An fMRI investigation of the relationship between future imagination and cognitive flexibility

R.P. Roberts[a,*], K. Wiebels[a], R.L. Sumner[a], V. van Mulukom[a,b], C.L. Grady[c], D.L. Schacter[d], D.R. Addis[a,e]

[a] School of Psychology and Centre for Brain Research, The University of Auckland, Auckland, New Zealand
[b] Centre for Research in Psychology, Behaviour and Achievement, Coventry University, Coventry, UK
[c] Rotman Research Institute at Baycrest Hospital and Departments of Psychiatry and Psychology, University of Toronto, Toronto, Canada
[d] Department of Psychology and Center for Brain Science, Harvard University, Cambridge, MA, USA
[e] Brain Research New Zealand, New Zealand

ARTICLE INFO

ABSTRACT

While future imagination is largely considered to be a cognitive process grounded in default mode network activity, studies have shown that future imagination recruits regions in both default mode and frontoparietal control networks. In addition, it has recently been shown that the ability to imagine the future is associated with cognitive flexibility, and that tasks requiring cognitive flexibility result in increased coupling of the default mode network with frontoparietal control and salience networks. In the current study, we investigated the neural correlates underlying the association between cognitive flexibility and future imagination in two ways. First, we experimentally varied the degree of cognitive flexibility required during future imagination by manipulating the disparateness of episodic details contributing to imagined events. To this end, participants generated episodic details (persons, locations, objects) within three social spheres; during fMRI scanning they were presented with sets of three episodic details all taken from the same social sphere (*Congruent* condition) or different social spheres (*Incongruent* condition) and required to imagine a future event involving the three details. We predicted that, relative to the *Congruent* condition, future simulation in the *Incongruent* condition would be associated with increased activity in regions of the default mode, frontoparietal and salience networks. Second, we hypothesized that individual differences in cognitive flexibility, as measured by performance on the Alternate Uses Task, would correspond to individual differences in the brain regions recruited during future imagination. A task partial least squares (PLS) analysis showed that the *Incongruent* condition resulted in an increase in activity in regions in salience networks (e.g. the insula) but, contrary to our prediction, reduced activity in many regions of the default mode network (including the hippocampus). A subsequent functional connectivity (within-subject seed PLS) analysis showed that the insula exhibited increased coupling with default mode regions during the *Incongruent* condition. Finally, a behavioral PLS analysis showed that individual differences in cognitive flexibility were associated with differences in activity in a number of regions from frontoparietal, salience and default-mode networks during both future imagination conditions, further highlighting that the cognitive flexibility underlying future imagination is grounded in the complex interaction of regions in these networks.

1. Introduction

Much recent research has focused on the notion that the brain is a fundamentally prospective organ (Schacter et al., 2007), using information gleaned from the present environment and past memories to generate predictions about the future. Indeed, much of our time is consumed by various types of future-oriented thoughts that range in their depth and flexibility (Szpunar et al., 2014). Like many species,

humans can enlist inflexible reproductions of memorized or instinctual behaviors in a future-directed fashion (Suddendorf and Corballis, 2007). Humans, however, can also construct mental simulations of novel future events in sufficient detail to support effective planning (Buckner and Carroll, 2007; Gilbert and Wilson, 2007; Schacter, 2012; Schacter et al., 2012; Schacter and Addis, 2007). In fact, it is likely that the ability to simulate experiences beyond the immediate present environment underlies the human capacity to respond flexibly to

unexpected changes in the environment (Buckner and Carroll, 2007; Suddendorf and Corballis, 2007).

The constructive nature of the episodic memory system (Bartlett, 1932; Schacter et al., 1998) makes it well-suited to support the construction of novel simulations. According to the constructive episodic simulation hypothesis (Schacter and Addis, 2007), the storage of episodic memories as a pattern of features distributed across the cortex (Damasio, 1989; Schacter et al., 1998; Squire, 1992) facilitates the extraction of episodic details—such as familiar people, places and objects—as content for simulations. Support for the idea that *access to* episodic memory is required for simulation comes from neuroimaging studies reporting that both memory and simulation engage a core network of regions overlapping substantially with the default mode network (DMN; Benoit and Schacter, 2015; Schacter et al., 2012; Schacter et al., 2007) as well as patient studies documenting corresponding deficits in episodic memory and simulation (Addis et al., 2009b, 2008; Andelman et al., 2010; Hassabis et al., 2007; Klein et al., 2002; Kwan et al., 2010; but see also Squire et al., 2010). In addition to episodic memory, semantic memory also plays a critical role in future simulation, providing a scaffold for event representations (Irish and Piguet, 2013). Indeed, without access to semantic memory, future simulation is impaired (Duval et al., 2012; Irish et al., 2012; Viard et al., 2014), and interestingly the network associated with semantic memory overlaps considerably with the DMN (Binder and Desai, 2011; Binder et al., 2009; Burianova et al., 2010) further suggesting a critical interplay between these systems during simulation.

According to the constructive episodic simulation hypothesis, extracted episodic details must also be *recombined* into a coherent event simulation. This recombinatory ability is thought to be central to *flexibly* imagining the future – to construct as well as disassemble and rework the components of scenarios to create different outcomes to enhance future behavior (Addis et al., 2016; Schacter and Addis, 2007). Despite this theoretical importance, little is known about the recombination process, including its neural correlates. Much of the existing evidence rests on neuroimaging reports of increased activity during the simulation of future events relative to remembering past events (e.g., Addis et al., 2010; Addis et al., 2007; Benoit and Schacter, 2015). Increased activity for future imagination relative to remembering the past has been interpreted as reflecting the recombination of episodic details into a coherent scenario because, by definition, the details comprising a novel event are less congruent than the details previously bound into a past event, and thus should impose higher demands on recombinatory processes. Regions across the DMN have been reported as exhibiting such effects, including frontopolar/dorsomedial and dorsolateral prefrontal cortex, lateral temporal and parietal cortex, precuneus, posterior cingulate, and hippocampus (Abraham et al., 2008; Addis et al., 2010, 2007, 2009a; Gilmore et al., 2016; Szpunar et al., 2007; Viard et al., 2011; for a meta-analysis, see Benoit and Schacter, 2015).

The hippocampus has been a focus in the study of recombination during simulation – perhaps unsurprising given the established role of this structure in relational processing, including the binding together of disparate elements during working memory as well as episodic encoding and retrieval (Axmacher et al., 2010; Eichenbaum, 2001; Hannula and Ranganath, 2008; Hannula et al., 2006; Staresina and Davachi, 2009). Indeed, the simulations generated by hippocampal amnesics are not only sparse in episodic detail but also less coherent than those of healthy controls (Hassabis et al., 2007). Hippocampal amnesics are diminished in their ability to imagine future events that draw heavily on semantic information (e.g. the presidential election in 2032), suggesting the hippocampus may also play a role in the binding together of semantic details to produce complex semantic representations (Race et al., 2013). Moreover, simulation-related hippocampal activity is greatest when constructing future events for the first time (Gaesser et al., 2013; van Mulukom et al., 2013), particularly when these events are specific in nature (Addis et al., 2010) and comprise

greater amounts of detail (Addis and Schacter, 2008; Madore et al., 2016b). These construction effects are evident even when controlling other possible determinants of hippocampal activity such as event novelty (Gaesser et al., 2013) and encoding (Martin et al., 2011; for additional discussion see Schacter et al., in press). Interestingly, Weiler et al. (2010) found that simulating less probable events (that likely involve more incongruent combinations of details) engages the hippocampus more than commonplace, high probability events, although the disparateness of details was not directly measured.

This evidence, however, is limited in that these studies provide only *indirect* support of the recombination process; as yet, the effects of explicitly modulating recombinatory demands on simulation-related brain activity have not been investigated directly. Moreover, the focus on the hippocampus has been at the expense of characterizing recombination effects in other DMN regions. Thus, the current study is the first to experimentally manipulate the disparateness of details comprising future simulations, thereby directly testing this hypothesized function of the hippocampus and exploring the effects on extra-hippocampal regions during future simulation.

In addition to recombinatory processes, we propose that successfully organizing disparate elements into a coherent scenario places demands on other domain-general processes supported by networks outside of the DMN. One such process is spontaneous cognitive flexibility (Eslinger and Grattan, 1993) which refers specifically to the ability to spontaneously generate a diversity of ideas (in contrast to reactive cognitive flexibility – the ability to shift mental set in response to changing environmental demands). Spontaneous cognitive flexibility (referred to hereafter as cognitive flexibility) involves the ability to "break conventional or obvious patterns of thinking" (Dietrich, 2004, p.1014) in the service of generating novel ideas, and as such can be indexed by divergent thinking[1] measures (Eslinger and Grattan, 1993; Tomer et al., 2002), such as the flexibility measure of the Alternate Uses Task (AUT; Guilford, 1967). Indeed, this domain-general ability supports many forms of creative processing, including music, poetry and, relevant here, imagination (Beaty et al., 2016). Consistent with the notion that cognitive flexibility is important for recombining disparate details during simulation, Addis et al. (2016) found that the amount of episodic detail comprising future simulations was positively associated with divergent thinking as measured by the AUT.

It is important to note that although divergent thinking has been linked with the DMN, in particular the temporal pole and hippocampus (e.g. Benedek et al., 2014a; Ellamil et al., 2012; Takeuchi et al., 2011) this activity reflects the associative component of the task and is distinct from the executive component of the task – namely, cognitive flexibility – that is grounded in frontoparietal control network (FPCN) activity, especially lateral frontopolar cortex, including the rostrolateral prefrontal cortex (Benedek et al., 2014b; Gilhooly et al., 2007; Niendam et al., 2012). Indeed, FPCN is particularly active during tasks that require cognitive flexibility and consistent with its domain-general role, the FPCN influences the activation of *other* task-specific networks (Cole et al., 2013). For instance, Beaty et al. (2015) found that FPCN regions (e.g., rostrolateral and dorsolateral prefrontal cortex) were functionally coupled with DMN regions during a divergent thinking task; moreover, the insula (part of the salience network, SN) was also coupled with the DMN in the early stages of the task, likely supporting the switching between large-scale networks (Menon and Uddin, 2010). In addition, the same study showed that more cognitively flexible individuals (i.e. those with the most creative responses in the AUT) exhibited increased coherence between FPCN and DMN regions. Additionally, it has been shown that during flexible future planning, the FPCN couples with DMN regions (Spreng et al., 2010), supporting

---

[1] While divergent thinking is often defined as synonymous with "creativity", in of itself, it is just one component of the creative thinking faculty, along with convergent thinking, working memory, sustained attention, etc. (Dietrich, 2004).