Isolated from input: Transmodal cortex in the default mode network supports perceptually-decoupled and conceptually-guided cognition

Abbreviated Title – Distant memories

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Abstract

The default mode network supports a variety of mental operations such as semantic processing, episodic memory retrieval, mental time travel and mind-wandering, yet the commonalities between these functions remains unclear. One possibility is that the default mode network supports cognition that is independent of the immediate environment; alternatively or additionally, it might support higher-order conceptual representations that draw together multiple features. We tested these accounts using a novel paradigm that contrasted decisions based on perceptual and conceptual features, while separately manipulating whether these decisions were driven by features in the environment or recovered from memory. Task-based fMRI identified regions that responded when stimulus independence and semantic retrieval were combined: these included left and right angular gyri and left middle temporal gyrus. Although these sites were within the default mode network, they showed a stronger response to demanding memory judgements than to an easier perceptual task, contrary to the view that they support automatic aspects of cognition. In a subsequent analysis, we showed that these regions were located at the extreme end of a macroscale gradient, which describes gradual transitions from sensorimotor to transmodal cortex. This shift in the focus of neural activity towards transmodal default mode regions might reflect isolation from specific sensory inputs, both when decisions are guided by conceptual as opposed to perceptual features and when cognitive states are generated in the absence of input.

Key words: transmodal cortex, default mode network, semantic, conceptual processing, stimulus independence.

Highlights

- Brain regions supporting meaning overlap with stimulus independence.
- Bilateral angular gyri and left MTG respond strongly to both features of cognition.
- These patterns reflect a shift in activity towards regions of transmodal cortex.
- Complex memory representations may emerge in cortical areas distant from input.

1. Introduction

Although early studies characterized the default-mode network (DMN) as "task negative", this network actively supports aspects of cognition (Spreng, 2012), including semantic processing (Binder, Desai, Graves, & Conant, 2009; Krieger-Redwood et al., 2016), episodic recollection (Rugg & Vilberg, 2013), working memory (Konishi, McLaren, Engen, & Smallwood, 2015; Spreng et al., 2014; Vatansever, Menon, Manktelow, Sahakian, & Stamatakis, 2015), autobiographical planning (Spreng, Gerlach, Turner, & Schacter, 2015; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010), self-generation of emotion (Engen, Kanske, & Singer, 2017) and imagining the future or the past (Schacter & Addis, 2007). Although we lack an over-arching account of a core function for the DMN, many of these situations involve memory retrieval – i.e., a requirement to focus cognition on previously-encoded knowledge, as opposed to information in the external environment. In line with this account, many regions within or allied to the DMN are considered to be heteromodal 'hubs' for memory-related processes, including the posterior cingulate cortex (Leech, Braga, & Sharp, 2012; Leech & Sharp, 2014), angular gyrus (Binder & Desai, 2011; Bonnici, Richter, Yazar, & Simons, 2016; Seghier, 2013), hippocampus (Moscovitch, Cabeza, Winocur, & Nadel, 2016) and anterior temporal lobes (Lambon Ralph, Jefferies, Patterson & Rogers, 2017; Patterson, Nestor & Rogers, 2007; Visser, Jefferies, & Lambon Ralph, 2010). In addition, cognitive states that activate the DMN tend to involve meaningful content that has personal relevance.

The current study was motivated by the hypothesis that there might be common neurocognitive processes underpinning perceptually-decoupled and conceptually-guided cognition in the DMN. During states of episodic recollection, we recreate past experiences that involve places, objects and people not currently present in the environment. Consequently, memory retrieval might necessitate a process of decoupling from sensory-motor systems, allowing cognition to be generated internally in a way that diverges from what is going on around us. These perceptually-decoupled states might recruit brain regions whose neural computations are functionally independent, or distant, from systems important for perceiving and acting. This is consistent with the observation that the distributed regions of the DMN are maximally distant from primary visual and motor cortex,

both in terms of their pattern of functional connectivity and in their geodesic distance across the cortical surface (Margulies et al., 2016).

In addition, DMN regions might support higher-order representations with predictive value across multiple situations and modalities, which integrate features from diverse sensory-motor regions. Contemporary accounts of semantic representation envisage an interaction between unimodal brain regions that support knowledge about specific features (e.g., knowledge that BANANAS are YELLOW and CURVED in visual cortex) and heteromodal regions within or allied to the DMN, which extract deeper similarity structures across these domains (i.e., allow us to understand that BANANA and KIWI are conceptually related, despite salient differences in colour, shape etc.). This view is also consistent with the observation that DMN lies at the extreme end of a gradient from heteromodal to unimodal cortex (Margulies et al., 2016), since increasingly abstract and complex representations might be formed at greater distances along the gradient, as the influence of specific features and modalities is reduced (Buckner & Krienen, 2013; Margulies et al., 2016; Mesulam, 1998). Within the DMN, angular gyrus (Binder & Desai, 2011; Bonner et al., 2013) and anterior temporal cortex (Lambon Ralph et al., 2017; Patterson et al., 2007) are both implicated in heteromodal semantic processing. However, their roles remain controversial since other regions such as left inferior frontal gyrus and posterior aspects of the temporal lobe frequently show stronger task-induced activation in fMRI. Angular gyrus, in particular, typically shows a pattern of task-induced deactivation, which is greater for harder judgements in both semantic and non-semantic tasks (Humphreys et al., 2015; Humphreys & Lambon Ralph, 2015). In addition, despite commonalities in the intrinsic connectivity of these regions, differences in semantic content have been proposed although not broadly accepted (Jackson, Hoffman, Pobric & Lambon Ralph, 2016): the anterior temporal lobes might support object identification, while angular gyrus is potentially more sensitive to thematic associations (Davey et al., 2015; Schwartz et al., 2011).

In this study, we contrasted situations designed to maximise two potential aspects of DMN function – i.e., sensory-motor decoupling and/or the need to focus cognition on conceptual identity as opposed to simple perceptual features. Our experiment builds on prior work by Konishi and colleagues (2015), who showed DMN

activation when participants recalled the location of simple shapes (triangles, squares and circles), rather than performing a perceptual match. Since the recall task was more demanding, these results contradict the view that DMN only supports easy or automatic aspects of cognition. The current study extended this paradigm by varying the information to be encoded and retrieved. Participants made match-to-sample judgements based on a perceptual feature (colour) or conceptual categories. We also manipulated whether these decisions were made when the relevant information was on the screen (0-back) or when information had to be retrieved from memory (1-back; see Figure 1).

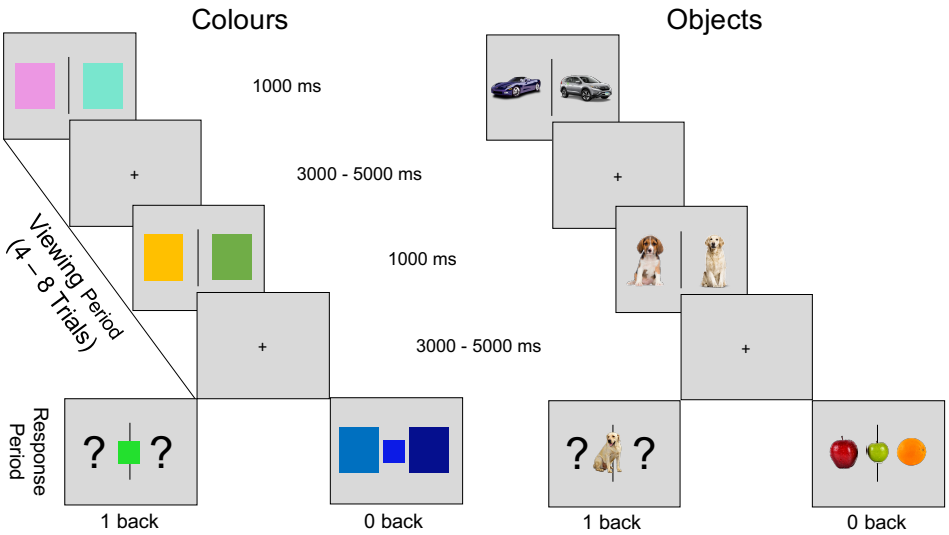

Figure 1

Our aim was to establish whether regions sensitive to perceptual decoupling and conceptual retrieval lay within the DMN, and whether these effects were located in overlapping or distinct regions. We also characterized the whole-brain maps from these manipulations in terms of their position on the macro-scale gradient from unimodal to heteromodal cortex described by Margulies et al. (2016). This allowed us to test the hypothesis that isolation from input is a critical feature shared by cognitive states activating the DMN.

2. Material and Methods

2.1 Participants

Thirty right-handed native British-speaking participants with normal or corrected-to-normal vision were recruited from the University of York (16 female; mean age 22.68, range 18-34 years). One participant's data was excluded due to excessive motion artifacts, leaving twenty-nine subjects in the final analysis for (15 female; mean age 22.57, range 18-24 years). In a subsequent analysis we used a set of 60 participants resting state data from the same pool of individuals (34 female; mean age 20.32, range 18-29 years). Both studies were approved by the York Neuroimaging Centre (YNIC) Ethics Committee. Participant's provided informed consent prior to the start of the experimental session.

2.2 Stimuli

The task paradigm had four conditions: (A) Object 0-back, (B) Object 1-back, (C) Colour 0-back and (D) Colour 1-back using a block design. In all conditions, pairs of items were presented separated by a central line. In the colour conditions, these were different coloured squares, while in the object conditions, these were familiar and meaningful objects, taken from the same semantic category (i.e., different types of cars, fruit, dogs; see Figure 1). Items were presented once with no repetition. The contrast between object and colour conditions allowed us to investigate regions that are important for the retrieval of conceptual information. The colour patches only varied on one feature (their colour), while the objects were meaningful multi-featural concepts. In addition, the contrast of 0-back and 1-back conditions allowed us to investigate the effect of stimulus-independent processing (1 back > 0 back).

2.3 Procedure

In the scanner, participants completed a total of four functional runs (average run time 8 min 32 s). Within each run, there were two blocks related to each of the 4 conditions (Object 1-back; Object 0-back; Colour 1-back; Colour 0-back). Each block began with written instructions stating the task type (0-back or 1-back). Blocks consisted of observing pairs of items (1000 ms); each pair was separated by a jittered inter-stimulus interval (ISI; 3000-5000 ms) in which a fixation cross was presented. At random intervals (4-8 trials), a third item was presented in the centre of the screen and participants were asked to indicate the location of one of the pair (left or right)

that was most similar to this probe (see Figure 1). This paradigm also required participants to match items that were present and compared this with items in memory. In the 0-back catch-trials participants had to decide which stimulus (left or right of the screen) was most similar to this centrally-presented probe (i.e., all items were present on the screen). In the 1-back catch-trials, participants had to decide which stimulus (left or right of the screen) had been most similar to this centrally-presented probe on the previous trial (i.e., the critical stimulus was absent). Blocks consisted of 5 probes in total and lasted on average 64 s.

2.4 MRI Acquisition

Data for both experiments were acquired using a GE 3 T HD Excite MRI scanner at the YNIC. A Magnex head-dedicated gradient insert coil was used in conjunction with a birdcage, radio-frequency insert coil tuned to 127.4 MHz. A gradient-echo EPI sequence was used to collect data from 38 bottom-up axial slices aligned with the temporal lobe (TR = 2s, TE = 18ms, FOV = 192x192mm, matrix size = 64x64, slice thickness = 3mm, slice-gap = 1mm, flip-angle = 90°). Voxel size was 3x3x3mm. Functional images were co-registered onto a T1-weighted anatomical image from each participant (TR = 7.8s, TE = 3ms, FOV = 290x290mm, matrix size = 256x256mm, voxel size = 1.13x1.13x1mm) using linear registration.

2.5 Pre-processing

All imaging data were pre-processed using a standard pipeline and analysed via FMRIB Software Library (FSL Version 6.0). Images were skull-stripped using a brain extraction tool [BET, (Smith, 2002)]. The first five volumes (10s) of each scan were removed to minimize the effects of magnetic saturation, and slice-timing correction with Fourier space time-series phase-shifting was applied. Motion correction (MCFLIRT, (Jenkinson, Bannister, Brady, & Smith, 2002)) was followed by temporal high-pass filtering (cut-off = 0.01Hz). Individual participant data was registered to their high-resolution T1-anatomical image, and then into a standard spare (Montreal Neurological Institute); this process included tri-linear interpolation of voxel sizes to 2x2x2 mm.

The resting state functional data used were pre-processed and analysed using the FMRI Expert Analysis Tool (FEAT). The individual subject analysis involved: motion correction using MCFLIRT; slice-timing correction using Fourier space time-series phase-shifting; 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); Gaussian low-pass temporal filtering, with sigma = 2.8s

2.6 Task based fMRI

For our task-based analysis, the time points of interest were the probe trials where participants had to make a decision about something present (0-back) or absent (1-back) from the screen. We therefore used a box-car regressor to model (i) the probe trial for each condition and (ii) the entire block. Modelling the entire block ensured any effect detected from our analysis can be attributed to the probe itself and not the general effect of the block. Box-car regressors for each probe/block, for each condition, for each run, were convolved with a double gamma hemodynamic response function. Regressors of no interest were included to account for head motion. We computed four contrasts: (1) 0-back > 1-back, (2) 1-back > 0-back, (3) Object > Colour and (4) Colour > Object. A fixed effect design (FLAME, http://www.fmrib.ox.ac.uk/fsl) was conducted to average the four runs, within each individual. Individual participant data were then entered into a higher-level group analysis using a mixed effects design (FLAME, http://www.fmrib.ox.ac.uk/fsl) whole-brain analysis. Finally, our analysis focused on a conjunction of 1-back > 0-back and Object > Colour to identify regions engaged in both stimulus independent processing and conceptually abstract representations.

2.7 Resting-state fMRI

We extracted the time series from regions identified by univariate analysis and used these as explanatory variables in a connectivity analyses at the single subject level. In each analysis, we entered 11 nuisance regressors; the top five principal components extracted from white matter (WM) and cerebrospinal fluid (CSF) masks based on the CompCor method (Behzadi, Restom, Liau, & Liu, 2007), six head motion parameters and spatial smoothing (Gaussian) was applied at 6mm (FWHM). WM and CSF masks were generated from each individual's structural image (Zhang, Brady, & Smith, 2001). No global signal regression was performed, following the method implemented in Murphy, Birn, Handwerker, Jones, & Bandettini (2009).

Whole brain analyses were cluster corrected using a z-statistic threshold of 3.1 to define contiguous clusters. Multiple comparisons were controlled using Gaussian Random Field Theory at a threshold of $p < .05$ [34]. All statistical maps

242 produced in these analyses are freely available at Neurosynth at the following URL:
243 http://neurovault.org/collections/2296/.
244
245 3. Results
246 Table 1 presents behavioural performance, in the form of response efficiency
247 (RT/ACC), for each of the four conditions of our task. These data were compared
248 using a 2 (task; 0-back vs. 1-back) by 2 (condition; object vs. colour) repeated-
249 measures analysis of variance (ANOVA). There was no significant differences
250 between stimulus type ($F(1,28) = 2.55$, $p = .116$) but a significant main effect of task
251 ($F(1,28) = 15.38$, $p < .001$). There was no significant interaction ($p > .05$). These
252 analyses demonstrate that performance on the 1-back task was less efficient than
253 for the 0-back task but that object and colour conditions were well matched in terms
254 of overall task difficulty.
255 Table 1. Behavioural results.

Condition	**Response Efficiency**	
	Mean	**SE**
Colour 1-back	1028	206
Colour 0-back	829	287
Object 1-back	1041	229
Object 0-back	841	295

256 Footnote: SE = standard error. Response efficiency = reaction time in milliseconds / percent accuracy.
257 We next generated statistical maps for describing patterns of neural activity
258 at the moments when participants responded in each of our four conditions. These
259 maps were compared at the group level using a GLM (see Methods). The contrast of
260 0-back > 1-back decisions captures perceptually-guided decision-making, revealing
261 increased activity in the bilateral ventral visual stream, from occipital pole through to
262 posterior fusiform cortex (see Figure 2). These regions have a well-documented role
263 in online visual processing. The contrast of 1-back > 0-back reflects stimulus
264 independence in decision-making. This comparison revealed greater activation in
265 bilateral angular gyrus and anterior temporal lobes, as well as medial structures in
266 the posterior cingulate cortex and medial prefrontal cortex. Many of these regions

fall within the DMN (58.44% of voxels fell within the DMN as defined by Yeo et al., 2011) and are spatially similar to the 'general recollection network' proposed by Rugg and Vilburg (2013). The comparison of Objects > Colours identifies brain areas that support the processing of multi-featural conceptual representations. This contrast revealed a similar set of regions to the stimulus independence contrast (left and right angular gyrus and anterior temporal lobe) with the addition of the right dorsolateral cortex (52.49 % of voxels fell within the DMN as defined by Yeo et al., 2011). The contrast of Colours > Objects yielded no significant whole-brain corrected results. To allow comparison with previous research, the spatial maps for the contrast of 1-back > 0-back from Konishi and colleagues are also displayed: similarities can be seen in posterior cingulate cortex, medial prefrontal cortex, right angular gyrus and dorsolateral cortex.

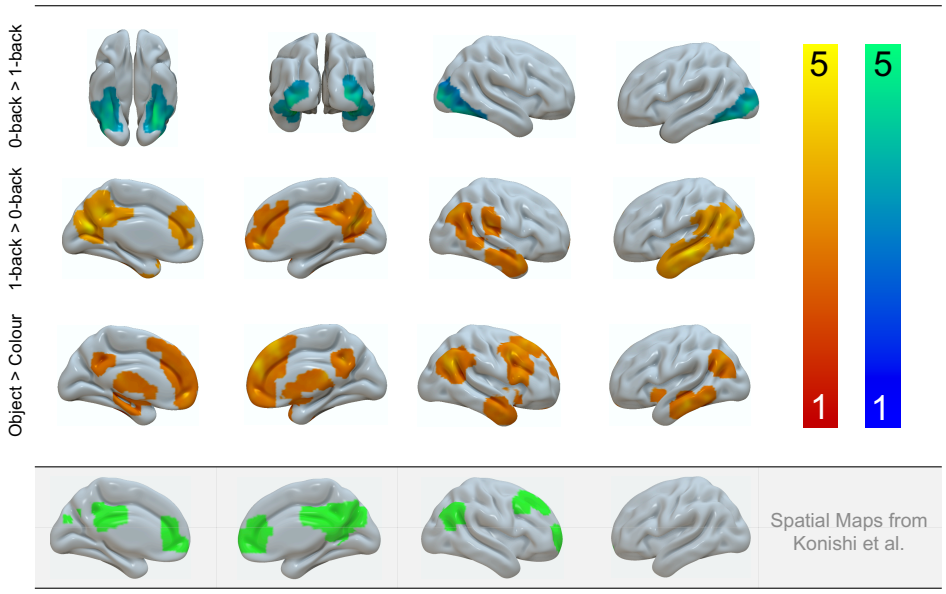

Figure 2

Our next analysis formally identifies regions that show a response to both stimulus independence and memory complexity. Figure 3 shows the results of a formal conjunction of the contrasts of Object > Colour and 1-back > 0-back, revealing three regions – bilateral angular gyrus and lateral medial temporal gyrus in the left hemisphere. The left hand panel of Figure 3 summarizes the parameter estimates from each of these regions in each condition of our task. In every case the strongest response was when decisions were made in the Object 1-back condition. Importantly, although these regions fell within the DMN (88.07% of voxels within the

conjunction mask fell within the DMN as defined by Yeo et al., 2011), their response profile indicated greater responding during a demanding condition (i.e. Object 1-back) ruling out a task-negative interpretation of these results.

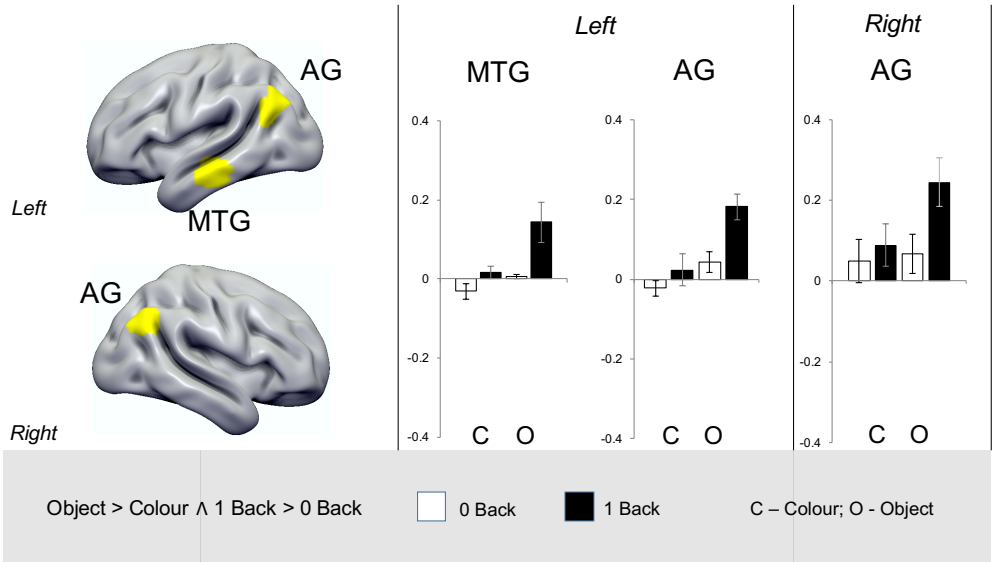

Figure 3

We also explored the intrinsic architecture of conjunction regions responding to Object > Colour and 1-back > 0-back in an independent resting-state data set (see Methods). The results of this analysis are presented in Figure 4 and reveal coupling beyond the seed regions to the posterior cingulate cortex, dorsolateral prefrontal cortex and pre-supplementary motor area bilaterally. Some of these regions fall outside the DMN, as defined by Yeo and colleagues, and instead are members of the frontoparietal network linked with cognitive control (40.15% of voxels within the DMN mask and 17.81% fell within the frontoparietal network, as defined by Yeo et al., 2011). These findings are consistent with previous work showing functional integration between the DMN and the executive network in demanding memory tasks, and at odds with the view that angular gyrus and lateral anterior temporal cortex only contribute to automatic aspects of retrieval or to task-negative states.

We also conducted a supplementary analysis contrasting Object and Colour decisions separately in the 1-back and 0-back conditions to confirm regions important for stimulus-independent semantic decisions (see Supplementary Figure 1). This analysis showed that 1-back trials involving meaningful objects activated regions including angular gyrus, middle temporal gyrus and right dorsolateral

prefrontal regions more than colours. In contrast, the comparison of Objects > Colours in the 0-back condition only revealed greater activity in fusiform cortex.

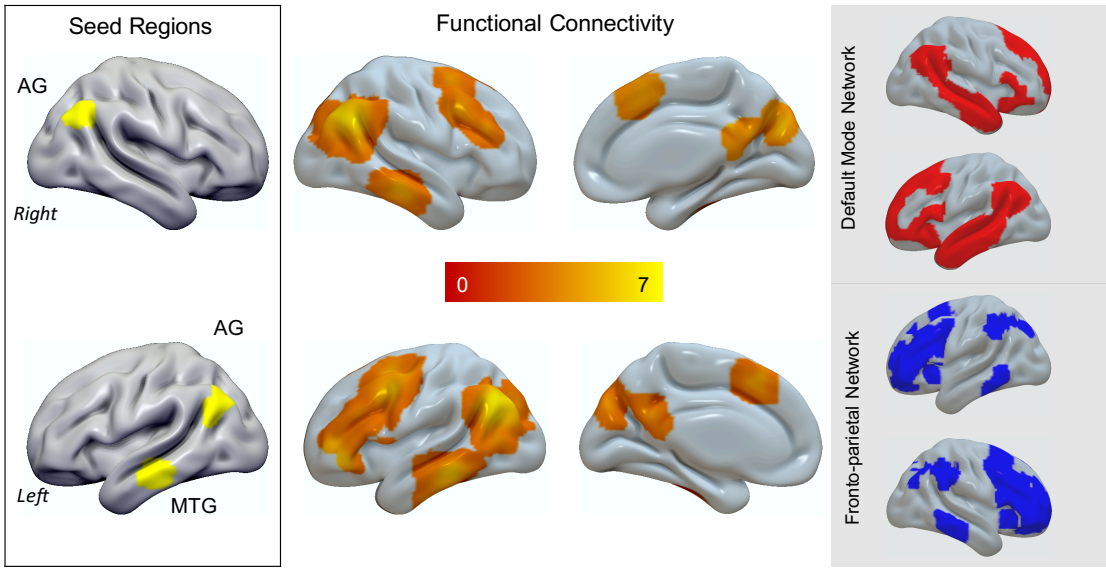

Figure 4

Together these analyses highlight a network of regions that are important when decisions are made in the absence of external sensory support, and when they involve multi-feature concepts (Figure 5). Common regions responding to the two task contrasts (1-back > 0-back; Object > Colour), and showing high intrinsic connectivity with conjunction regions in the left hemisphere, include angular gyrus and middle temporal gyrus. In the right hemisphere, all three maps include angular gyrus and two also include dorsolateral cortex. Both of these right hemisphere regions responded to a similar 1-back > 0-back contrast involving abstract shapes (circle, triangle, square) in the study by Konishi and colleagues (2015). The current study therefore provides a replication of the key conclusion that these regions of the DMN show activation when retrieving categorical information from memory, even when the task is relatively hard.

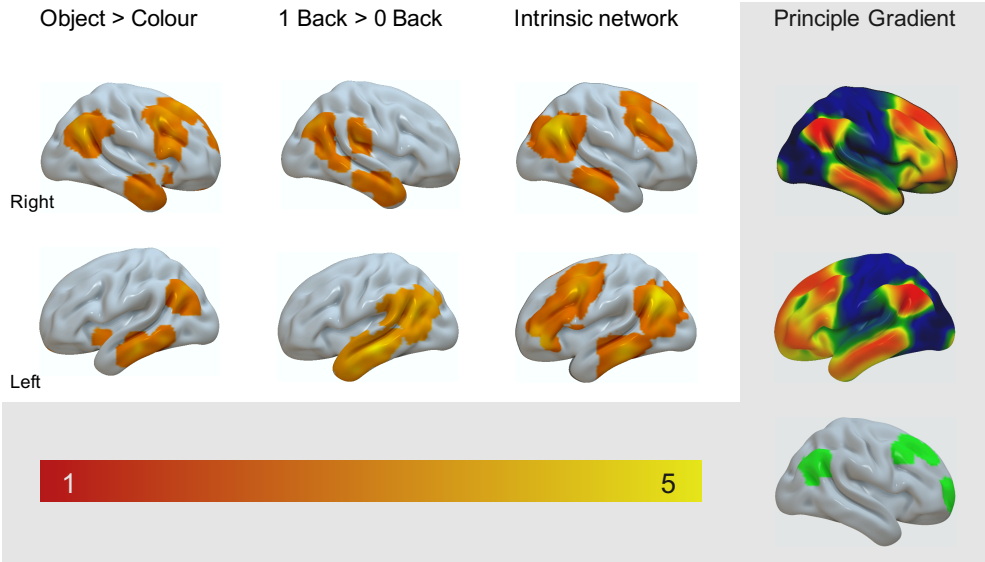

Figure 5

In Figure 5, these spatial maps are presented alongside the principal gradient from Margulies and colleagues (2016), which describes a functional spectrum of intrinsic connectivity across the cortical surface, extending from primary sensory motor systems to regions of the DMN at the other extreme. More similar colours on this gradient reflect greater similarity in connectivity. It can be seen that common regions implicated in stimulus-independent and conceptual processing are localized towards the transmodal end of the principal gradient.

Our final analysis characterizes the similarity between the neural patterns captured by our task and the spatial distribution of the principle gradient from Margulies et al., (2016) in a more formal manner. Following Margulies et al., we divided the principle gradient into 20 equally sized bins. Next for each participant we calculated the average signal in each bin for each condition of our task. The left hand panel in Figure 6 presents these data plotted across the principle gradient separately for each condition; the shaded bars represent the 95% confidence intervals. It can be see that the conditions are most distinct towards the transmodal end, with the highest values when participants made judgments about objects from memory. To quantify these patterns, we compared their distribution using a 2 (stimulus independence) X (stimulus complexity) X 20 (Gradient Bin) ANOVA. This revealed a significant 3-way interaction [$F(19, 532) = 5.136$, $p < .001$]. To follow up this interaction, we performed a principle components analysis (PCA) on the condition level data, describing the dynamics captured in the left hand panel of Figure 6. The

results revealed two components with eigenvalues greater than 1 accounting for over 86% of the variance (component 1 = 70.49%; component 2 = 15.73%) across the principal gradient bins. The first two components are presented in the right hand panel of Figure 6. The second component describes a gradual transition showing increasing levels of BOLD activity from the unimodal end of the gradient towards the transmodal end. Projecting the values from component 2 back onto the task conditions, and averaging them at the group-level, revealed that this pattern of variance loaded almost exclusively on the 'object' 1-back condition. There was a significant positive fit between the spatial map of the principle gradient and recruitment in the Object 1-Back task, but not other conditions.

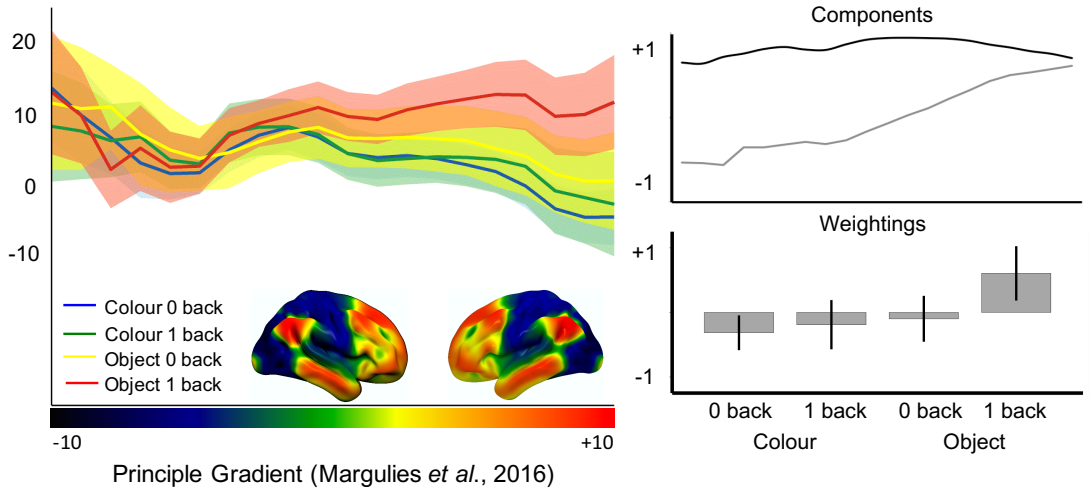

Figure 6

4. Discussion

Our experiment establishes that overlapping regions in the DMN are sensitive to both perceptual decoupling (i.e., the requirement to make decisions based on memory, as opposed to the immediate environment) and conceptual processing (i.e., decisions based on semantic rather than perceptual information). We also showed that these regions fell at the extreme end of a gradient from unimodal to heteromodal cortex (Margulies et al., 2016). Therefore, isolation from input appears to be a critical feature shared by at least two manipulations that activate the DMN. Distance from sensory-motor cortex might be necessary to form heteromodal conceptual representations, which are thought to be abstracted from individual

features and modalities. Also, when cognition is driven by internal rather than external representations, brain regions that have intrinsically weak connectivity with unimodal input regions might play an important role, since memory retrieval can create mental simulations that differ markedly from the external environment. These findings have broad implications for the role of DMN in cognition, and also contribute to our understanding of specific DMN regions, particularly angular gyrus and lateral temporal lobe. We first consider the results in terms of their implications for functional accounts of these regions. Secondly, we consider the macroscale organisation of the cortex, focusing on approaches which can explain the functional similarity of these distributed clusters and their relative position on the cortical surface.

Functional implications for the angular gyri: There were stronger responses in left and right angular gyri, as well as in left middle temporal gyrus, when conceptual decisions were based on information that was no longer present in the environment. These findings are inconsistent with several existing accounts of the contribution of angular gyrus to memory and semantic cognition. First, they do not easily align with the proposal that specific aspects of meaning are represented in angular gyrus – namely thematic associations, but not item identity (Davey et al., 2015; Schwartz et al., 2011). Our conceptual task involved matching items on the basis of their identity, yet it still robustly activated this region. Secondly, the findings are at odds with the proposal that the angular gyri only activate during contrasts of easier versus harder tasks, and for “automatic” and not “controlled” patterns of retrieval (Humphreys et al., 2015; Humphreys & Lambon Ralph, 2017). The 1-back condition was harder than the 0-back condition and still elicited a greater response.

Our findings are potentially more consistent with suggestions that the angular gyri contribute to semantic and episodic retrieval tasks via processes that allocate attention in a bottom-up fashion, i.e., to strongly-activated memory representations. The angular gyri show a stronger response to a range of memory retrieval situations in which the retrieved representations are detailed, specific or precise (Binder et al., 2005; Price, et al., 2015; Bonnici et al., 2016; Davey at al., 2015). The 1-back trials required attention to be focused on conceptual information represented internally, consistent with the purported role of inferior parietal cortex

405 in reflexive attention to memory (Cabeza et al., 2011). We did not obtain the same
406 findings for the colour condition, which required more similar colours to be matched
407 (e.g., two bright greens compared with a darker green), perhaps because these
408 stimuli did not activate pre-existing representations in memory.

409 Functional implications for temporal cortex: Angular gyrus shows strong
410 intrinsic connectivity with ventral anterior temporal cortex (Davey et al., 2016;
411 Jackson et al., 2016), which is proposed to support the integration of multiple
412 features and modalities to capture 'deep' conceptual similarities between items with
413 diverse 'surface' features (e.g., items such as PINEAPPLE and KIWI that have different
414 colours, sizes, shapes, phonology etc.; for a review see Lambon Ralph et al., 2017).
415 Semantic dementia patients with atrophy focussed on this region show highly
416 consistent degradation of conceptual knowledge across tasks (Bozeat et al., 2000;
417 Jefferies & Lambon Ralph, 2006), while neuroimaging studies of healthy participants
418 localise the response during heteromodal conceptual processing to ventral anterior
419 temporal lobes and anterior middle temporal gyrus (Murphy et al., 2017; Visser et
420 al., 2011). Word meaning can be decoded within anterior middle and inferior
421 temporal gyri, while patterns of activation in superior temporal gyrus instead reflect
422 the presentation format (Murphy et al., 2017).

423 The ventral anterior temporal lobes are thought to provide a "graded hub" in
424 which different unimodal features are gradually integrated to form heteromodal
425 concepts, with visual information reaching this region along the ventral visual
426 pathway (fusiform cortex), auditory and motor information arriving from superior
427 temporal gyrus and frontal cortex, and social/emotional information merging from
428 the temporal pole (Lambon Ralph et al., 2017). Nevertheless, the peak response in
429 the anterior temporal lobes in the current study was in lateral MTG, and not in the
430 site of the putative hub in ventral anterior temporal cortex (Murphy et al., 2017).
431 Visser et al. (2012) observed evidence compatible with two gradients of information
432 convergence in the temporal lobes: first, there is a posterior-to-anterior axis, since
433 posterior temporal lobe regions proximal to visual and auditory cortex show largely
434 unimodal responses, while more anterior regions integrate across these types of
435 input to support heteromodal conceptual processing. Secondly, there may be
436 integration from superior and inferior regions, implicated in auditory and visual

437 processing respectively, towards middle temporal gyrus, which shows a more
438 heteromodal response along the length of the temporal cortex. The site we observed
439 in the conjunction of semantic and perceptually-decoupled decisions in the current
440 study appears to correspond with the extreme heteromodal end of *both* of these
441 temporal lobe gradients.

442 Implications for the default mode network: We replicated prior
443 demonstrations that transmodal regions in the DMN are engaged when participants
444 make decisions that rely on information from memory rather than input from
445 perception, even though the 1-back task was more difficult than the 0-back task
446 (Konishi et al., 2015). This pattern of task-positive behaviour adds to a growing body
447 of evidence that the DMN contributes in an active manner to demanding external
448 cognitive tasks (Konishi et al., 2015; Krieger-Redwood et al., 2016; Spreng et al.,
449 2014; Spreng et al., 2015; Spreng et al., 2010; Vatansever et al., 2015). The
450 contribution of DMN to controlled cognitive states appears to reflect situations in
451 which DMN regions work in tandem with the frontoparietal network. Prior work has
452 established the combination of these networks is important for tasks including
453 controlled semantic retrieval (Krieger-Redwood et al., 2016), working memory
454 (Vatansever et al., 2015), autobiographical planning (Spreng et al., 2014; Spreng et
455 al., 2015), retrieving memories of close personal friends (de Caso et al., 2017) and
456 the control of spontaneous thoughts in a deliberate manner (Golchert et al., 2017).
457 Our study shows that right angular gyrus, within the DMN, and right dorsolateral
458 prefrontal cortex, a member of the frontoparietal network, activate together when
459 participants make judgments about meaningful objects from memory rather than
460 colours (see Supplementary Figure 1). Our functional connectivity analysis
461 demonstrates that these regions are correlated at rest. The right dorsolateral cluster
462 replicates the spatial distribution observed from the prior study by Konishi et al.
463 (2015) and overlaps with a region of greater grey matter associated with more
464 deliberate mind-wandering (Golchert et al., 2017). Both 1-back retrieval in our
465 paradigm, and more deliberate spontaneous thought, require memory retrieval to
466 be shaped in a goal-directed fashion. It is possible that a range of states requiring the
467 goal-directed control of memory depend on co-operation between these two large-
468 scale networks.

At the most general level, our study supports the idea that similar responses across disparate brain regions (e.g., lateral middle temporal gyrus and angular gyrus) and across apparently different cognitive manipulations (semantic vs. non-semantic processing; decisions based on memory or perception) can be explained in terms of the topographical organisation of the cortex. Prior work highlighted that regions of transmodal cortex, such as the DMN, show the greatest distance from unimodal sensorimotor cortex in both functional and structural space (Margulies et al., 2016). Our findings build on this observation by showing that this dimension of connectivity is related to the combined requirement to match items on the basis of conceptual as opposed to sensory features and the need to retrieve relevant information from memory as opposed to the ongoing visual presentation of this information. Using both standard and novel methods of analysis, we demonstrated that the neural activity associated with this type of activity is prevalent in transmodal regions (Figure 5) and can be represented as a whole brain shift in the balance of neural activity, away from sensorimotor regions and towards the transmodal end of the gradient (Figure 6). This topographical shift in the distribution of neural processing is consistent with theoretical accounts that assume that more abstract cortical functions are facilitated through functional isolation from incoming input (Buckner & Krienen, 2013; Margulies et al., 2016; Mesulam, 1998; Smallwood, 2013). Both angular gyrus and middle temporal gyrus respond to heteromodal aspects of meaning, in line with their position at the heteromodal end of the principal gradient (Binder & Desai, 2011; Bonner et al., 2013; Humphreys & Lambon Ralph, 2015; Simanova et al., 2014). Moreover, the two task contrasts – highlighting perceptual decoupling and semantic decisions – might emphasise processes that utilise heteromodal cortex, explaining their common recruitment. In line with this, a recent study found that strong connectivity between subnetworks of the DMN predicted poor performance on tasks that required encoding and retention of recently presented information, but not poor retrieval of previously-encoded knowledge, consistent with a failure to engage with the external world (Poerio et al., 2017).

There are a number of limitations that should be borne in mind when considering the results of this study. First, our comparison of semantic and colour decisions allowed us to demonstrate a neural pattern associating conceptual

processing with stimulus independency. This comparison is too crude a manipulation to determine which aspects of the semantic judgements gave rise to this response in the DMN; for example, is it the richness of concepts such as Labrador or apple, their heteromodal nature, the fact that they are acquired over a lifetime, and/or their broad predictive value in the real world, which dissociates them from colours? Future studies could probe different features of retrieval, such as whether the target is a concrete or abstract concept, whether it has to be identified at a specific or superordinate level, and whether there are differences according to the modality of the representation being probed. Second, the nature of our design precludes the ability to separate different aspects of memory retrieval engaged during 1-back decisions. In our paradigm, these decisions require both the integration of appropriate information from memory, as well as the inhibition of the non-probed item representation. Interestingly, studies have implicated dorsolateral prefrontal cortex in the suppression of memories (Anderson et al., 2004) whereas both the angular gyrus has been linked to the integration of appropriate semantic features (Wagner et al., 2015) and the retrieval of specific information (Davey et al., 2015). It is possible that the angular gyrus and dorsolateral prefrontal cortex are performing distinct roles in the integration of relevant associations and the suppression of irrelevant information during retrieval. Future work could address this question by manipulating the featural overlap between the target and distractor in this paradigm. Finally, although we showed that two aspects of cognition recruit common regions in the DMN, and that this pattern can be recovered in a whole-brain gradient analysis, we did not recover a conjunction across the entire DMN, and other tasks that activate DMN might elicit a peak response in other nodes of this network. Our findings are consistent with the view that the DMN supports aspects of cognition that require integration of, and isolation from, unimodal systems, yet since each node of the DMN receives a different balance of local inputs, these regions might differ to some extent in their relevance for any given task.

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721 **Figure Legends**

722

723 **Figure 1.** *Experimental design.* The four different match-to-sample judgments that
724 participants made in this experiment.

725

726 **Figure 2.** *Neural activity produced when making decisions based on meaningful*
727 *objects and when decisions are made from memory.* (a) Activity elicited when
728 decisions were made based using information from perception (b) Activity when
729 decisions were made on the basis of information from memory and (c) when
730 information from memory was more complex. Spatial maps were cluster corrected
731 at Z = 3.1 FWE.

732

733 **Figure 3.** *Locating peak activity during stimulus independent decisions regarding*
734 *complex stimuli.* (a) A conjunction of the neural activity when making decisions
735 based on meaningful categories and when decisions are made in the absence of
736 perceptual input revealed three regions: bilateral angular gyrus and in the left
737 middle temporal gyrus. (b) Percent signal extracted from these regions revealed an
738 additive effect (i.e. these regions responded significantly more to the object
739 condition when information was not present on the screen compared to all other
740 conditions). The conjunction analysis was based on whole-brain cluster corrected
741 spatial maps from Figure 1. Error bars indicated 95% confidence intervals.

742

743 **Figure 4.** *Peak areas during stimulus independent decision regarding complex stimuli*
744 *involve both regions of the default mode network (DMN) and the fronto-parietal*
745 *network (FPN).* These regions show functional connectivity at rest with both the pre-
746 supplementary cortex and the dorso-lateral pre-frontal cortex. Although the regions
747 identified in our conjunction analysis fall within the DMN they show functional
748 communication with regions in the FPN, including the right dorso-lateral prefrontal
749 cortex. The spatial networks in the grey panel are from the decomposition of Yeo
750 and colleagues. The conjunction analysis was based on whole-brain cluster corrected
751 spatial maps from Figure 1. For the connectivity analyses spatial maps were cluster
752 corrected at Z = 3.1 FWE.

Figure 5. *Regions linked to during stimulus independent decisions regarding complex stimuli form localized clusters in transmodal cortex.*

Figure 6. *Stimulus independent decisions regarding meaningful objects leads to a whole-brain shift towards the transmodal-end of the gradient.* (a) A regions-of-interest analysis using bins of the principal gradient revealed that the decisions that are made on objects rather than colours when these stimuli are not available to perception led to higher activity towards the transmodal-end of the principal gradient. (b) Decomposition using PCA revealed that this difference was related to a gradual shift in the locus of neural activity away from regions on the principal gradient related to perception and action and towards transmodal regions of cortex. Error bars indicated 95% confidence interval.

Supplementary material

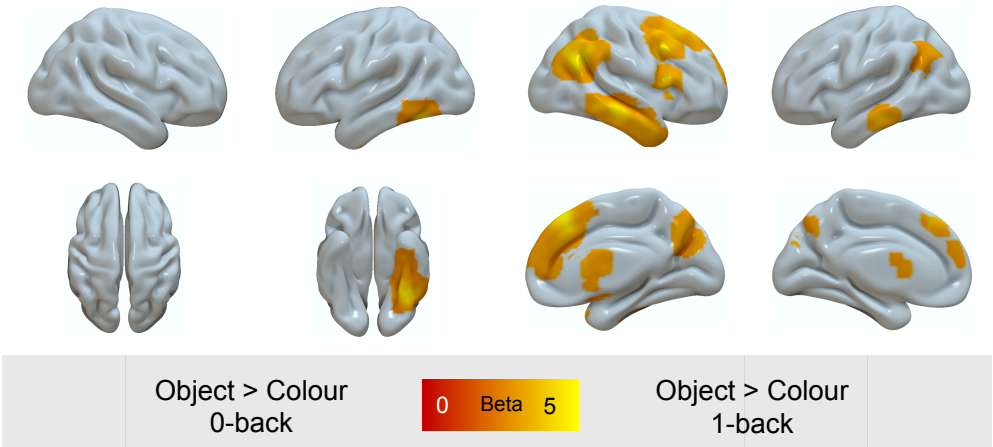

Figure S1. *Comparison of complex memory representation in the presence or absence of relevant perceptual input.* Spatial maps were cluster corrected at Z = 3.1 FWE.