have found that when experience is focused on events from the past, this is often associated with lower levels of happiness (Poerio et al., 2013; Ruby et al., 2013; Smallwood & O'Connor, 2011). By contrast, thoughts about the future, but not the past, have been linked to reductions in levels of social stress (Engert et al., 2014) and may contribute to the processes through which people consolidate personal goals (Medea et al., 2016). Neurocognitive investigations have also highlighted differences between these classes of experiences. Self-generated thoughts about the past were linked to higher connectivity between lateral temporal lobe regions and the hippocampus, reflecting the heightened role of episodic memory when we retrospect, and relatively greater decoupling between medial prefrontal cortex and medial visual cortex than for individuals who tend to think more about the future (Smallwood et al., 2016a). Together, these observations support the hypothesis that the *content* of self-generated thought in part determines its relationship to other neurocognitive measures.

As well as taking into account the content of self-generated thought, it is important to consider the *context* in which self-generated thought occurs (Smallwood & Andrews-Hanna, 2013). Studies have shown that, although participants' executive control capacity relates to lower levels of off-task thought when tasks are complex (Mcvay & Kane, 2009; Unsworth &

Robison, 2016), the relationship can reverse when tasks are less demanding (Bernhardt et al., 2014; Kane et al., 2007; Levinson et al., 2012; Rummel & Boywitt, 2014; Smallwood et al., 2013). Indeed, task demands modulate different types of off-task thought, with a focus on the future more common in easy tasks (Ruby et al., 2013; Smallwood et al., 2009). Under these conditions mind-wandering is described as more intentional (Seli et al., 2016; Seli et al., 2016b), and is less likely to be detrimental to task performance (Thomson et al., 2014). It is often assumed that self-generated thought is more common during tasks that lack complex demands (Teasdale et al., 1993) because there is a greater availability of cognitive resources to devote to self-generated thought. Together these lines of evidence suggest that understanding the context in which self-generated occurs can be important in understanding its neurocognitive basis.

The current study aims to elucidate the relationship between pupil diameter and the extent to which attention is deployed to the external environment. We measured pupil diameter in the context of a paradigm in which we manipulated the degree of external task focus by means of the addition of a working memory load (see Figure 5.1). We have previously used this paradigm to vary the amount of attention that participants devote to an ongoing task, a manipulation that is reflected in the speed and effectiveness with which decisions are made, as well as in changes in reports of task focus. In a prior study we acquired functional magnetic resonance imaging data during this task and found that performance of the easy task is accompanied by greater engagement of regions of the default mode network (Konishi et al., 2015), a neural system important in self-generated thought (Allen et al., 2013; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016; Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015; Mason et al., 2007; Stawarczyk, Majerus, Maquet, & D'Argembeau, 2011).

Using this paradigm, we conducted two experiments on healthy participants in which we acquired measures of pupil diameter while they performed alternating blocks of the 0-back and 1-back versions of this paradigm. We acquired two different indicators of the focus of attention. In Experiment 1 we acquired measures of behavioural task performance, and in Experiment 2 we also measured the content of ongoing thought using Multi-Dimensional Experience Sampling (MDES; Karapanagiotidis et al., 2016; Medea et al., 2016; Smallwood et al., 2016b; Smallwood & Schooler, 2015). We measured both subjective and objective indicators of attention to explore whether they had the same signature in terms of baseline pupil size. Our motivation for measuring subjective indicators of attention only in the second

experiment was to address the concern that the act of introspecting on experience would alter the nature of any pupil-behaviour relationships observed in the first experiment.

Although we also examined evoked responses in the pupil signal, the primary focus of our analysis was baseline pupil diameter, given prior work indicating that this measure provides an index of whole brain neural gain that describes the stability of cognition at a given moment (Hauser et al., 2016; Mittner et al., 2016a). Importantly, while the content of mind wandering episodes has been investigated with behavioural and fMRI measures (Gorgolewski et al., 2014; Karapanagiotidis et al., 2016; Medea et al., 2016; Smallwood et al., 2016a), previous pupillometric studies only differentiated between states of on-task or off-task (or within off-task states, such as mind wandering or external distraction), but did not explore content-related questions (e.g. Franklin et al., 2013; Grandchamp et al., 2014; Smallwood et al., 2011; Unsworth & Robison, 2016). Given evidence of neural differences associated with different forms of content during mind-wandering, we sought to re-evaluate the links between on-going experience and the pupil signal to explore which aspects of experiential content it reflects. In this way, our study is the first to explore the hypothesis that physiological changes may underpin differences within the content of experience during the mind-wandering state. Finally, we also explored whether any relationship between the pupil signal and on-going experience depends the nature of the external task to identify if the pupil marker can provide an index of attention in a manner that is independent of the context within which it is assessed.

5.3   Method

5.3.1   Task Paradigm

The task used in both studies was programmed using PsychoPy2 (Peirce, 2007, 2008). The task featured a 0-back and a 1-back condition that continuously switched from one to the other throughout the experimental session (see Figure 5.1). Our paradigm is the same used in Konishi et al. (2015). In both conditions participants saw different pairs of shapes (Non-Targets, NT) appearing on the screen divided by a vertical line. The shape pairs could be: a circle and a square, a circle and a triangle, or a square and a triangle for a total of 6 possible pairs (two different left/right configurations for each). The pairs never had shapes of the same kind (e.g. a square and a square). In both tasks, a block of NT was followed by a target requiring participants to make a manual response. The target was a small stimulus presented in either blue or red. In the 0-back condition the target was flanked by one of two shapes and

participants had to indicate by pressing the appropriate button which shape matched the target shape. In the 1-back condition, the target was flanked by two question marks and participants had to respond using the left and right arrow keys, depending on which side the target shape was on the previous trial.

Each block lasted between 40 to 120 seconds before switching to the other condition; the change of condition was signaled by a message ("SWITCH") that remained on screen for 4 seconds. The number of NTs preceding the targets varied between 2 and 6, the number of targets per block varied between 2 and 5 and the total number of blocks was 8 for each condition. The total number of targets was 15 to 20 per condition. The blue and red colours used in the two conditions were matched for luminance as displayed on an LCD monitor, and the colour/condition pairing was counterbalanced across participants. The starting order of conditions was counterbalanced across participants and a single session of the task lasted ~15 minutes for Experiment 1 and ~20 minutes for Experiment 2 (due to the addition of thought probes). Each participant completed two sessions for study 1, and two to six sessions in the span of three different days (two sessions a day) for study 2. Presentation rate of the stimuli was jittered in the following way: fixation crosses ranged from 1.8-2.2 seconds (average 2s) in steps of 0.05s, Non-targets were varied from 1.3–1.7 seconds (average 1.5s) in steps of 0.05s. Target durations ranged from 2.1-2.5 seconds (average 2.3s) in steps of 0.05s and lasted for the full duration, regardless of participant response.
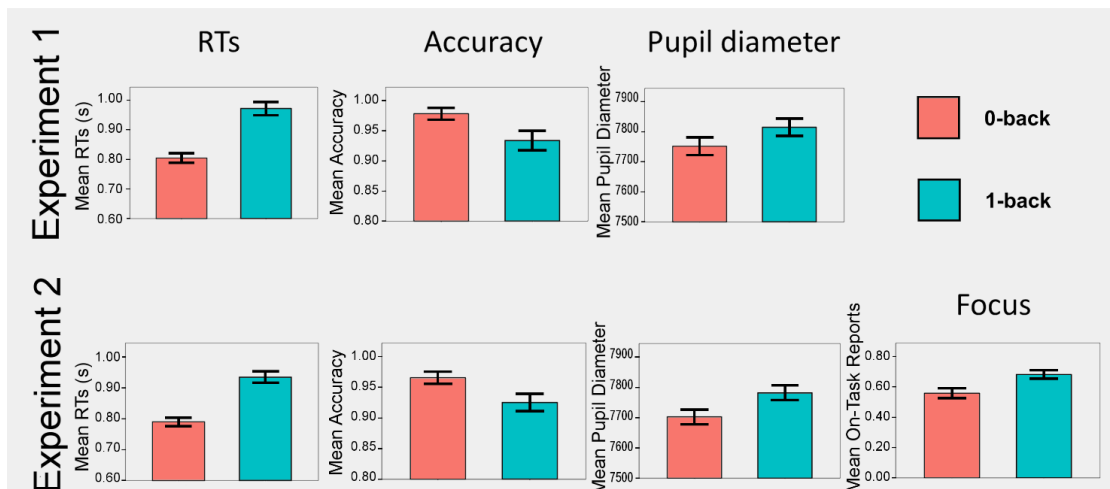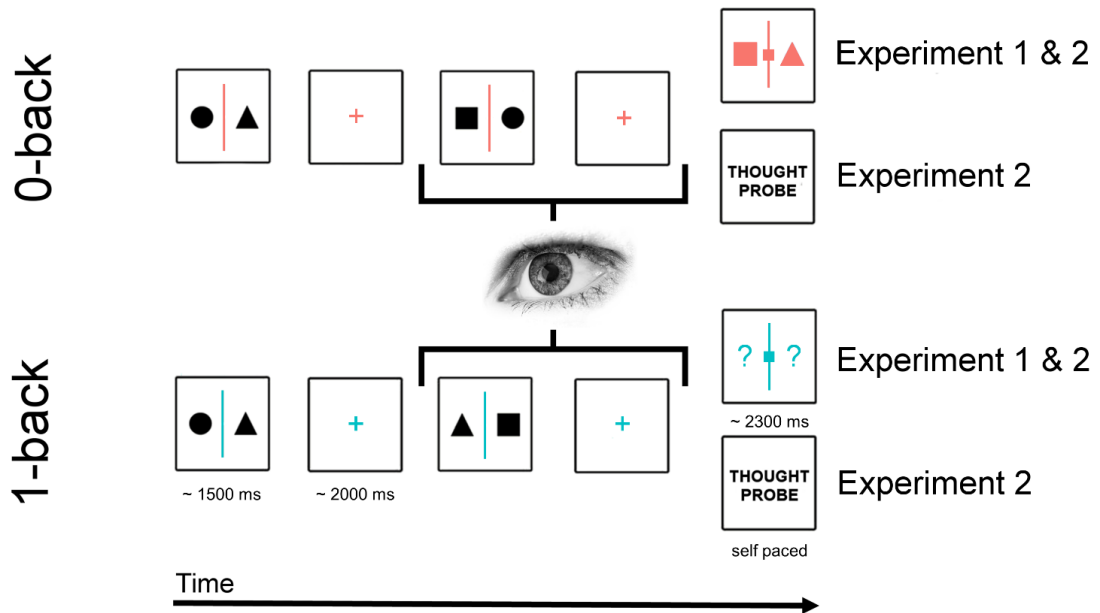
Figure 5.1 - Top panel illustrates our paradigm: in both conditions, after a certain number of Non-Targets (NTs) participants were faced with a target decision (in Experiment 1 & 2), or a thought probe (only in Experiment 2). In the 0-back condition, the decision is based on the presently perceived stimulus (is the square on the left or the right?); the NTs are thus irrelevant to the task, allowing for long periods in the 0-back condition when attention is unconstrained by the ongoing task. Conversely, in the 1-back condition the target decision is based on the previously attended NT (was the square on the left or the right?). Under these conditions, participants must maintain external attention on the NTs in order to perform accurately in the task. We selected a time window of ~3.5 seconds, corresponding to the NT and fixation cross immediately preceding a target or a thought probe, to analyse the effects of average pupil size on behaviour and internal reports. Bottom grey panel shows how our conditions modulate behaviour and on-task reports. In both studies participants are slower and less accurate in the 1-back condition; additionally, their pupils are larger and they report being more on-task.

5.3.2 Multi-Dimensional Experience Sampling (Experiment 2)

In order to sample participants' ongoing experiences in Experiment 2, we used a probe-caught, experience sampling method (Kahneman et al., 2004; Smallwood & Schooler, 2006). The task was designed so that there was a 20% chance of a thought probe being presented in place of a Target in a condition block. The experience sampling protocol consisted of a series of ten questions (shown in Table 5.1), the first of which always prompted participants to rate their focus level ("Just before this question appeared, were you focused on the task or were you thinking about something else?") on a continuous slider scale from "completely off task" to "completely on task". Before the experiment began, participants were instructed on the meaning of being completely on task (e.g. "I'm focused and only thinking about the computer task") and completely off task (e.g. "I was thinking about something unrelated, like a past vacation or what I'll have for dinner"). The other nine questions were split into five questions regarding the content, and four questions regarding the form of the thoughts experienced by the participants. Participants answered using a slider scale that always had "not at all" and "completely" at the extremes, apart from one question regarding the thoughts' valence, for which the scale went from "negative" to "positive". These questions have been used in previous investigations (Medea et al., 2016; Smallwood et al., 2016a).

Type	Question	Dimension	Left Extreme	Right Extreme
Content	My thoughts were focused on the task I was performing.	Focus	Not at all	Completely
Content	My thoughts involved other people.	Other	Not at all	Completely
Content	The content of my thoughts was:	Emotion	Negative	Positive
Content	My thoughts involved past events.	Past	Not at all	Completely
Content	My thoughts involved myself.	Self	Not at all	Completely
Content	My thoughts involved future events.	Future	Not at all	Completely
Form	My thoughts were in the form of words.	Words	Not at all	Completely
Form	My thoughts were in the form of images.	Images	Not at all	Completely
Form	My thoughts were vague and non-specific.	Vague	Not at all	Completely
Form	My thoughts were intrusive.	Intrusive	Not at all	Completely

Table 5.1 - The table shows the questions asked to participants for each thought probe. The first question always regarded their on-task focus level, while the other 9 were randomised each time. Participants responded on a continuous scale which had a left and a right extreme for each question, as described in the table.

Mind wandering episodes are rich, heterogeneous phenomena in content and form (Smallwood & Schooler, 2006, 2015). One way to capture the variety and heterogeneity of each episode is to conduct a principal component analysis (PCA) to determine patterns of covariance in the participants' responses to the thought probes (e.g. when participants think about the past, they might also tend to think about themselves and in the form of images). Factor analyses have been previously used with success in a range of mind wandering studies (Klinger & Cox, 1987; Medea et al., 2016; Ruby, Smallwood, Engen, et al., 2013; Ruby, Smallwood, Sackur, et al., 2013; Smallwood et al., 2016a; Stawarczyk, Cassol, et al., 2013). In the current study, as in our prior work, we differentiate between the immediate content of experience (e.g. whether it is related to the task, its episodic or emotional features), from the *form* that these thoughts are expressed (e.g. whether these experiences are intrusive, expressed as images or words). We recorded a total of 673 thought probes. Following Medea et al. (2016), Ruby et al. (2013a), Ruby et al. (2013b), Smallwood et al. (2016), we decomposed these data at the trial level using exploratory factor analysis with varimax rotation and selected three components for both the content questions and three components for the form questions which explained ~80 % of the variance in both cases. These are presented in Figure 5.5 (grey panel). For the content of thoughts, this resulted in: 1) a Past/Off Task/Others component, weighting on thinking about the past and about other people, while being off task; 2) a Future/Self component, weighting on thinking about the future and on one's self, and 3) a Positive/On Task component, weighting on having positively valenced thoughts, while being on task. For the form of thoughts, the analysis identified: 1) an Images component, weighting on thinking in images and also not thinking in words, 2) an Intrusive component, weighting on reporting one's thoughts as being intrusive, and 3) a Vague component, weighting on having vague thoughts. These are very similar to the solutions produced in prior investigations using this approach (see Medea et al., 2016, Smallwood et al., 2016, for demonstration of similar solutions in three different samples of participants). For the purpose of our analysis, we projected these solutions back onto the trial level data: this way, aside for the raw scales for each question, every thought probe had six additional values, representing the weights of the six principal components (three for the content and three for the form of thoughts) found with the factor analysis.

5.3.3 Participants

Forty-two participants (18-28 years, mean age 19.4; 8 males) completed Experiment 1; nine participants were removed from the analyses due to excessive amount of missing pupil data (as defined below in the pre-processing section) and one was removed as target accuracy was at chance; after filtering of participants, thirty-two participants (57 total sessions) were used in the analyses. Forty-two participants (18-39 years, mean age 21.5; 11 males) completed Experiment 2; five participants were removed from the analyses due to excessive amount of missing pupil data, one participant was removed due to abnormally slow reaction times; thirty-six participants (104 total sessions) were finally used in the analyses.

5.3.4 Apparatus and Setup

Pupil size was recorded using an EyeLink 1000 Desktop Mount (SR Research Ltd., Mississauga, ON, Canada), at a rate of 250hz, from the right eye only of participants. Pupil diameter was measured in arbitrary units as recorded by the eye-tracker. The study was conducted in a small, dark room with no windows, resulting in ambient light levels below 0.1 cd/m^2. Visual stimuli were presented on an 18-inch LCD monitor located 60 cm from the chinrest (with forehead support) that participants used, and the eye-tracker was placed right below the computer screen. Presentation of all stimuli was controlled with PsychoPy2 v.1.81.03 together with the ioHub Python package (http://www.isolver-solutions.com/iohubdocs/) to interface with the eye-tracker.

5.3.5 Procedure

Participants were provided an information sheet for the experiment at least 24 hours ahead of the testing day; on the day, participants were welcomed in the lab and signed a consent form. They were then introduced to the task paradigm and the eye-tracker setup, after which they completed a practice trial of the task, which included full instructions. Participants were instructed to respond as fast and accurately as possible to the targets; participants were also instructed on the definition of being on-task (e.g. being completely focused on the task, or having thoughts regarding the task), and being off-task (e.g. thinking about something completely unrelated, such as planning a future holiday). A randomized target order 9-point calibration routine was performed and a separate validation was performed using the EyeLink

1000 software. Once calibration was completed, the experiment began. Participants were asked to maintain fixation in the centre of the screen for the entire duration of the experiments, except when responding to the thought probes in Experiment 2. All investigation was conducted according to the principles expressed in the Declaration of Helsinki; the study and the process for gaining informed consent was approved by the University of York Department of Psychology's Ethics Committee, and by the Ministry of Defence Research Ethics Committees.

5.3.6   Pre-processing of Eye-tracking Data

The following pre-processing steps were taken in order to remove possible artefacts before data analysis, for each session, for each participant. If pupil data was missing in time periods longer than 1 second, the trial was discarded, while it was linearly interpolated for periods shorter than 1 second. If more than 25% of the data was missing (e.g. for excessive blinking, drowsiness, falling asleep), the entire session was discarded and not used in subsequent analysis. Pupil data was z-scored and trials in which pupil measures had values larger than 3.5 or smaller than -3.5 were discarded. Gaze fixation in the centre of the screen was monitored automatically, and if it diverged outside of a 88 pixel central boundary (approximately 2.7 visual degrees given our setup), the trial was discarded. The pupil time series was also median filtered (order 5) to remove spikes, and low-pass filtered with a 10hz cut-off and then downsampled to 80ms (12.5hz).

5.3.7   Analysis

Pupil data was analysed using linear mixed models as implemented in R through the package *lme4* (Bates et al., 2015). For both experiments we ran models to investigate how baseline pupil size predicted behaviour (target RTs), and for Experiment 2 we also ran models to investigate how pupil size predicted on task focus and mind wandering reports (PCA components) in the two task conditions. We selected a time window of interest comprising the non-target (NT) and fixation cross immediately preceding either a correctly reported target, in case of behaviour, or a thought probe, for the analysis of the self-reports. This resulted in an average time window of 3.5 seconds. In all our models the average pupil diameter in that time window, and task condition, were included as fixed effect predictors; on task reports, PCA components extracted from the mind wandering reports (Experiment 2), and reaction times

(Experiment 1 and 2; log-transformed in order to normalise their distribution) were the predicted variables in our models. Participants and sessions were modelled as random factors, in a nested fashion; sessions were also modelled as a fixed factor, in order to investigate possible learning effects. We then compared models that had task condition to a null model through a Likelihood Ratio Test, to see if it would improve the model's fit. Next, we compared models that progressively included a session and a baseline pupil factor, to see if the additional predictors would improve model fit; If the additional factors improved model fit, we compared models that included the interactions between the predictors, to models only having the individual predictors but with no interaction. Finally, because stimulus-evoked pupil response (Beatty, 1982) has been previously shown to differentiate between on-task and off-task attentional states and accurate/inaccurate performance (Smallwood, Brown, et al., 2011; Unsworth & Robison, 2016), we also looked at the amplitude of the pupil response (calculated as the difference between the peak response and the average pupil size during that time window) for the presentation of the critical NTs (immediately preceding a target or a thought probe), by including it as a fixed effect in place of the baseline pupil in a new set of analyses. Fixed effects on the predicted variables were plotted using the *effects* (Fox, 2003) and *ggplot2* (Wickham, 2009) R packages.

5.4   Results

5.4.1   Task Condition Effects on Behaviour and Pupil Size (Experiment 1 & 2)

We analysed participants' accuracy and response time data for both of our studies using paired sample t-tests. We replicated the task-condition effects found in Konishi et al. (2015). Participants were both slower, and less accurate, to targets in the 1-back task relative to the 0-back (Experiment 1 RTs: $t(35) = 10.00$, $p < .001$, Experiment 1 accuracy: $t(35) = 3.93$, $p < .001$; Experiment 2 RTs: $t(31) = 7.99$, $p < .001$, Experiment 2 accuracy: $t(31) = 5.08$, p<.001). In Experiment 2 we also replicate the effects of differential task focus for the two conditions (Konishi et al., 2015), so that participants reported to be more off task in the 0-back condition than in the 1-back ($t(35)=4.80$, $p <. 001$). Finally we found that average pupil diameter (PD) was larger throughout the 1-back task relative to the 0-back, in both studies (Experiment 1 PD: $t(35) = 2.02$, $p = .051$; Experiment 2 PD: $t(31) = 3.03$, $p = .005$). We also analysed the effect of task condition on the average pupil response (divided in 17, 80ms time bins) to the critical non-targets immediately preceding a target, which was also significant in both experiments (Experiment 1: $t(16) = 11.27$, $p < .001$; Experiment 2: $t(16) = 11.32$, $p < .001$).

All results are shown in Figure 5.1 (bottom panel); the pupil waveform to the critical NTs and fixations preceding a target is shown in Figure 5.2 for both experiments.
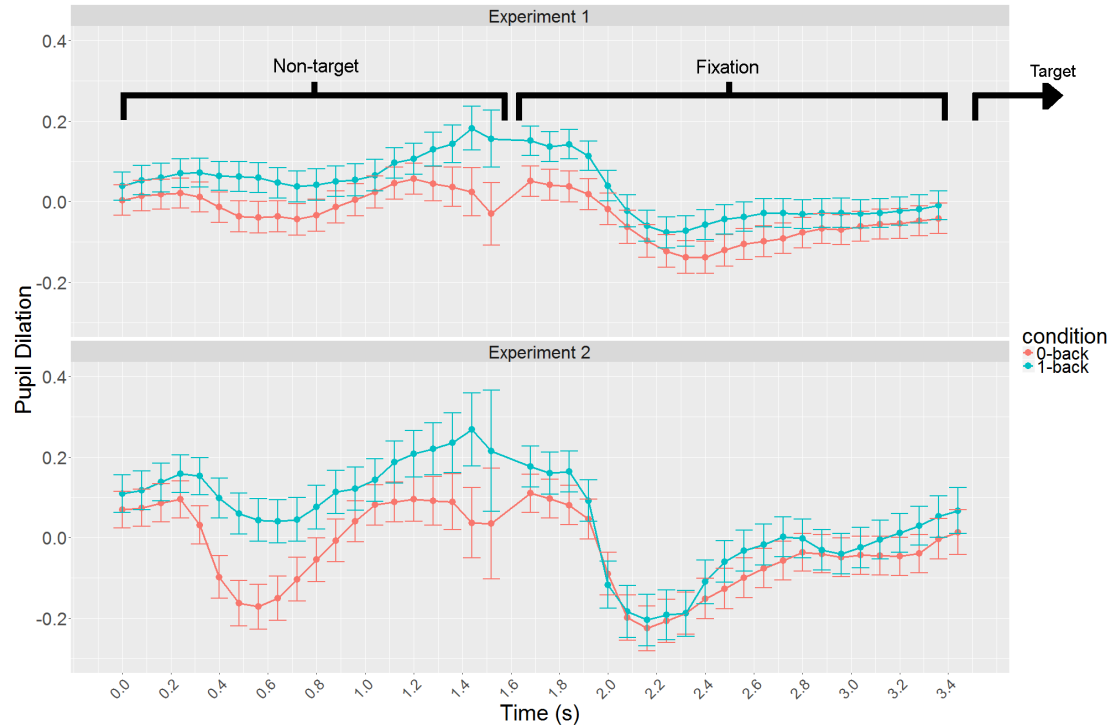
Figure 5.2 - The pupil dynamics evoked by the NT and fixation cross stimuli preceding a target in the 0-back and 1-back conditions, in the two experiments. A baseline difference in pupil size is evident in the two conditions, in both experiments. A task-based modulation of the pupillary light reflex constriction (similarly shown before by Steinhauer, Condray, & Kasparek, 2000; and in the general context of arousal by Bitsios, Szabadi, & Bradshaw, 1996, 2004) is also evident in the NTs. X-axis represents time (in seconds) since onset of the NT, showing the window of ~3.5 seconds used in our analyses. Error bars towards the tail of the stimuli are larger due to the presentation time jittering used. The Y-axis represents z-scored pupil size. Error bars represent 95% confidence intervals. In both studies, a larger pupil baseline is present in the 1-back than in the 0-back condition.

5.4.2   Effects of Condition, Session, and Pupil Size on Target Reaction Times (Experiments 1 & 2)

Task condition significantly predicted RTs in both Experiment 1 ($\chi^2(1) = 258.15$, $p < .0001$) and Experiment 2 ($\chi^2(1) = 322.17$, $p < .0001$), with longer RT in the 1-back condition. Adding the session factor to the model significantly improved the fit in both Experiment 1 ($\chi^2(1) = 7.15$, $p = .007$) and Experiment 2 ($\chi^2(1) = 15.56$, $p < .0001$), with later sessions predicting faster RTs. Adding the baseline pupil factor also significantly improved the fit of the model in both Experiment 1 ($\chi^2(1) = 6.69$, $p = .009$) and Experiment 2 ($\chi^2(1) = 22.01$, $p < .0001$), with larger pupils predicting slower RTs. In both datasets, the best fitting models (in terms of lower

AIC, BIC, and degrees of freedom) contained individual fixed effects of condition, session, and baseline pupil. We also checked if the evoked pupil response to the critical NTs could predict subsequent performance: adding the stimulus-evoked pupil response also significantly improved model fit in both datasets, compared to models comprising of task condition and session as fixed effects: Experiment 1 (χ^2 (1) = 12.71, p = .0003), Experiment 2 (χ^2 (1) = 36.91, p < .0001), with a larger evoked response predicting slower RTs. No interactions between the factors were significant. Finally, we checked if baseline pupil and task-evoked response (as dependent variables) were related to target accuracy, using repeated measures ANOVA, with condition and session as additional independent variables. A main effect of accuracy (F (1, 29) = 6.17, p = .019) indicated that baseline pupil was higher prior to incorrect responses in Experiment 2, alongside the known effect of condition (F (1,29) = 7.86, p = .009); no effect of session or interaction effects were found, no effects were found for task-evoked response, and no significant effects were found in Experiment 1, although it is likely that low power in these last analyses had an impact, given the few mistakes done by participants in Experiment 1: Experiment 1 had a total of 50 mistakes (6 in 0-back, 44 in 1-back) on 1998 total targets, while Experiment 2 had 128 mistakes (27 in 0-back, 101 in 1-back) on 3095 total targets.

These analyses therefore show that slower and inaccurate responding was preceded by larger pupils in both the 0-back and the 1-back task, and that RTs became faster across sessions. The relation between baseline pupil size and accuracy is shown in Figure 5.3. All other results are shown in Figure 5.4.
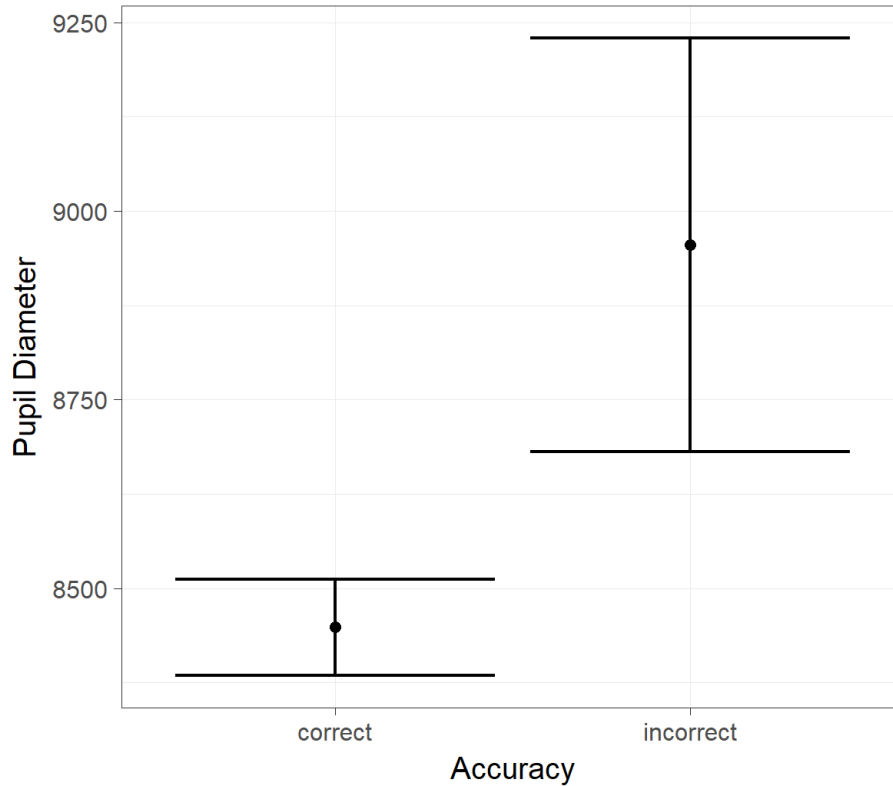
Figure 5.3 - The relation between baseline pupil size (y-axis, shown in the raw Eyelink 1000 values) and target accuracy in Experiment 2. Error bars represent 95% confidence intervals. Large baseline pupils prior to mistake in a similar task had been previously observed in Smallwood et al. (2011).

5.4.3 Effects of Condition, Session, and Pupil Size on Reports of Task Focus (Experiment 2)

Our next analysis examined the relation between baseline pupil size and the response to the task focus questions. Task condition significantly predicted task focus in Experiment 2 (χ^2 (1) = 44.38, p < .0001), as participants reported being more on task in the 1-back condition. Adding a session factor to this model seemed to have a very weak, but non-significant effect in improving model fit (χ^2 (1) = 3.28, p = 0.07), with later sessions predicting lower task focus. Adding baseline pupils to this model significantly improved the fit (χ^2 (1) = 22.06, p < .0001), with larger baseline pupils predicting more on task focus reports. We then tested for interaction factors between the three fixed effects. Adding an interaction factor between task condition and baseline pupil slightly improved model fit, nearing significance (χ^2 (1) = 3.04, p = .081). To understand this trend we compared the effect of the pupil signal in each task separately. This subsequent analysis confirmed differences in pupil size for reports of task focus exist in the 0-back task (χ^2 (1) = 21.59, p < .0001), that were not clear in the 1-back task

(χ^2 (1) = 2.02, p = .155). All other interactions did not improve model fit. Similarly to what done for the RTs analyses, we also checked if the evoked pupil response could predict subsequent report of task focus, but found no evidence for this. All results are shown in Figure 5.4.
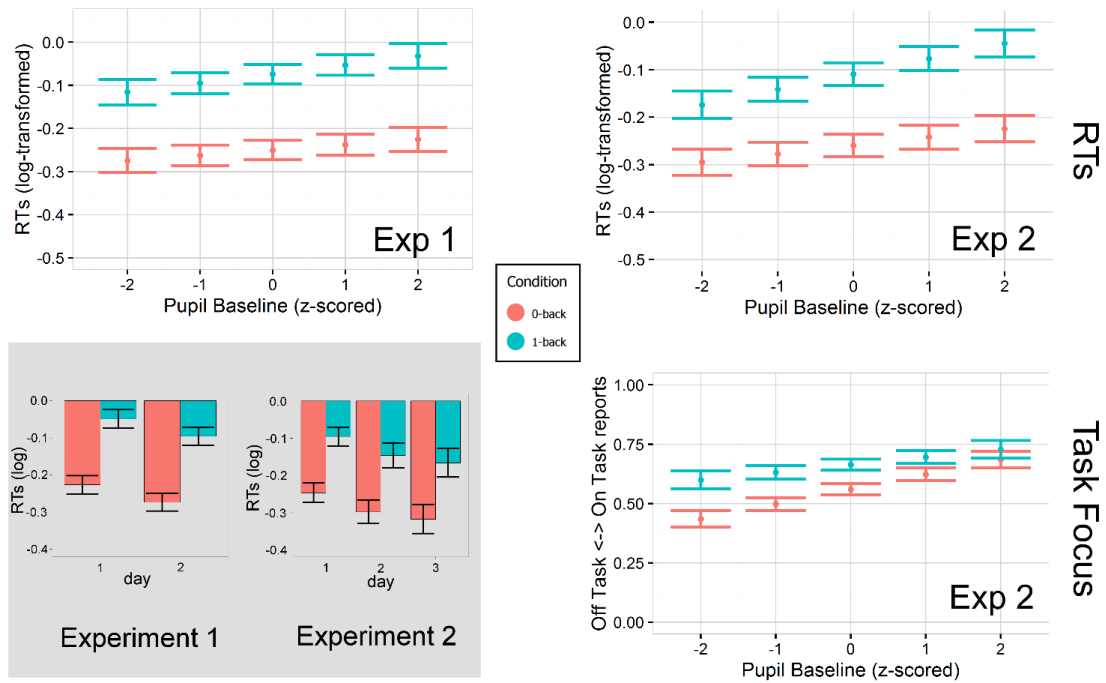
Figure 5.4 - Illustrated on white background are the main effects of task condition and baseline pupil size on reaction times (log-transformed) and on-task reports. Larger pupils, and task condition, predict slower reaction times in both of our studies (top two panels). Additionally, larger pupils predict reports of being on-task in the 0-back condition (bottom right panel). Grey panel shows task learning effects: over successive days, participants' RTs become faster for both conditions, in both studies.

5.4.4   Effects of Condition, Session, and Baseline Pupil Size on Experience Sampling Reports (Experiment 2)

Having demonstrated a relationship between the pupil signal and the degree of task focus, we next examined how this related to the different types of mind-wandering as described by the decomposition analysis. Task condition significantly predicted self-reports regarding the Off task/Past (χ^2 (1) = 7.04, p = .007), Future/Self (χ^2 (1) = 12.52, p < .001), Images (χ^2 (1) = 25.97, p < .0001), Positive/On Task (χ^2 (1) = 4.05, p = .044), and Intrusive (χ^2 (1) = 4.82, p = .028) components: in the 0-back condition, compared to the 1-back, participants reported being more off task and thinking more about the past, thinking more about the future, thinking

more in images than in words, and described having more intrusive thoughts. Adding a session factor only improved fit for the Future/Self component ($\chi^2(1) = 11.75$, $p = <.001$), with reports of thoughts related to the Future and the Self increasing across sessions: the mean value for the Future/Self component in session 1 was -0.08, rising to 0.29 in session 6 (sess. 2 = -0.03; sess. 3 = -0.10; sess. 4 = 0.12; sess. 5 = 0.14). Adding baseline pupils to the model only improved fit for the Past/Off task ($\chi^2(1) = 8.17$, $p = .004$) and Intrusive component ($\chi^2(1) = 15.94$, $p < .0001$). There were no interactions between task condition and baseline pupils for any of the PCA components. All results are shown in Figure 5.5.
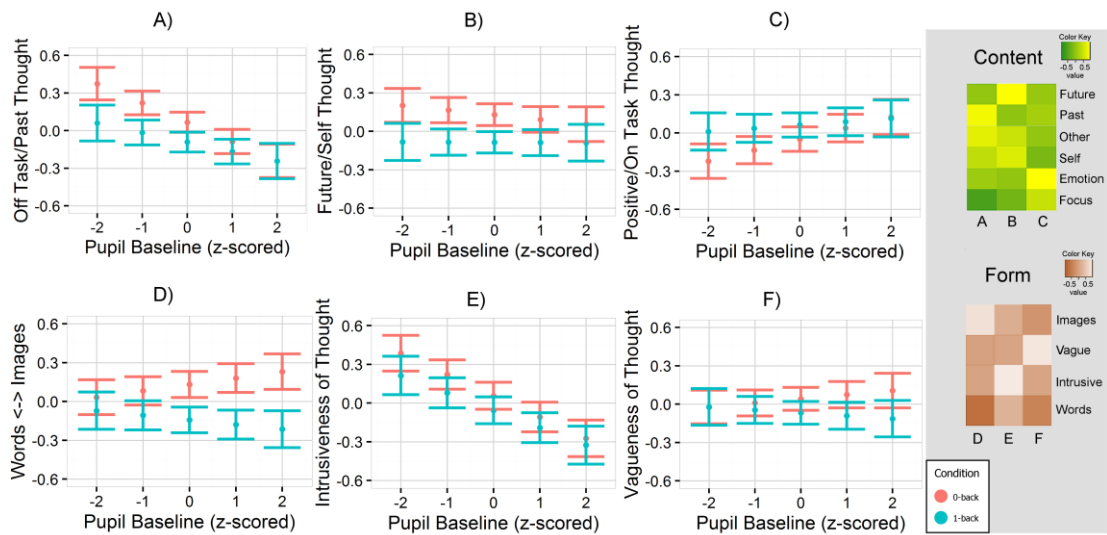
Figure 5.5 - Grey panel (right) illustrates the PCA decomposition of the thought probes in the 6 components of thought, divided by content and form. Numerical values represent the weights of each individual scale for each principal component. In the white panel are illustrated the main effects of task condition and baseline pupil size on the 6 components of thought. Task condition predicts reports for 4 components: in the 0-back condition, participants report being more off task, having more thoughts about the past (P), the future (F), more intrusive thoughts (IN), and thinking more in images than in words (I/W). Additionally, smaller pupils predicted more reports of off task and past thoughts (P), and of intrusive thoughts (IN).

Analysing the components obtained from the PCA controls for the patterns of covariance in the participants' responses, allowing us to explore our data with the minimum number of analyses. Our next analysis explored the relationship between pupil diameter and each individual question. This analysis revealed that task condition was a significant predictor for the following scales, so that the in the 0-back task, thoughts about the Past ($\chi2$ (1) = 10.04, p = .001), Future ($\chi2$ (1) = 5.43, p = .019), Self ($\chi2$ (1) = 18.13, p = <.001) were more frequent, that thoughts had a more Intrusive quality ($\chi2$ (1) = 7.81, p = .005), and were more often in

the form of Images ($\chi 2$ (1) = 14.64, p = <.001); the 0-back task also predicted less thoughts in the form of Words ($\chi 2$ (1) = 22.98, p = <.001). Adding a session factor only improved model fit for the Past ($\chi 2$ (1) = 5.07, p = .024), Future ($\chi 2$ (1) = 10.88, p = <.001), and Images ($\chi 2$ (1) = 6.12, p = .013), with these types of reports increasing across sessions. On the other hand, adding a baseline pupil factor only improved fit for the Past scale (compared with the model including both task condition and session, $\chi 2$ (1) = 8.82, p = .003), and Intrusive scale (compared with the model including task condition, $\chi 2$ (1) = 13.75, p = <.001). With the exception of the effects of the Emotion component, these patterns are broadly consistent with the results of the PCA analysis. Finally, we tested if the evoked pupil response (instead of the baseline pupil) could be a predictor for the mind wandering reports in all of our models, and whether between-subject effects of average pupil size predicted trait differences in mind wandering reports. In neither case did these analyses reveal significant effects. All results concerning the principal components and the individual scales are summarised in

Table 5.2.

Components	condition	+session	+pupil
Off Task/Past	0.007*	0.709	0.004*
Future/Self	<.001*	<.001*	0.601
Positive/On Task	0.044*	0.717	0.128
Images<>Words	<.0001*	0.103	0.724
Vague	0.062	0.066	0.827
Intrusiveness	0.028*	0.188	<.0001*
Raw Scales	**condition**	**+session**	**+pupil**
Emotion	0.162	0.946	0.787
Past	0.001*	0.024	0.003*
Future	0.019*	<.0001*	0.513
Self	<.0001*	0.094	0.664
Other	0.541	0.839	0.251
Images	<.001*	0.013*	0.589
Words	<.0001*	0.329	0.105
Vague	0.156	0.227	0.711

Intrusive	0.005*	0.489	<.001*

Table 5.2 - The table illustrates the effects of the three fixed factors of interest in improving model fit. The number indicates the p-values resulted from likelihood testing models of increased complexity against each other. Asterisks highlight statistical significance on the likelihood tests, indicating that the additional fixed effect improved model fit.

5.5 Discussion

In two experiments we found evidence of larger pupil size predicting slow and inaccurate response times in a simple working memory task. A link between larger baseline pupils and slower or inaccurate responding has been observed before in different paradigms, such as Unsworth & Robison (2016) using a sustained attention task; Gilzenrat et al. (2010) in an oddball task; Bradshaw (1968) in a reaction-time task; and Smallwood et al. (2011) in a 1-back task similar to ours. Our data, therefore, adds to a growing body of evidence that unusually large pupils are a signature that external information is not being processed correctly.

We also found evidence of a link between baseline pupil size and ongoing experiential states. In our data, off task states were associated with significantly smaller pupil size than was observed for on-task reports, replicating prior studies (Grandchamp et al., 2014; Mittner et al., 2014; Unsworth & Robison, 2016). Our analysis of the content of thoughts suggests that reduced pupil size is a marker for experiential states that are focused on the past, or that are particularly intrusive in nature. Prior studies using the same decomposition procedure have identified that past thoughts are most strongly linked to unhappiness (Ruby et al., 2013). A recent fMRI experiment (Smallwood et al., 2016a) demonstrated that past thoughts depended on coupling between the hippocampus and the lateral temporal lobe and decoupling between the medial prefrontal cortex and the occipital cortex, extending into the lingual gyrus. The coupling between the hippocampus and the posterior core of the DMN can plausibly be accounted for by a role of episodic memory in past related thought. More importantly, neural activation in the lingual gyrus is a correlate of large pupils (Kuchinsky et al., 2016; Murphy et al., 2014) so that it seems plausible that the observed association between small pupils and past thinking, as well as the decoupling between the mPFC and the lingual gyrus observed in prior studies, describes a pattern of increased perceptual decoupling that is important when we think about the past. This hypothesis could be tested by measuring external attention directly

using EEG and exploring if thinking about the past reduces the coupling between cortical activity and events in an ongoing task (see Baird et al., 2014). More generally, it seems possible that a combination of intrusive thoughts, as well as a tendency to focus on the past may constitute the experiential correlates of a state of rumination (Poerio et al., 2013; Smallwood & O'Connor, 2011). In line with this view, past research has shown that when participants have smaller pupils, this exacerbates their perceptions of sadness when viewing other individuals, a process that is linked to activations in the anterior cingulate and anterior mid insula (Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006). Moving forward, our study suggests that reductions in the size of pupils might be a useful marker in clinical research for the occurrence of internal thoughts that are related to the past and are intrusive in nature.

Our data also highlights the theoretical value of taking into account both the content of experience and the context in which it occurs, in studies of mind-wandering (Smallwood & Andrews-Hanna, 2013). We found that pupil size was a more reliable predictor of attentional state in the context of the less demanding 0-back task than in the 1-back task. Although the interaction was not significant ($p = .081$), post–hoc analyses indicated a significant effect of pupil on cognition in the non-demanding 0-back task ($p < .0001$) and no evidence of an effect in the more complex 1-back task ($p = .155$). This may reflect the fact that in the less demanding condition of our experiment there is more freedom for attention to fluctuate for intrinsic reasons, and that these are being reflected in the pupil signal. Regardless of the specific interpretation, our data underscores the importance of characterising internal experience across multiple external conditions when attempting to explain their links to ongoing measures of physiology.

We also observed that the pupil signal was sensitive to the content of experience, indicating the need to take it into account. Our findings suggest that a focus on the past, and experiences with an intrusive aspect during the mind-wandering state, are associated with periods when the size of pupils is minimal. Other aspects of mind-wandering such as focus on the future, by contrast, were not associated with fluctuations in pupil size, but were instead modulated by the level of external demands in the concurrent task and the amount of time on task. This shows that the pupil signal does not capture information on all aspects of the mind-wandering state, a complex heterogeneous state whose behaviour changes in a complex fashion across different task conditions. Given these data it seems that the studies of mind-wandering reviewed in the introduction might have failed to reveal a consistent association with the pupil

signal because they have routinely failed to account for this contextual and experiential complexity. Moving forward, it is a priority for studies to take account of different experimental and situational influences in their experimental design.

In conclusion, our study suggests that there are two different physiological states that relate to reductions in the extent to which attention is devoted to the external environment, which differ on their psychological qualities. Assuming that spontaneous changes in baseline pupil size are related to intrinsic variation in arousal (Aston-Jones & Cohen, 2005), our data suggests that states of very high and very low arousal may induce situations when attention is not focused on external processing. However, our data suggests that these different states may not have identical psychological features. In both studies, slow responding to targets was preceded by unusually large pupils whereas smaller pupils were predictive of being off-task, and in particular of thoughts that were related to the past and that were intrusive in nature. In the future, it will be important to distinguish these two states of non-optimal external attention through the use of other metrics, such as their neural correlates or their associations to personality. More generally, as our study shows that different patterns of baseline pupil size discriminate between different attentional states, it underscores that it is dangerous to make generalisations directly from behaviour to experience because, at least in the context of our paradigm, these metrics do not agree (see Konishi & Smallwood, 2016) for a consideration of this issue).

5.5.1   Limitations and Future Directions

Our analysis used a short a priori defined window of ~3.5 seconds as determined by the jittering that our paradigm employed. This relatively short analysis window means our data is unable to determine whether there are longer-term trends in the pupil signal that may relate to ongoing experiential or behavioural states. Current accounts suggest that the pupil signal provides an indirect but reliable marker of activity in the locus coeruleus-norepinephrine system (Aston-Jones & Cohen, 2005) and that it characterizes the relative stability of ongoing cognitive and affective states, with smaller pupils indicating periods of greater stability (Hauser, Fiore, Moutoussis, & Dolan, 2016; Mittner, Hawkins, Boekel, & Forstmann, 2016b). With a longer analysis window it would be possible to explore whether the pupil signal can describe periods of experiential stability. This is an important question for future studies to address. Second, in our paradigm we did not ask participants to distinguish between intentional and unintentional mind wandering. These have been shown to be states that differ

in the context in which they arise, and in their relationship with task performance (Seli et al., 2016; Seli et al., 2016b; Thomson et al., 2014); furthermore, a recent study has shown these states to have dissociable relations to cortical thickness and intrinsic functional connectivity (Golchert et al., 2016). It is thus possible that intentional and unintentional off-task thought would have differential pupillometry signatures. Third, a recent study (Van Den Brink et al., 2016) has shown that the relation between pupillometric measures and attentional states can be modulated by time-on-task effects, which were not directly analysed in our study aside from the effect of multiple task sessions; future research could explore how time-on-task effects modulate more complex states such as the content of mind wandering. Fourth, recent work by Allen and colleagues (2016) has shown that aspects of the pupil signal are sensitive to meta-cognitive accuracy of perceptual judgements. The capacity to reflect on the contents of experience, known as meta-awareness, has been linked to the mind-wandering state (Schooler et al., 2011) and so it is possible that the pupil signal could shed light on our awareness of ongoing experience, perhaps highlighting how people catch their minds' wandering. Finally, one motivation for conducting this experiment was to identify whether there was information about internal states that can be derived from the pupil signal, with the ultimate aim of inferring mental states in the absence of introspection. Our study demonstrates that response time markers of sub-optimal performance have a similar property under conditions in which participants are, and are not, required to introspect on the contents of experience; this provides some evidence that introspection might not disrupt all markers of external cognition; importantly, however, this is different to showing that introspection does not alter the nature of ongoing experience. To assess this question, it will be necessary to develop independent methods of assessing information processing linked to the pupil signal, such as can be achieved by using fMRI or EEG, and understand if these metrics change when participants are asked to introspect on their own experiences.

Chapter 6. The Role of Practice in Task-Positive and Task-Negative Default Mode Network Activity

6.1 Introduction

Phenomena like mind-wandering illustrate that the focus of human cognition seamlessly switches between the external environment and our stimulus independent, inner thoughts, depending on the context (Smallwood & Schooler, 2015). While these transitions are frequent in everyday life, an adaptive cognitive system should be able to limit mind-wandering episodes when external demands are high, as in these situations MW leads to inaccurate performance (Kane & McVay, 2012; McKiernan, D'Angelo, Kaufman, & Binder, 2006; Teasdale et al., 1995), while allowing these off-task thoughts to arise in non-demanding situations (Kane et al., 2007; Levinson, Smallwood, & Davidson, 2012).

This closely matches the pattern of activation of the Default Mode Network (DMN), a set of regions of the brain that are active when cognition is focused internally and at rest, and that reduce their activity when executive demands increase (Gusnard & Raichle, 2001; Mckiernan, Kaufman, Kucera-thompson, & Binder, 2003; Raichle et al., 2001; Raichle & Snyder, 2007); indeed, the DMN is now known to be directly implicated in mind-wandering and internal cognition (Andrews-Hanna, Reidler, Huang, et al., 2010; Andrews-Hanna et al., 2014; Christoff et al., 2009; Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007; McGuire et al., 1996; McKiernan et al., 2006; Stawarczyk, Majerus, Maquet, et al., 2011).

However, core areas of the DMN, specifically the medial prefrontal cortex (mPFC) and posterior cingulate cortex (PCC), have been found to be also coupled with task-positive behavior (Crittenden, Mitchell, & Duncan, 2015; Konishi et al., 2015; Simony et al., 2016), including tasks that require cognition to be stimulus-oriented, that is, focused on the external environment (Gilbert et al., 2005; Small et al., 2003); furthermore, although mind-wandering is known to normally hinder task performance (Mcvay & Kane, 2009; Smallwood & Schooler, 2015; Unsworth & McMillan, 2012), activation in these areas has been associated with better performance in some tasks (Gilbert et al., 2005, 2006; Vatansever et al., 2015).

The flexibility in task-positive and task-negative behaviour of the DMN was illustrated in a study (Konishi et al., 2015) that modulated the executive demands of a task. The task used in

Konishi et al. (2015) featured a 0-back and a 1-back condition. In the 1-back condition, participants saw several non-target stimuli (NTs) before a target was presented, requiring a response based on the previously seen NT; to make a correct response, participants had to correctly encode every NT, and then retrieve it when a target appeared. In the 0-back, response to the targets was based on the information they could see on the screen at the time of the response; furthermore, the targets were preceded by several non-targets (NTs), which, differently from the 1-back condition, were not needed to make a correct target response. Hence, for long periods of the 0-back, participants' attention was free to drift off without this affecting their performance. Thus, using a hard, 1-back working memory task, and an easy 0-back task, activity in the DMN was found both for non-demanding phases of the 0-back, in which participants were free to mind wander, and for demanding phases of the 1-back, in which participants had to respond to a target by retrieving a previously encoded non-target stimulus. In particular, an overlap in activity was found in PCC and mPFC for both of these phases, which encouraged cognitive processes to prioritise internal, over external, information.

Moreover, the DMN is known to increase its activity as practice on a task increases, and this is closely related to an increase in mind-wandering (Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007); this is likely a consequence of the fact that as a task is practiced, the processes needed to perform it are automatized and the demands on the executive system decrease (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977; Teasdale et al., 1995). With the present study we investigated the role of task practice on the recruitment of the DMN in both the context of stimulus-independency, and task-positive behaviour: by following the work of Mason et al., (2007), the aim of the present study was to observe how task practice affects DMN activation using a paradigm which has been previously shown to selectively varies participants' executive demands, mind-wandering rates, and DMN recruitment (Konishi et al., 2015).

The work by Mason and colleagues (2007) showed that repeated practice of classic working memory tasks with a high executive demand, leads to an increase in DMN activity and mind wandering reports. The task used in Konishi et al. (2015) instead recruited the DMN for specific instances of task-positive behaviour related to retrieval of internal information, along with instances of stimulus-independency; by making participants perform the task repeatedly over several days, it is possible to investigate what is the effect of practice on DMN activity in a task that specifically recruits the network for normal performance. One possibility is that the

differences in the two task conditions used in Konishi et al. (2015) would increase, leading to a further increase in DMN activity both for periods of 0-back NTs and also in the context of task-positive behaviour, for the 1-back targets. Alternatively, and similarly to the work of Mason et al. (2007), after participants become very familiar with the task, an increase in DMN activity could be seen in the easier of the two tasks. In Mason et al. (2007) the increase in DMN activity was seen in tasks that were practiced relative to new tasks; in the present study, it could be seen in the 0-back condition relative to the 1-back. Finally, there is the chance that no differences will be observed between the results of the present study and the one of Konishi et al. (2015).

6.2 Methods

6.2.1 Participants

Thirteen healthy, right-handed participants (9 males, age range = 19-30 years, mean = 22.6 years) completed the study and received a total payment of £25 for their participation; participants were recruited by advert from the Department of Psychology and the York Neuroimaging Centre at the University of York. All investigation was conducted according to the principles expressed in the Declaration of Helsinki and all participants provided written informed consent at least 24 hours prior to completing the experiment. The Ethics Committee of the York Neuroimaging Centre and the Ministry of Defence Research Ethics Committee approved this study, including the process for gaining informed consent.

6.2.2 Task Paradigm

We used a variation of the 0-back/1-back task used in Konishi et al. (2015) and (Konishi, Brown, Battaglini, & Smallwood, 2017): the task features a 0-back and a 1-back working memory condition that continuously switch from one another throughout the experimental session (see Figure 5.1, top panel). The 1-back condition requires the participants' constant external attention for optimal performance, while the 0-back condition allows long periods of task disengagement without affecting performance. Furthermore, the two conditions differ on the type of target response required: in the 0-back condition, participants choose a response (left or right) based on information present on the currently observed stimulus, while in the 1-back condition participants base their response on the stimulus seen some seconds before.

Each condition block lasted on average 76 seconds (range = 42-165s) and the change of condition was signalled by a message ("SWITCH") that remained on screen for ~3 seconds. On each trial, the number of non targets (NTs) preceding targets randomly varied between 2 and 5; the number of targets per block varied from 3 to 5; the number of blocks per session was 2 for each condition; each session lasted 5 minutes and participants completed 5 sessions on each of the 3 days of testing. The average number of NTs for each session was 60 (~30 per condition), so that the total number of NTs analysed per participant was, on average ~900. The average number of targets for each session was 16 (avg. of 8 per condition), so that the total number of targets analysed per participants was, on average 240 (~120 per condition).

Presentation rate of the stimuli was jittered in steps of 0.05 seconds in the following way: fixation crosses ranged from 1.8 to 2.2 seconds; non-targets ranged from 1.3 to 1.7 seconds; targets from 2.1 to 2.5 seconds and remained on the screen for the whole duration, regardless of a participant's response; "switch" messages from 2.8 to 3.2 seconds.

6.2.3   Behavioural Analyses

The effects of task practice (sessions) and task condition on participants' reaction times were investigated using linear mixed models (LMM) as implemented in R through the package lme4 (D. Bates, Maechler, Bolker, & Walker, 2015). Reaction times were first log-transformed in order to normalise their distribution, and were then fitted in a series of LMMs which sequentially included task condition, and task session as fixed effect predictors of RTs. Participants and sessions were also modelled as random factors in the LMMs, in a nested fashion. We then compared models that that had both, either one, or zero predictors, with a likelihood ratio test, to see if the additional predictors would improve the model's fit. Fixed effects on the predicted variable were plotted using the effects (J. Fox, 2003) and ggplot2 (Wickham, 2009) R packages. Only correct targets were taken into consideration in all of our RT analyses. Finally, we analysed the effects of task condition and session on response accuracy using repeated measures ANOVA.

6.2.4   fMRI Data Acquisition

Imaging data was acquired at the York Neuroimaging Centre (YNiC) using an eight-channel phased-array head coil on a GE 3.0 Tesla Signa Excite HDx MRI scanner. Blood oxygen

level-dependent (BOLD) contrast images with fat saturation were acquired using a gradient single-shot echo planar imaging (EPI) sequence with the following parameters: scan duration 5 min and 10 seconds, repetition time (TR) 2000 ms, echo time (TE) 30ms, 155 volumes, flip angle 90°, matrix 64x64, field of view (FOV) 192mm, slice thickness 3mm, 36 slices with interleaved (bottom-up) acquisition order. The first 10 seconds were removed to allow magnetization equilibrium.

The functional data were co-registered onto high-resolution structural images which were available as they had been previously acquired for each of the participants (TR 7.8 ms, TE minimum full, flip angle 20°, matrix size 256 x 256 x 176, voxel size 1.13 x 1.13 x 1 mm). To facilitate the co-registrations, a high-resolution T1-weighted in-plane anatomical image was also acquired for all participants, using a fluid attenuated inversion recovery (FLAIR).

6.2.5   fMRI Pre-processing

All fMRI pre-processing and analyses were performed using FSL (Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012; Smith et al., 2004) version 5.0.8. We extracted the brain from the skull using the BET toolbox (Smith, 2002) for both the FLAIR and the structural T1-weighted images, and these scans were registered to standard space using FLIRT (Jenkinson & Smith, 2001). The following pre-statistics processing was applied to the resting state data; motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002); slice-timing correction using Fourier-space time-series phase shifting; non-brain removal using BET; spatial smoothing using a Gaussian kernel of FWHM 6mm; grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor; high pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100 s).

6.2.6   First Level Analysis

First and higher level analyses were conducted using the FSL FEAT toolbox (Smith et al., 2004). For our first-level analysis we modelled the time-series data of each 5-minute session for each participant, using general linear modelling (GLM) and including previously estimated standard motion parameters: we used an event-related design that included the onset and duration of the four types of events of interest, i.e. targets and non-targets for both of our two task conditions. Six contrasts were defined: 0-back targets > 1-back targets and the

reverse; 0-back non-targets > 1-back non-targets and the reverse; 0-back non-targets & 1-back targets (internal attention) > 1-back non-targets & 0-back targets (external attention), and the reverse. Only correct targets were included in the analysis.

6.2.7   Higher Order Analyses

Our second-level, analysis combined each first-level analysis for each subject using FSL's Local Analysis of Mixed Effects (FLAME) with fixed-effects, in order to extract the average activation for each of our contrasts. In addition to this, one other "session" covariate was projected onto the second level: this consisted in a vector of standardised values for each of the participants' fifteen sessions in order to observe any changes due to learning effects: for example, to observe the effect of task practice, a value of -1.56 was given for the 1st session, -1.34 for the 2nd... until value 1.56 for the 15th and last session.

Finally, the group-level analysis combined the second-level analyses for all participants using FLAME with mixed-effects, and one-sample t-tests were used to evaluate differences in our contrasts of interest. All analyses were cluster corrected using a z-statistic threshold of 2.3 and then corrected for multiple comparisons at $p < 0.05$ FWE. We also performed the same analyses using a more stringent z-statistic threshold of 2.6 which yielded almost identical results, and so we here report the more conservative threshold; the only exception regards the analysis concerning the session effect, which we discuss further below.

6.3   Results

Our experimental objectives were twofold: 1) we aimed to replicate the findings of (Konishi et al., 2015), in which DMN activity was found for blocks of stimulus-independent cognition and also for task-positive behaviour; 2) considering that DMN activity increases across sessions for tasks with a high executive demand (Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007), we asked participants to return to the lab over multiple days in order to observe the effects of practice on the afore mentioned task (Konishi et al., 2015), in which DMN activity is present in relation to task-positive behaviour, along to instances of stimulus independency. Understanding if, and how, the role of the DMN changes with practice, might help to elucidate the multiple roles of this network, from stimulus-independent mind

wandering (Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007), to performing a simple 1-back working memory task (Konishi et al., 2015).

6.3.1 Effects of Session and Condition on Accuracy

Firstly, we analysed the effects of task condition and task session on target accuracy, using repeated measures ANOVA. These revealed a significant effect of condition on accuracy, with participants being less accurate in the 1-back condition relative to the 0-back ($F(1, 12) = 11.26$, $p = .008$), and task session, ($F(14, 153) = 1.95$, $p = .026$), with accuracy improving across sessions. The interaction between the two within-subject variables was not significant ($F(14, 153) = 0.656$, $p = .813$).

6.3.2 Effects of Session and Condition on Reaction Times

Secondly, we used LMMs to analyse the effects of task practice and task condition on participants' reaction times. Both task condition ($\chi^2(1) = 335.27$, $p < .0001$) and session ($\chi^2(2) = 52.09$, $p < .0001$) contributed to improving the model's fit. As in (Konishi et al., 2017), participants' RTs were faster in the easier 0-back task than in the 1-back, and also decreased throughout the sessions, with practice. The interaction between the two fixed effects was non-significant ($\chi^2(1) = 0.0024$, $p < .961$). These analyses thus show an effect of learning through task practice across sessions, which does not seem to differ by condition; this replicates the findings of (Konishi et al., 2017). Results are shown in Figure 6.1 (panel C).

6.3.3 Task Differences – Targets

The two contrasts between periods of target response revealed different patterns of activations in the two conditions: targets in the 0-back condition (Figure 6.1, panel A) activated a set of core DMN regions more than targets in the 1-back condition, namely the mPFC, PCC, and dorsomedial prefrontal cortex (DMPFC). The opposite contrast (1-back Targets > 0-back Targets; panel B) revealed three main clusters of activation comprising the salience network (Seeley et al., 2007), in anterior cingulate cortex (ACC), bilateral insula, and one cluster in right dorsolateral prefrontal cortex (DLPFC), all areas found in the same contrast in Konishi et al., (2015). Results are summarised in Table 6.1 and shown in Figure 6.1, together with the

results of Konishi et al. (2015) for the same contrast, and the effect of task condition and task session on RTs, mirroring the results of (Konishi et al., 2017).
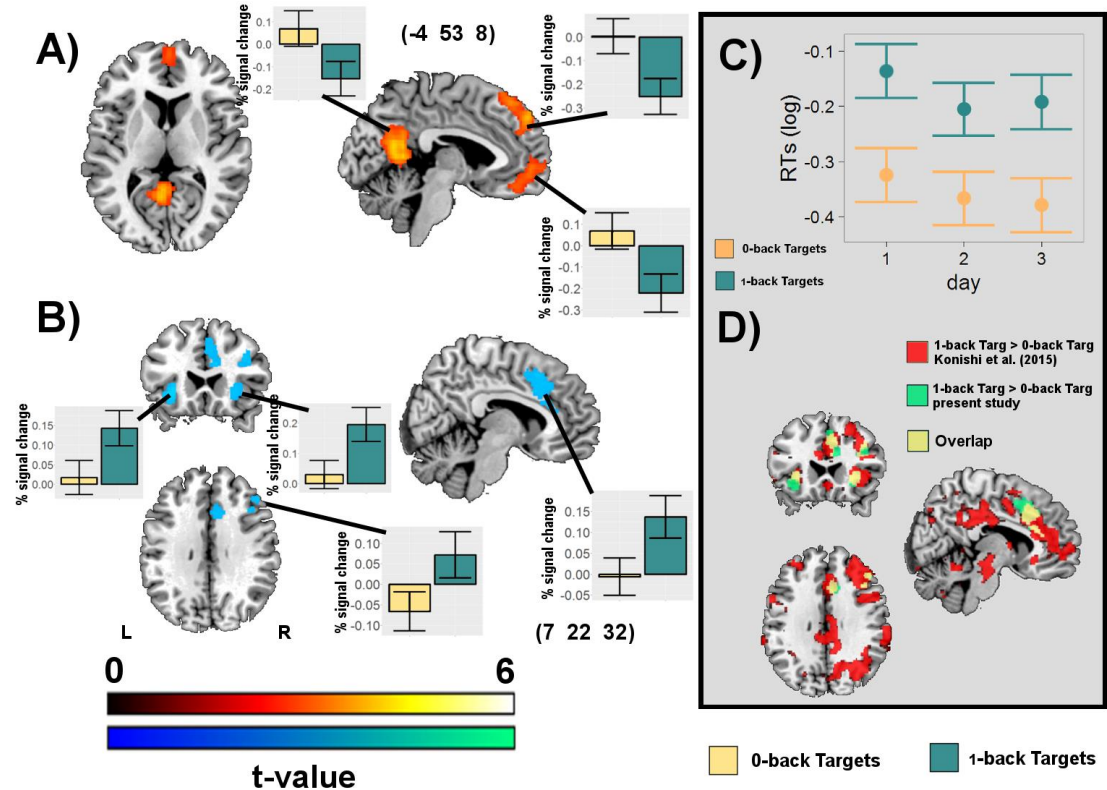
Figure 6.1 - Illustrated are the differences in brain activity during target presentation for the two task conditions, and the effect of practice on RTs. A) Activity in PCC, mPFC and DMPFC for 0-back targets. B) 1-back targets recruit the salience network (ACC and bilateral insula), and right DLPFC. C) For both conditions, RTs become faster as participants practice the task over multiple sessions. D) Illustrated, in yellow, is the overlap between the 1-back > 0-back target contrast of this study and Konishi et al. (2015), which is evident in the salience network and right DLPFC.

6.3.4   Task Differences – Non Targets

We identified a large set of regions that were significantly more active when participants attended to non-targets (NTs) in the 0-back condition compared to NTs in the 1-back condition. These included the medial prefrontal cortex (mPFC) and the posterior cingulate cortex (PCC), the two main hubs of the default mode network (DMN). These replicate the findings of Konishi et al., (2015) demonstrating that in the non-response period of this task the DMN is more active in the easier 0-back than more demanding 1 back. The opposite contrast (1-back NTs > 0-back NTs) yielded a cluster in the left intraparietal sulcus

(IPS)/superior parietal lobule (SPL), an area involved in goal-driven attention (Duncan, 2010; Luo et al., 2010; Singh-Curry & Husain, 2009) and part of the central executive network (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Sridharan, Levitin, & Menon, 2008). Results are summarised in Table 6.1 and shown in Figure 6.2, together with the results of Konishi et al. (2015) for the same contrast, and the dorsal attention network (Yeo et al., 2011).
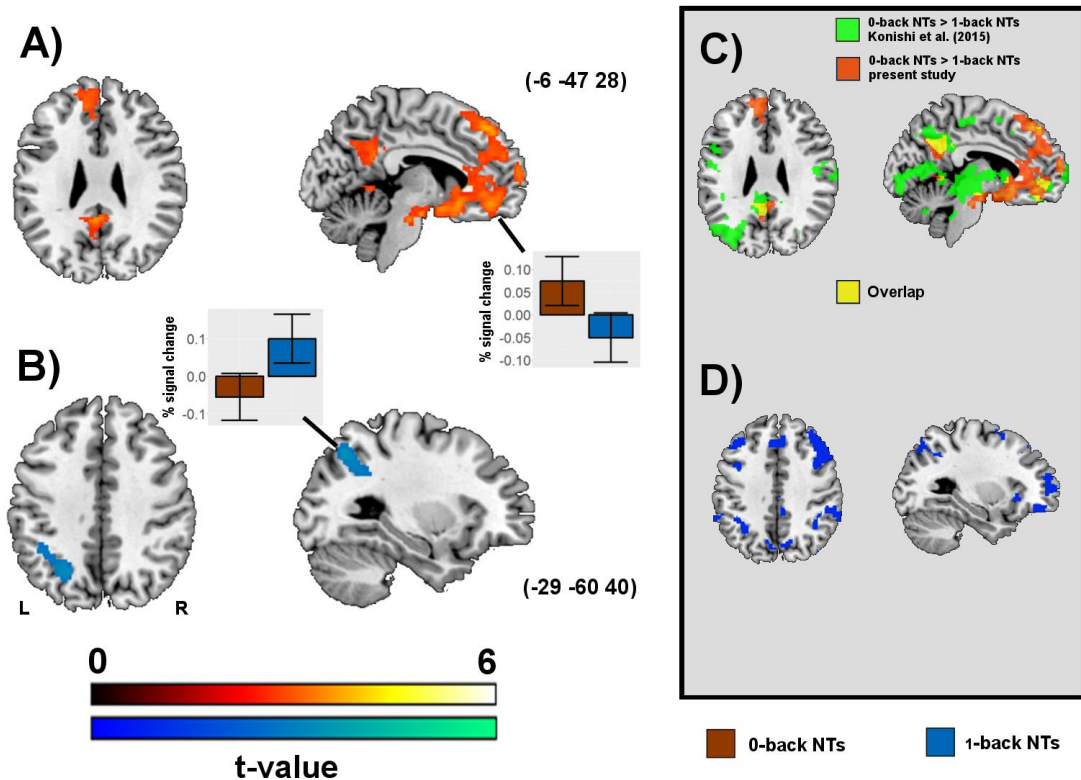
Figure 6.2 - Task-related differences in brain activity during presentation of non-targets. A) Stimulus-independent DMN activity during periods of 0-back NTs. B) 1-back NTs activity reveals a cluster in left IPS/SPL, part of the executive network. C) Overlap in PCC and mPFC (in yellow) during 0-back NTs between the present study and Konishi et al. (2015). D) The executive network/dorsal attention network as parcellated by Yeo et al. (2011).

6.3.5   Internal > External Attention

Periods of target response in the 0-back task, and the encoding of the non-targets in the 1-back task reflect situations when cognition is dependent on perceptual input, while the response periods in the 1-back task and the non-targets in the 0-back reflect periods of stimulus-independency. Contrasting periods of the task that required the participants' external attention produced a cluster in primary visual cortex (V1); conversely, the blocks of internal cognition

activated regions of the anterior cingulate cortex (ACC) and right insula. Results are summarised in Table 6.1 and shown in Figure 6.3, next to the visual and the salience network, with which they overlap (Seeley et al., 2007; Yeo et al., 2011).
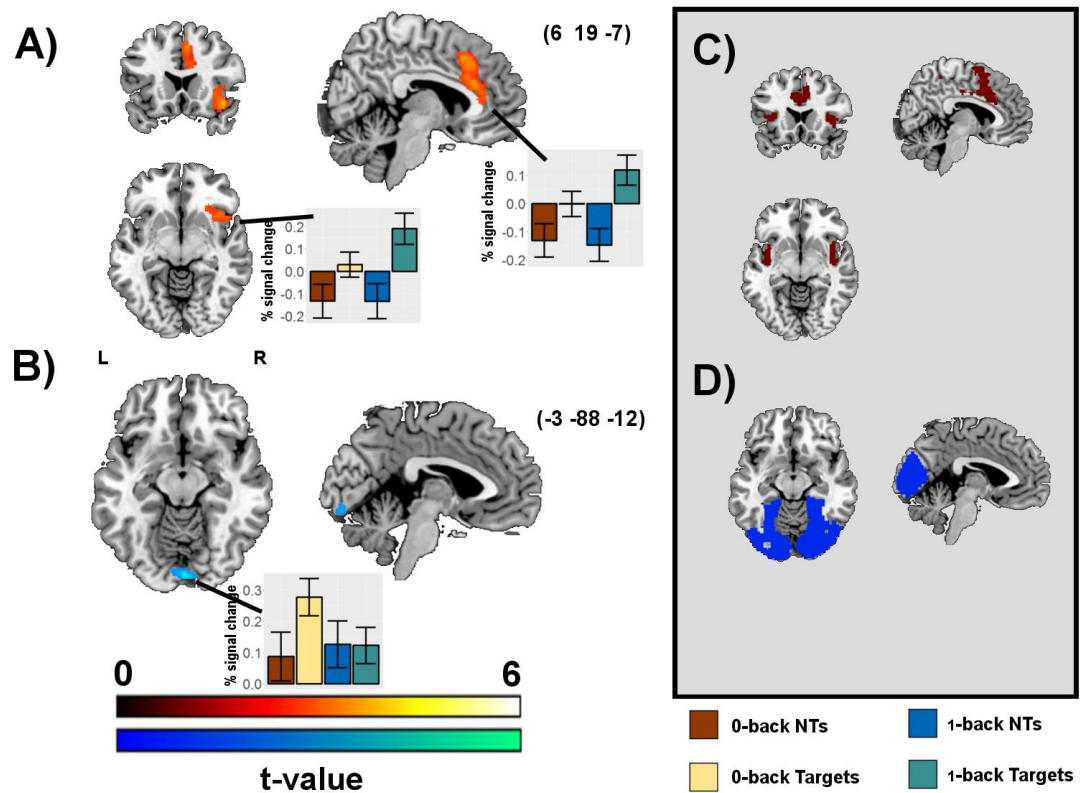
Figure 6.3 - Brain activity during task periods that promoted internal (1-back targets and 0-back NTs) or external (0-back targets and 1-back NTs) attention. A) The "internal" contrast yields the salience network, showing activity in ACC and right insula. B) The external contrast results in a cluster in primary visual cortex. C) The salience network, as parcellated by Yeo et al. (2011). D) Visual network, as parcellated by Yeo et al. (2011).

6.3.6   Session Effects on BOLD Response

Finally, we examined if these effects were moderated by task practice, that is, the number of sessions completed by the participants. We found that task practice changed the pattern of activation for the Internal > External contrast: a cluster in the medial prefrontal cortex (mPFC) resulted more active during the earlier task sessions, for the internal attention condition. The opposite effect, looking at clusters active during the later sessions, yielded no significant activations. Results are summarised in Table 6.1 and shown in Figure 6.4, next to the results of Konishi et al. (2015), showing overlap in the mPFC between the two maps.
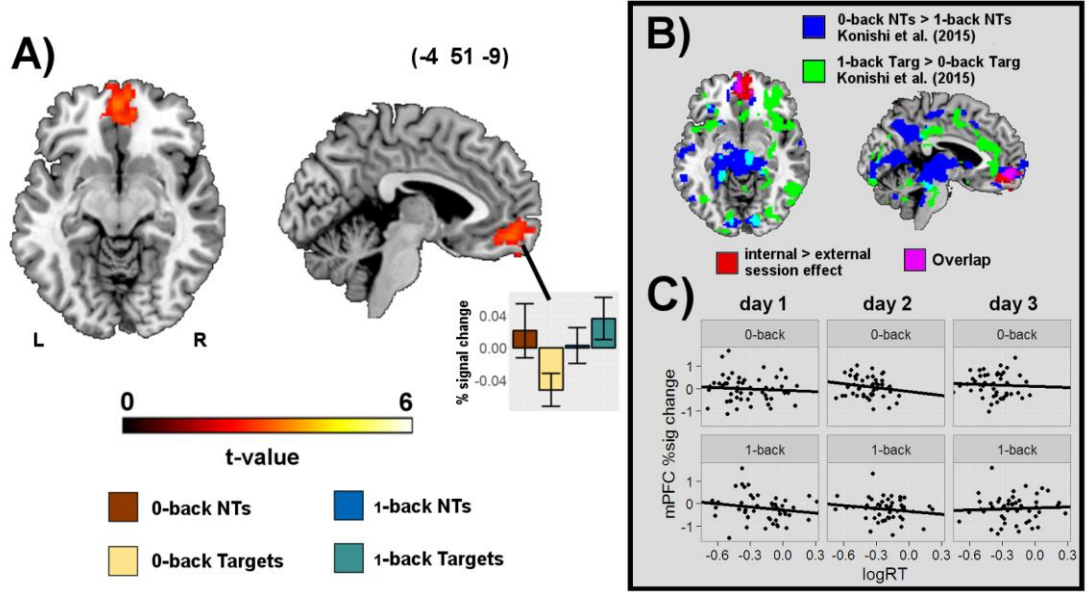
Figure 6.4 - A) The task session analysis reveals one cluster in mPFC which is more active during the initial sessions for task periods of internal attention (1-back targets and 0-back NTs). B) Overlap shown in purple between activity in this mPFC cluster and in the conjuction analysis of Konishi et al. (2015), which looked at common activity in 1-back targets and 0-back NTs. C) The relationship between RTs and mPFC activity during target presentation for both conditions, shown across the three days of testing; mPFC activity is linearly related to faster RTs (aside from the last day of testing in the 1-back), discounting the possibility that, at least in this context, it relates to stimulus-independent phenomena such as mind wandering.

Contrast	Covariate	Region	Cluster Size (voxels)	Peak Z	MNI Coordinates (x,y,z)	Cluster Centre of Gravity (x,y,z)	P value
NTs - 0-back > 1-back	-	DMN	10335	4.29	24 -40 -18	-5 3 0	<0.0001
NTs - 1-back > 0-back	-	Left IPS	568	3.75	-28 -66 46	-30 -59 43	0.0049
Targets - 0-back > 1-back	-	DMPFC	1516	4.4	-4 52 42	-9 40 44	<0.0001

Contrast		Region	Size	Peak	Coord 1	Coord 2	p-value
Targets - 0-back > 1-back	-	mPFC	1431	3.84	6 46 -18	0 49 -9	<0.0001
Targets - 0-back > 1-back	-	PCC	1187	4.3	-4 -60 10	-2 -57 18	<0.0001
Targets - 1-back > 0-back	-	ACC	686	3.69	8 24 22	7 18 37	0.0027
Targets - 1-back > 0-back	-	Left Insula	581	4.23	-34 22 -6	-34 17 0	0.0072
Targets - 1-back > 0-back	-	Right Insula	554	3.55	34 18 2	35 18 -1	0.0093
Targets - 1-back > 0-back	-	Right DLPFC	441	4.06	38 32 24	39 28 24	0.0284
Internal > External	-	ACC	792	3.67	6 28 22	5 25 28	0.0002
Internal > External	-	Right Insula	450	3.81	42 18 -12	38 17 -10	0.0098
External > Internal	-	V1	571	4.34	-24 -88 10	-19 -88 1	0.0024
Internal > External	Session	mPFC	927	3.61	-2 52 -12	0 52 -8	0.0090

Table 6.1 – Clusters showing significant activity for the left-column contrasts. The p-values represent the level of significance after correcting for the number of voxels in the brain

6.4 Discussion

Our results show several similarities with those of Konishi et al. (2015): in this study, non-targets stimuli in the 0-back condition, which don't require participants' attentional engagement, significantly activated the PCC and the mPFC more than the non-targets in the 1-back condition, which in turn needed to be encoded by the participants in order to perform the task correctly. The relation between DMN activity and periods of stimulus-independency are well-known, and have been directly linked to mind-wandering episodes (Andrews-Hanna et al., 2010; Christoff et al., 2009; Mason et al., 2007; Stawarczyk et al., 2011). On the other hand, presentation of targets in the 1-back condition, compared to the 0-back, was related to significant more activation of the ACC and bilateral insula, regions that activate for salient stimuli such as targets that prompt a behavioural response (Seeley et al., 2007), and right DLPFC, a region of the executive network often active during sustained attention and working memory (Curtis & D'Esposito, 2003); this pattern mirrors the findings for the same contrast in Konishi et al. (2015). Furthermore, at the behavioural level participants RTs showed the same pattern as in Konishi et al. (2015) and (Konishi et al., 2017), with faster RTs in the 0-back condition compared to the 1-back, and with RTs decreasing over the multiple sessions, as participants practiced more and more the task.

However, there were also important differences in the results of our two studies: activation of the mPFC and the PCC during target stimuli, which in Konishi et al. (2015) was found significantly more in the 1-back condition than in the 0-back, was shown to migrate to the 0-back condition with task practice, in the present study. The present study expanded the research of Konishi et al. (2015) by increasing the amount of time and practice that participants had on the task; while in our 2015 study participants performed a single experimental session, in this study participants came on three different days to be tested, performing the task three times as much, on average. In order to test if the differences in our results could be due to the effects of increased task practice, we ran another set of analyses, this time including task session as a covariate: selective activation of the mPFC was found for stimulus-independent periods (0-back NTs and 1-back Targets) during early task sessions (Figure 6.4, panel A), but not when looking at the overall results. These results mirror what found in Konishi et al. (2015) with participants performing a single session of the task; moreover, activity in the mPFC found for 1-back targets in Konishi et al., (2015), seems to decrease, relative to the 0-back task, with increasing task practice in the present study. This

pattern of activity is consistent with the results of Mason et al., (2007), in which increased task practice was related to an increase of activity in the mPFC (and PCC) for the easier, practiced tasks, compared to novel tasks. In our study, participants did not encounter novel tasks, but instead practiced both an easy and a hard task; after these tasks became well practiced, activity in the DMN and especially the mPFC, was mainly present in the easier, 0-back task, both for NTs and target stimuli. Moreover, activity of the mPFC seen during presentation of 0-back targets is more easily reconducible to task-positive behavior than mind wandering episodes, as it is directly related to faster RTs (Figure 6.4, panel C): notably, the relation between fast RTs and mPFC activity was not only true for the 0-back condition, but also for the 1-back with the exception of the third day of testing.

Activation of these areas, and in particular of the mPFC, during presentation of targets in simple choice reaction tasks such as our 0-back condition, has been shown before in multiple studies (Burgess et al., 2007; Gilbert et al., 2005, 2006), and has also been linked to better performance in these tasks. To test if the relationship between mPFC activity and better performance was also true for the targets in our 0-back condition, we decided to run a series of LMMs with the BOLD response in our mPFC cluster as the predicted variable, the log-transformed RTs as the main predictor, and with participants and sessions as nested random effects. Faster RTs were indeed predictive of higher mPFC activity either on their own ($\chi^2(2) = 23.67$, $p < .0001$) or taken into account together with task condition and task session ($\chi^2(1) = 3.87$, $p < .049$), confirming the fact that activity in the mPFC during target presentation could not be indicative of poor performance; this also suggests that mPFC activity in this context was likely not linked to mind wandering episodes, which are known to hinder task performance. The relationship between mPFC activity, RTs, task condition and task sessions (show over the 3 testing days) is illustrated in Figure 6.4, panel C.

One interpretation of these results is that throughout the three sessions, participants have learned to optimally encode the stimuli, while limiting their off-task thoughts to windows of time that wouldn't hinder task performance, such as the 0-back NTs. Activity in the mPFC and PCC has been previously linked to improved performance in spatial tasks (Small et al., 2003) and simple reaction tasks much similar to our 0-back condition (Gilbert et al., 2006; Vatansever et al., 2015). Furthermore, theoretical accounts of the mPFC have hypothesised it to have a key role in learning associations between different contexts and events (Euston, Gruber, & McNaughton, 2012); in modulating the relative influence between stimulus-oriented and stimulus-independent thought (Burgess et al., 2007); in learning and predicting

the likely outcomes of negative and positive actions (Alexander & Brown, 2012); and in the control and timing of goal-directed actions in the context of simple reaction time tasks (Bekolay, Laubach, & Eliasmith, 2014). In particular the two latter accounts have gained traction by explaining mPFC activity with very low-level functions: both theorise the mPFC as a crucial area in controlling goal-directed actions and learning their relation with their consequences. Our results are consistent with these accounts: mPFC activity was increased during the first part of the experiment (Figure 6.4, panel C), where most of the learning likely took place, and was also related to improved performance, especially in our simple reaction task (0-back condition). Related to our design, it is possible that the mPFC supports learning of optimal task-behavior across a number of sessions, which would initially revolve around the more difficult 1-back task; once this is achieved and the process is automatised, optimal 1-back task behavior could be supported mainly by the DLPFC, by maintaining working memory of the encoded NTs, and the salience network, by switching focus between external stimuli (a target triangle cue on the screen) and internal stimuli ("I remember that the triangle was on the right").

Accompanying these low-level accounts, a higher-level view of this pattern of results could see the mPFC and the DMN as areas crucial to conscious processing and decision-making: this would explain the activity in the initial sessions of the harder 1-back condition, when participants are still consciously focusing and learning to perform the task optimally, and the mPFC/DMN activity in the 0-back task across sessions, when participants are free to drift off to their own thoughts. Moreover, it is possible that once an easy task (such as the 0-back) is practiced enough, the DMN is able to support both mind wandering and task performance in an optimal manner, as it appears from our results. This is supported by a series of studies (Burgess et al., 2007; Gilbert et al., 2005, 2006) that found a relation between mPFC activity and improved performance in simple reaction time tasks similar to the 0-back used in the present study; the authors of these studies hypothesise that the mPFC regulates cognition between two modalities, an internal, stimulus-independent one, and an external, stimulus-oriented one. Importantly, they argue (Gilbert, Dumontheil, Simons, Frith, & Burgess, 2007) that mPFC activity in low-demand situations, such as in a task like the 0-back, could represent not only a state of stimulus-independent thought (during the NTs), but also a state of watchfulness of the external environment (e.g. waiting for a target to appear); while the former state is the one usually attributed to mPFC and DMN activity, the latter explanation might also be justified by the consistent finding that mPFC activity is directly related to positive task performance (such as faster RTs), as it was in the present study.

Secondly, in this experiment we examined the pattern of brain activation during periods of stimulus-independency (SI) versus stimulus-dependency (SD), which were present differentially in the two task conditions: non-targets needed to be encoded in the 1-back (SD), but not in the 0-back condition (SI), as in the latter, task performance completely depended on encoding of the target stimuli (SD); finally, to respond correctly to targets in the 1-back condition, participants needed to retrieve internal information regarding the previously encoded set of non-targets, and thus 1-back targets likely reflect a state of stimulus-independency relative to targets in the 0-back condition. During periods of stimulus-dependency, in which participants' attention was coupled with the external environment, we observed activation in a cluster in primary visual cortex. Conversely, during periods of stimulus-independency we observed significant more activation in areas of the ACC and right insula, regions comprising the salience network (Seeley et al., 2007).

The pattern or relative deactivation of primary visual cortex during periods of SI, compared to periods of SD, might reflect a process of perceptual decoupling: this term refers to the disengagement of attention from the external environment during internal cognition, such as during mind wandering episodes (Schooler et al., 2011; Smallwood, Beach, et al., 2008; Smallwood, McSpadden, & Schooler, 2007). Perceptual decoupling is known to reduce the capacity to encode external stimuli at the behavioural level (Smallwood, Baracaia, Lowe, & Obonsawin, 2003; Smallwood, Obonsawin, & Heim, 2003), such as hindering comprehension of read material (Schooler et al., 2004; Smallwood, McSpadden, et al., 2008); moreover, perceptual decoupling during periods of mind wandering has been shown to reduce cortical processing of external events in EEG studies (Barron et al., 2011; Kam et al., 2010; Smallwood, Beach, et al., 2008), and in at least one pupillometry study (Smallwood, Brown, et al., 2011). Previous research (Christoff et al., 2009; Smallwood, Tipper, et al., 2013; Smallwood, Brown, Baird, & Schooler, 2012) has shown a role of the DMN in maintaining internal cognition insulated from external distractions, and the pattern of activation of V1 found in this study likely reflects the same process at play, with decreasing activation of visual cortex during periods of stimulus-independency.

Moreover, in the present study periods of stimulus-independency (the "internal" condition) showed activation in ACC and right insula, regions of the salience network (Seeley et al., 2007); evidence from fMRI studies suggests that the primary role of the salience network involves integrating, detecting and then selecting "the most relevant among internal and extra-personal stimuli, in order to guide behaviour" (Menon & Uddin, 2010). In this context,

the salience network has also been shown to be heavily implicated in regulating behaviour and cognitive control through its regulation of DMN activity (Bonnelle et al., 2012) and the switching between the DMN and the executive network (Goulden et al., 2014; Sridharan et al., 2008). As previously noted, the paradigm used in this study encourages frequent switching between a stimulus-independent and a stimulus-dependent modality of cognition. While in the 1-back condition, participants have to continuously switch between perceiving and encoding newly encountered NTs (SD), and recalling their previous position to make a correct response when presented with a target stimulus (SI); in the 0-back condition, participants switch between responding to targets based on the stimulus they perceive (SD), while drifting off to their own self-generated thoughts during the presentation of the NTs, the encoding of which is not needed to perform the task. Fitting in this theoretical context, one interpretation for the pattern of activation of the salience network that is found in the Internal > External analysis (Figure 6.3, panel A), is that these areas are continuously selecting the most relevant stimulus for the individual, whilst regulating the switch between different networks needed to perform the task: this is evident in the 1-back condition, with the salience network active during presentation of target stimuli (Figure 6.1, panel B), helping to integrate between the perceived stimulus (two question marks plus the target shape in the middle: e.g. "where was the triangle?") and the internally memorised NT ("the triangle was on the right"), which was in turn encoded through activity of the executive network (Figure 6.2, panel B). This activity of the salience network during 1-back targets is also accompanied by activity of the right DLPFC, which is known to be crucially involved in working memory tasks such as the 1-back (Curtis & D'Esposito, 2003).

In conclusion, the present study's replicates the main results of Konishi et al. (2015) and expands them to investigate the role of task practice in modulating DMN recruitment both for task-positive behaviour, and mind wandering. Periods of stimulus-independency in the 0-back task, when participants on-task focus is at its lowest, engaged the PCC and mPFC, core hubs of the DMN. In the other task condition, 1-back targets recruited the right DLPFC, a known working memory area which is thought to redirect and maintain attention to internal information, regardless of task difficulty (Barch et al., 1997; Curtis & D'Esposito, 2003), and the salience network, both regions found in Konishi et al. (2015) for this contrast. Furthermore, the contrasts referring to periods of focused internal and external attention, revealed different patterns of activation, with the former engaging the salience network, and the latter engaging a confined cluster in primary visual cortex. Activity of the salience network, particularly engaged by 1-back targets (Figure 6.3, panel A), likely indicates a

124

process of recognising the relevant target (Menon & Uddin, 2010) and switching between different networks (e.g. DMN, executive network) needed to perform this task (Goulden et al., 2014); activity in primary visual cortex, which is maximal for 0-back targets and is then reduced for the other task stimuli (Figure 6.3, panel B), might reflect a pattern of perceptual decoupling, in which external attention is reduced when focusing on internal stimuli (Schooler et al., 2011).

Activity in the PCC and mPFC, which in Konishi et al. (2015) was present for both 1-back task-positive and 0-back stimulus-independent instances, was here observed throughout the testing sessions for the latter, but only at the outset of testing for the former. The role of the mPFC, and the DMN in general, for specific cognitive processes is still not pinpointed: while activity in these areas has been classically linked to periods of task-negative and stimulus-independent mind wandering (Andrews-Hanna, Reidler, Huang, et al., 2010; Christoff et al., 2009; Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007; Stawarczyk, Majerus, Maquet, et al., 2011), it has been shown that it can also be engaged by simple reaction time tasks (Gilbert et al., 2006; Vatansever et al., 2015), or more complex working memory tasks (Konishi et al., 2015; Spreng et al., 2014). One account of mPFC activity (Burgess et al., 2007; Gilbert et al., 2007) sees this area as a gateway for internal and external cognition, regulating the focus on internal information while maintaining watchfulness of the external world, depending on the environment's demands. Following the results presents in the literature and the ones of the present study, it is likely that the role of the mPFC adapts to repeated task practice: activity in this area was observed early on in the harder of two tasks (Figure 6.4, panel A), and then migrated to the easier 0-back condition across sessions, potentially reflecting a role of the mPFC in supporting the learning process of a task that relies on internal information, along with its acknowledged role both in simple reaction time tasks, and during stimulus independent mind wandering.

Chapter 7.   General Discussion

7.1   Summary of Findings

The field of mind wandering research has rapidly developed over the past two decades, in large part thanks to the advances in neuroimaging methodologies such as fMRI. Scientists have used many different experimental paradigms for the study of MW, but a standard paradigm has never emerged. Furthermore, certain neurophysiological correlates (NCs) of MW have been identified, but some are not exclusive to the MW phenomenon (e.g. the DMN), while there are mixed results for others (e.g. big or small pupils during MW episodes): for these reasons, we are still not yet able to identify a MW episode by only relying on its NCs, which should be the end goal of a covert, objective marker of the phenomenon. The research presented in these chapters aimed to develop a paradigm to study mind wandering, and then use it to investigate MW's neural and pupillary correlates, in order to understand their potential as objective markers of this phenomenon.

7.2   Developing a Mind Wandering Paradigm

A dual-task paradigm (the 0-back/1-back) was developed by alternating an easy reaction-time task and a harder working-memory task, so as to modulate the participants' internal experiences. In the three studies presented here, this paradigm effectively modulated both objective and subjective indicators of participants' performance and task focus. First, by taking advantage of the known modulatory effect of task demands on MW frequency, our paradigm varied participants' external attention, as MW reports increased in the 0-back condition, and decreased in the harder 1-back. Secondly, participants showed consistent behavioural differences in accuracy and RTs in the two tasks, resulting in improved performance in the easier 0-back task. These results agree with the *context-regulation* hypothesis idea that the consequences of mind wandering depend on the context in which it emerges: when arising in a non-demanding task, MW frequency did not appear to impact task performance. Finally, the pupillometric and neural measures acquired in the different studies also showed sensitivity to our manipulation, resulting in differences in baseline pupil size and brain activity patterns in the two task conditions: baseline pupil size was larger in the 1-back

task, signalling increased cognitive effort, while DMN activity was overall more pronounced in the easier 0-back task.

The 0-back/1-back paradigm confirmed that it is possible to modulate MW occurrence, and potentially MW content, in an experimental setting by varying the executive demands of a task. Alternating a demanding and an easy task required participants to maintain focus during certain critical periods, and at the same time allowed them to drift off during other instances, without affecting task performance. This setup allows the experimenter to investigate the different physiological correlates of on-task and off-task states, and their behavioural consequences.

7.3   A Marker for Mind Wandering

This paradigm was then used to investigate the potential of pupillometric and fMRI measures as objective markers of mind wandering. Developing a covert marker of a subjective phenomenon such as MW would allow experimenters to measure aspects of this experience without relying on self-reports: these, while remaining the current golden standard for accessing individuals' internal thoughts, suffer from several issues, the chief of which is their inherent subjectivity (Konishi & Smallwood, 2016).

7.3.1   Baseline Pupil Size as a Marker of Mind Wandering

The study presented in Chapter 5 explored the pupillary dynamics of MW and of external attention. The results of this study replicated findings in the literature that both small and large baseline pupil sizes are linked to states in which attention is not optimally tuned to the external environment (Aston-Jones et al., 1999; Mittner et al., 2014; Smallwood, Brown, et al., 2011; Unsworth & Robison, 2016; Van Den Brink et al., 2016); however, this study provided evidence that these states might have different qualities. While small pupil sizes were linked to self-reports of mind wandering, and in particular of intrusive thoughts and thoughts regarding the past, large pupils tracked task errors and slow RTs. Moreover, while some aspects of MW were sensitive to the pupil signal, such as intrusive and past thoughts, others were not, but instead were modulated by task context: for example, thoughts about the

future, or thoughts in the form of images, were more likely in the easier 0-back task. At the same time, task context also modulated the capacity of the pupil signal to predict self-reported task focus, as shown in the 0-back condition.

These findings are particularly important in for the development of a marker of MW: while triangulating a psychological phenomenon such as MW is best achieved through a combination of self-reports, behavioural indices, and physiological measures (Konishi & Smallwood, 2016), this study shows that these might not always agree, and that generalisation from one measure to another should be made with caution. While MW has been linked to poor behavioural performance in previous studies, the results of Chapter 5 suggests that it is not advisable to use solely behavioural indices as markers of MW, as in our study these measures were differentially linked to the pupil signal: behavioural performance can be modulated by other types of attentional fluctuations such as external distractions, which have been shown to have a different pupil fingerprint than MW (Unsworth & Robison, 2016).

The results of Chapter 5 agree with other recent findings (Mittner et al., 2014; Unsworth & Robison, 2016; Van Den Brink et al., 2016) that baseline pupil size can track a variety of off-task states and lapses of attention. However, the findings presented in this chapter highlight the sensitivity of the pupil signal to task context, and the content of MW. This suggests the potential of using baseline pupil size as a marker of MW, but critically, only while taking into account its content, and the context in which it occurs.

7.3.2   The Default Mode Network as a Marker of Mind Wandering

The DMN has been notoriously linked to off-task and MW states (Andrews-Hanna, Reidler, Huang, et al., 2010; Christoff et al., 2009; Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007), together with a range of other cognitive processes, from semantic memory (Binder & Desai, 2011) Using the 0-back/1-back paradigm, this study showed evidence that the DMN can be recruited by a simple working memory task, provided that it requires participants to process internal information. This result joins a recent series of studies (Spreng et al., 2014; Vatansever et al., 2015) showing that DMN activity is not only relegated to off-task, stimulus-independent instances, but can actively contribute to task performance.

Along with supporting a range of cognitive processes, DMN activity has been previously shown to increase as a task becomes well practiced, and that this is closely linked to an

increase in MW (Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007). The study presented in Chapter 6 explored the effects of task practice on the DMN, by replicating the study of Chapter 4 and allowing participants to become very familiar with the 0-back/1-back paradigm over several testing sessions. While MW-related DMN activity did not appear to be influenced by task practice in our paradigm, task-positive mPFC activity was found in the harder 1-back condition in the initial sessions, similarly to what found in Chapter 4. Importantly, task-positive mPFC activity migrated to the easier 0-back condition across task sessions, reflecting a potential role of this area in supporting the initial phases of a task relying on internal information (1-back).

The results from the studies presented in Chapter 4 and Chapter 6 join other recent findings (Gilbert et al., 2006; Spreng et al., 2014; Vatansever et al., 2015) showing that the DMN can be actively recruited for task performance. In these studies, we did not acquire a direct measure of mind wandering to link this phenomenon to DMN activity: however, there is now increasing evidence that the DMN is not exclusively active during off-task states such as mind wandering, and furthermore, that it can directly contribute to on-task states. Aside from shifting our perception of this network, which for a long time was dubbed as "task-negative", these findings underscore the caution needed, in thinking of using DMN activity as a marker for MW. Indeed, these studies suggest that a measure of DMN activity in isolation, without considering the task context in which it occurs, is not informative in discerning an individual's state of on-task from a state of off-task.

Overall, the results from the three empirical chapters presented in this thesis hint to the fact that, a complex and heterogeneous phenomenon such as mind wandering might be better understood when taking account both the content of the experience, as well as the context in which it occurs. Indeed, these have both shown that they can have an influence not only on MW itself, but on its behavioural and physiological indices as well.

7.4 Directions for Future Research

Developing a marker for a complex phenomenon such as mind wandering is not an easy feat. In the fMRI domain, the DMN was long considered an indicator of being off task, but recent findings show that is it not always the case. Pupillometry has been also used in a similar manner, but the findings presented in this thesis suggest that its predictive power is dependent

on the content of the experience, and the context in which it occurs. Finally, behavioural indices of attentional state, such as error rates and RTs, are not selective enough: a participant could make a slow response because he was lost in his own thoughts, because he was distracted by a loud noise, or even because he was being overly cautious.

Ideally, a marker of mind wandering would have certain qualities. It would be covert and objective, that is, it would be measurable without relying on participants' introspection. Importantly, a perfect marker would be both necessary and sufficient to describe the individual's internal experience. Until this point, mind wandering research has identified correlates of MW which appear to be necessary, but not sufficient, for this phenomenon's existence: a prime example is the DMN, which is routinely found to precede reports (Allen et al., 2013; Christoff et al., 2009; Stawarczyk, Majerus, Maquet, et al., 2011) of MW, but whose activity can also appear in other contexts. On the other hand, the field relies of self-reports, which are sufficient for the researcher to describe an episode of MW, but not necessary for the phenomenon to exist. In future research, necessity and sufficiency for a marker might be achievable in specific contexts by combining self-reports and multiple physiological measures.

The studies presented in this thesis analysed at most two of these potential markers at the time (one physiological, and one behavioural or self-reported measure), in order to understand participants' attentional states. For example, the combination of brain activity and RTs can inform us that mPFC activity is linked to fast RTs and is thus likely not linked to a state of MW; alternatively, pupillometry and thought probes were combined to understand the link between baseline pupil size and the content of one's thoughts. This approach might not be enough to develop a marker of MW which would be independent of a participant self-report. If that's to be achieved, it is likely that a combination of at least two, if not three, physiological measures would be needed, together with behavioural and self-report measures for at least the first phase of development. A future study could, for example, combine fMRI with pupillometry using our paradigm: following the findings in the literature and the results presented in this thesis, it is conceivable that a pattern of DMN activity and abnormally small pupils preceding a slow response to a target, would be linked to a state of MW. This could be initially assessed with experience sampling, which remains the current golden standard to understand a participant's inner world. By stacking different measures that all relate to MW (e.g. fMRI, self-reports, pupillometry, etc.), it is possible to identify the variance that is

common between them and thus increase the chances of triangulating the desired phenomenon.

Context is also extremely important when inferring MW. For example, some measures are particularly suited for certain contexts: in a difficult task, behavioural indices might tell us something about participants' attentional state; however, if the task is too easy, a participant might be able to perform perfectly without having to focus too hard. An experienced driver can drive home while lost in his own thoughts without making any mistake, while a novice would likely pay a distraction dearly: behavioural mistakes and attentional states would only be linked in the latter case, in this example. Conversely, pupillometry appears to be more informative of a participants' fluctuations in attention during an easy task. Similarly to context, certain markers could be sensitive to the content of MW, as pupillometry appears to be.

For these reasons, future research should first attempt to develop a marker of MW focusing on very specific contexts, and it should take into account the content of the experience. As recent studies have found, a marker of MW while driving (He, Becic, Lee & McCarley, 2011) can differ from a marker of MW while reading (Bixler & D'Mello, 2016; Faber, Bixler, & D'Mello, 2017); in the same way, a marker for creative, future-related MW might differ from one tracking ruminative thoughts. Generalisation to any context, and content, would be a successive step, potentially achievable after recognising the commonalities between the different markers.

7.5   Concluding Remarks

To conclude, the research presented in this thesis developed a new task for the study of mind wandering. This paradigm was then used in a series of studies investigating the neural and pupillary correlates of this phenomenon, in order to understand their potential as objective markers. These studies show that the default mode network, the most consistent network associated with MW and off-task states, can be also recruited for task-relevant goals, and its activity is modulated by context and task-practice. Furthermore, this data shows that the pupil signal is able to track MW states, but that it is also highly sensitive to task-context and to the content of the thoughts experienced. These results suggest that it will be crucial, for future research aiming to develop an objective marker of a complex and heterogeneous phenomenon

131

such as mind wandering, to take into account the content of the experience, and the context in which it occurs.

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