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Original Article

Creativity in verbal associations is linked to semantic control

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Although memory is known to play a key role in creativity, previous studies have not isolated the critical component processes and networks. We asked participants to generate links between words that ranged from strongly related to completely unrelated in long-term memory, delineating the neurocognitive processes that underpin more unusual versus stereotypical patterns of retrieval. More creative responses to strongly associated word-pairs were associated with greater engagement of episodic memory: in highly familiar situations, semantic, and episodic stores converge on the same information enabling participants to form a personal link between items. This pattern of retrieval was associated with greater engagement of core default mode network (DMN). In contrast, more creative responses to weakly associated word-pairs were associated with the controlled retrieval of less dominant semantic information and greater recruitment of the semantic control network, which overlaps with the dorsomedial subsystem of DMN. Although both controlled semantic and episodic patterns of retrieval are associated with activation within DMN, these processes show little overlap in activation. These findings demonstrate that controlled aspects of semantic cognition play an important role in verbal creativity.

Key words: creativity; default mode network; semantic control; semantic control network.

Creativity and communication depend on our capacity to deploy information from memory in a flexible way. As an illustration, we can generate an association between "any" 2 words (even unrelated items) by identifying a specific context in which they interact or co-occur (e.g. we can associate the words MELON and BOOKCASE by thinking about cookery books); this behavior is highly creative since there is no obvious way in which these words are linked. Creativity is assumed to reflect the ability to generate unusual patterns of retrieval from memory—including from the semantic store (encompassing the meanings of words and objects; Mednick 1962; Abraham and Bubic 2015; Chen et al. 2015; Kenett 2018; Kenett and Faust 2019; Liu et al. 2020) and/or from episodic memory (which represents our individual experiences; Addis et al. 2016; Beaty et al. 2016; Benedek and Fink 2019; Madore et al. 2015, 2016a, 2016b). Previous research has shown that executive and default mode networks (DMN) are recruited during creative thought (Beaty et al. 2014, 2015, 2016, 2019), yet the component processes reflected by these network interactions remain unclear. Neuroscientific studies of memory have revealed distinct neural networks that are engaged during controlled as opposed to more automatic patterns of retrieval from both semantic and episodic memory (Whitney et al. 2009; Barredo et al. 2015; Davey et al. 2016; Kim 2016; Vatansever et al. 2021), yet these studies typically only examined judgments about pre-linked words, minimizing the contribution of creativity. This study therefore investigated neural recruitment as participants formed links between words that varied in their degree of association along a continuum from strongly related (lowest creativity) to unrelated (highest creativity), linking neural activation and behavioral performance to distinct aspects of memory.

Previous studies have found that the efficient activation of broader conceptual information increases the likelihood of creating unique conceptual combinations (Kenett et al. 2014, 2016; Benedek et al. 2017; Kenett and Faust 2019). This pattern of retrieval may be connected to controlled semantic cognition, as opposed to the retrieval of conceptual knowledge that comes unbidden to mind, since semantic control processes are thought to be key to the retrieval of weak, ambiguous, or nondominant aspects of knowledge (Badre and Wagner 2007; Hoffman et al. 2010; Jefferies 2013; Krieger-Redwood et al. 2015). In these circumstances, a left-lateralized semantic control network (SCN) is strongly activated: this includes left inferior frontal gyrus (IFG), posterior middle temporal gyrus, and dorsomedial prefrontal cortex (dmPFC; Noonan et al. 2013; Jackson 2021). More challenging semantic tasks also recruit domain-general control regions within the bilateral multiple-demand network (MDN; Duncan 2010); however, SCN is thought to be at least partially distinct from MDN, since the peak SCN response in left anterior and ventral IFG lies outside the MDN (Wang et al. 2020; Gao et al. 2021). Given this research, we would anticipate that if verbal creativity reflects the capacity to retrieve semantic information in a more unusual way, activation within the SCN should be critical.

Retrieval from episodic memory can also be largely uncontrolled, or constrained to suit the task demands, and there are

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shared neurocognitive features of uncontrolled and controlled retrieval across semantic and episodic tasks (Rajah and McIntosh 2005; Burianova and Grady 2007; Barredo et al. 2015; Kim 2016; Irish and Vatansever 2020). DMN regions associated with information integration (Irish and Vatansever 2020; Lanzoni et al. 2020) and memory-guided cognitive states (Murphy et al. 2018) show common recruitment during both semantic and episodic retrieval (Burianova et al. 2010; Kim 2016). Left angular gyrus (AG) in the core DMN may be an integrator of multimodal information across both semantic and episodic memory (Seghier 2012; Bonnici et al. 2016; Ramanan et al. 2017; Carota et al. 2021). In addition, the left IFG within the SCN shows a stronger response to both weakly associated words in semantic memory, and for words paired together fewer times in episodic memory (Vatansever et al. 2021). Damage to this site is associated with deficits in retrieving weaker semantic and episodic relations, and difficulties when these sources of information are in conflict (Stampacchia et al. 2018, 2019).

Although research has shown that creativity draws on both DMN (Beaty et al. 2014, 2015, 2016; Marron et al. 2018; Beaty et al. 2020; Evans et al. 2020; Frith et al. 2021) and control regions (e.g. MDN), including lateral frontal cortex and dmPFC within the SCN (Abraham et al. 2012; Gonen-Yaacovi et al. 2013; Chen et al. 2020), both semantic and episodic memory draw on these networks: this leads to uncertainty about how we generate creative patterns of thought using these long-term memory representations. The highly creative brain shows a fine balance between integration and segregation of sensorimotor (Chen et al. 2019; Matheson and Kenett 2020), control networks and DMN, whereas the less creative brain is dominated by motor and visual processing (Zhuang et al. 2021). Moreover, individuals with strong and flexible connectivity between executive networks and DMN score more highly on tests of intelligence (Sripada et al. 2019) and produce more creative ideas (Beaty et al. 2014, 2015, 2016, 2017, 2019). SCN regions are argued to be important for the interaction between executive and DMN regions, because they fall at the juxtaposition of DMN and MDN (Wang et al. 2020); SCN is unique in showing shared intrinsic and structural connectivity to both DMN and MDN, which are often anticorrelated (Davey et al. 2016). Recently, research has explored functional subdivisions within DMN based on the original resting-state parcellation of 1,000 brains, which provided a 17-network solution separating the DMN into 3 distinct subsystems (Yeo et al. 2011). A "dorsomedial" DMN (dmDMN) subnetwork—comprising nodes in dorsomedial prefrontal, lateral temporal, and inferior frontal cortex—partially overlaps with the SCN (Fig. 1). This observation is consistent with current accounts of DMN function that emphasize the role of this network in information integration and internally oriented cognition across both controlled and less constrained contexts (Leech et al. 2011; Braga et al. 2013; Crittenden et al. 2015; Konishi et al. 2015; Krieger-Redwood et al. 2016; Sormaz et al. 2018; Wens et al. 2019; Lanzoni et al. 2020; Smallwood et al. 2021; Wang et al. 2021). In contrast, a "core" DMN subsystem shows greater task-related deactivation, particularly during challenging decisions, and no overlap with SCN (Fig. 1). These DMN subsystems have been differentially implicated in semantic (dorsomedial DMN) and episodic (core) processes (Zhang et al. 2021).

In this study, we asked how controlled and less-controlled aspects of semantic and episodic retrieval support the generation of creative and more stereotypical verbal associations. We presented pairs of words parametrically varying in their strength of association, from strongly related to unrelated trials. Although both semantic and episodic memory representations might support the identification of links between items, the availability of relevant information in semantic and episodic memory might differ across strongly, weakly, and unrelated word-pairs: for example, in the absence of strong semantic links, participants might fall back on past episodes, or alternatively, in the absence of common linking episodes, participants might identify links mediated by specific semantic features. In addition, the neurocognitive processes that support controlled retrieval (from either semantic or episodic memory) might be crucial in generating creative responses, since engaging control mechanisms can promote nondominant patterns of retrieval, whereas retrieval that is well-aligned across both semantic and episodic memory stores may be associated with low control demands. Accordingly, we tested 5 intersecting hypotheses about the neural basis of verbal creativity: (i) creative verbal behavior will relate to specific components of long-term memory; (ii) the generation of creative links will be associated with divergence across semantic and episodic stores such that only one aspect of long-term memory drives the response; (iii) in these circumstances, control processes will be recruited to constrain retrieval from long-term memory, allowing the production of nondominant information; (iv) this creative behavior will be associated with recruitment of the left-lateralized SCN; and (v) the degree of creativity will modulate recruitment across distinct subsystems of DMN, since the dorsomedial subsystem, but not the core DMN, overlaps with the SCN.

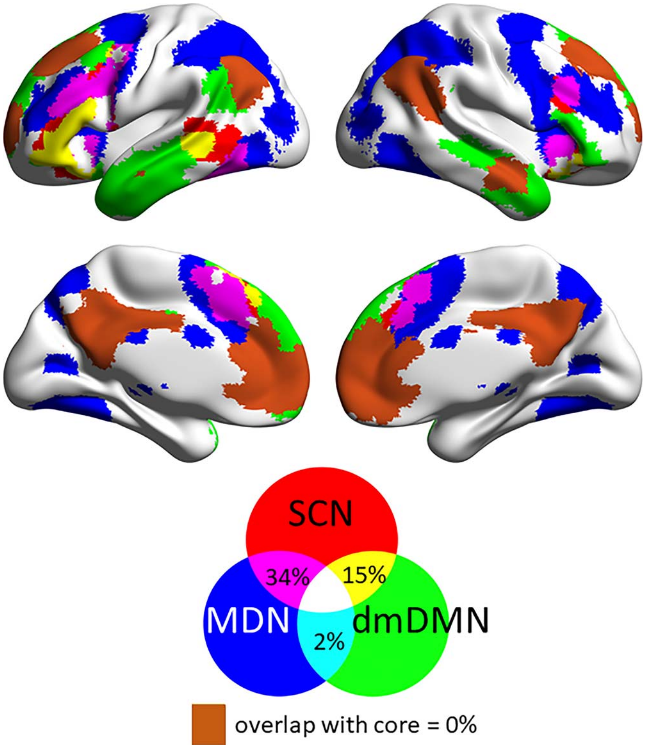

Fig. 1. The dmDMN subsystem defined from a 17-network parcellation of resting-state connectivity by Yeo et al. (2011) overlaps with the SCN (15% overlap; Jackson 2021). The dmDMN minimally overlaps with the multiple demand network (MDN, 2% overlap; Duncan 2010). In contrast, the core DMN subsystem shares no overlap with either control network.

Method

Participants

Task-based fMRI

We recruited 36 participants (23 females, mean age = 22 years, range = 19–32 years). None of the participants had a history of psychiatric or neurological illness, drug use that could alter cognitive functioning, severe claustrophobia, or pregnancy. All volunteers provided written informed consent and were debriefed after data collection. Ethical approval was obtained from Ethics Committees in the Department of Psychology and York Neuroimaging Centre, University of York. All participants were right-handed, native English speakers with normal/corrected vision, and were compensated for their time with payment and/or course credit. This study was not preregistered in a time-stamped, institutional registry prior to the research being conducted.

Three participants were not included in data analysis (1 withdrew during scanning, 1 had an anomaly in MRI, and 1 had missing volumes in MRI). Two further participants were removed post-analysis, 1 due to poor behavioral performance (no link made on 32% of trials) and 1 for excessive movement in 2 out of 3 runs (>1.2-mm absolute). Therefore, the final sample included 31 participants (21 females, mean age = 22 years, range = 19–32 years).

All data included in the analyses presented in this manuscript have no (absolute) movement greater than 1.2 mm. For 2 of the 31 participants in our final sample, 2 out of 3 runs of data are included, due to excessive movement on 1 of the runs.

Task materials and procedure

Pre-scan behavioral tasks

Before the neuroimaging session, participants practiced link formation at home. They were given 15 word-pairs ranging in strength of association and were asked to generate a link between the words, type this into an answer field, and then rate the link they formed on a 1–4 scale (the same scale used in the scanner). This allowed participants to familiarize themselves with the paradigm, and provided a check that they understood the paradigm.

Participants also performed the unusual uses task (UUT). The UUT is a standard assessment of divergent thinking (DT), a component of creative thought, in which participants are asked to name as many uses as they can for a given object. An initial screen presented the following instructions: "In this task you will be presented with the name of an object for 10 s. // You will then be taken to a blank screen where you are required to list as many uses for that object as you can think of in 2 min. // This will be repeated for 3 different objects." The 3 objects were: brick, newspaper, and shoe. Participants typed their uses in the answer box, which stayed on screen for the full duration of 2 min, after which the next object appeared for 10 s, followed by the 2-min generation screen. In line with our main experimental task, where participants received no explicit directions to be creative, participants were not given instructions to be creative when generating uses for the items. This methodology may have limited the degree to which participants behaved creatively, as some studies suggest that without the explicit instruction to be creative, fluency increases and creativity decreases. However, it has also been argued that creative individuals develop a habit for uniqueness: even without explicit instruction to be creative, more unique ideas are produced by these individuals (Reiter-Palmon et al. 2019). Therefore, the UUT scores in our study are a measure of incongruent DT (i.e. participants are scored on the creativity of their ideas, without having been explicitly told to be creative). Both of these paradigms were presented using Qualtrics (www.qualtrics.com).

Participants were given 1 point for each idea that deviated from the intended-use for the object, and zero points for typical uses. For example, for the item "brick" zero points were given for responses such as "wall," "building," "use in foundations"; and 1 point was given for each unusual use such as "doorstop," "weapon," "put garden pots on," "phone stand." Therefore, participant scores are based on the total number of unusual uses generated across all 3 items, and their final score gives a measure of how unusual an individual's thinking is in a fluent DT task (i.e. but not "originality"). This is similar to the rater-based scoring method, which is more appropriate for smaller sample sizes (Forthmann et al. 2020), however, instead of using several likert-scales to assess each response, we used a binary intended-use (0), unusual-use (1) scoring method, measuring the number of unusual uses generated, with no subjective rating as to the quality of the idea. All methods of scoring have their limitations and based on the sample size and instructions given to participants, we felt this was the most appropriate method to capture verbal DT in our study. Furthermore, due to the length of our main experimental task, it was not possible to acquire multiple types of DT (nor, other aspects of creativity); therefore, our correlations with UUT require replication with other DT and creativity measures, as well as validation with other instructions and scoring methods (e.g. instruction-scoring relationships that are congruent, incongruent, and partially congruent; Reiter-Palmon et al. 2019). A supplemental analysis scoring responses for originality using frequency-based methods (2 independent-raters; acceptable ICC = 0.6) and flexibility (2 independent-raters; good ICC = 0.8) showed similar results (Supplementary Tables S7 and S8).

fMRI behavioral tasks

Each trial lasted 13.5 s and was structured as follows. Participants were presented with word-pairs on the screen for 4.5 s (Fig. 2). During this period, participants were tasked with identifying a link between the words. They were given no specific instructions to be creative. The words varied in the degree to which they had a preexisting semantic link. We manipulated semantic association strength between the word-pairs using word2vec (Mikolov et al. 2013) to identify trials ranging from completely unrelated (i.e. minimum word2vec = −.05) to strongly related (i.e. maximum word2vec = 0.72). Word2vec uses word co-occurrence patterns in a large language corpus to derive semantic features for items, which can then be compared to determine the degree of their relationship. Following link generation for each trial, there was a fixation period of 0.5 s, followed by 1 s to rate the strength of the link that was identified. Participants were specifically instructed to rate the strength of the link they had made, and not the preexisting strength of association between the words. They provided ratings on a 1–4 scale (weak—strong), using their right hand, or alternatively pressed a button with their left hand to indicate no link was made. Following the link rating, participants performed a series of left–right chevron decisions (details below). There were 144 word-pair trials in total, presented across 3 runs, and these were pseudo-randomly assigned such that each run contained an even number of high, medium, low, and unrelated associate pairs.

Post-scan behavioral tasks

Immediately following the scanning session, post-scan behavioral testing included a series of questions about in-scanner performance. Participants were asked to: (i) recall and describe the link that they formed in the scanner; (ii) rate the strength of the link that they formed on a 5 point scale (for the second time, since the same judgment was made in the scanner); (iii) report the degree to which the link on that trial relied on semantic-to-episodic memory (a 5 point scale with semantic on one end, combination in the middle and episodic at the other end), and (iv) rate their confidence in their recall of the association they formed in the scanner

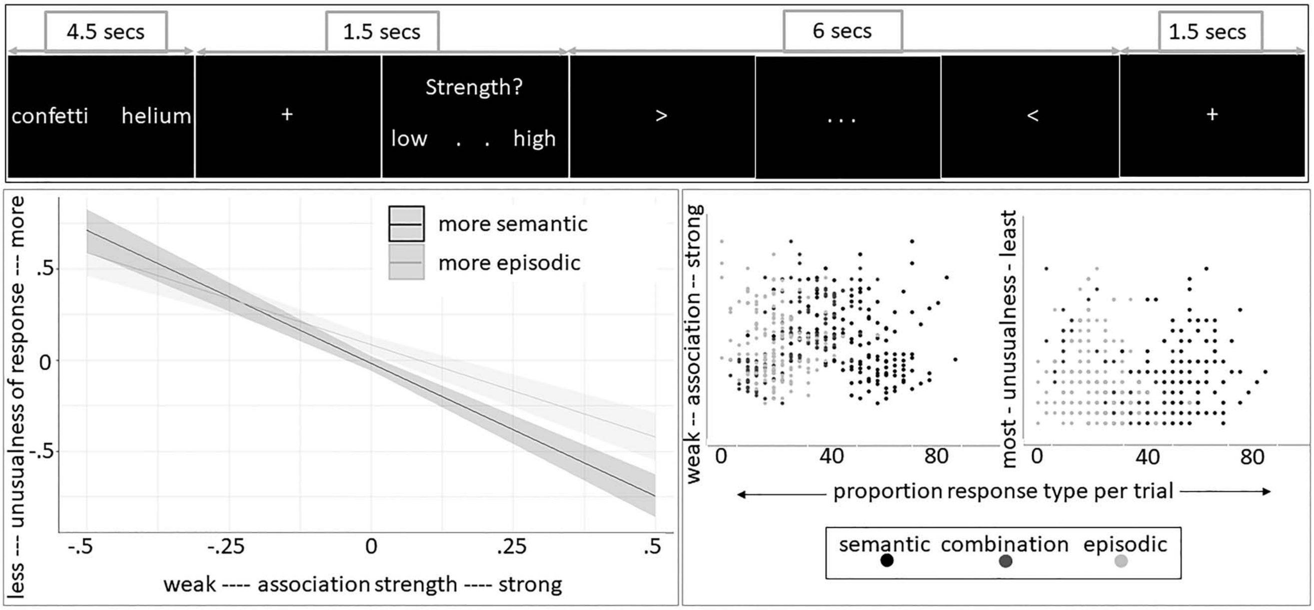

Fig. 2. Top: Task schematic. Participants covertly generated a link between the 2 words; next they rated the strength of the link that they had formed, and then engaged in a series of fast-paced left–right chevron decisions. Bottom left: The interaction effect from the linear mixed model (participant level data), with the semantic-to-episodic dimension plotted against each other. Bottom right: Two plots of the trial-level data showing: (i) the distribution of memory types used to generate associations plotted against association strength (word2vec) and (ii) homogeneity of response types. Participants rated the memory used on a 5-point scale, with most semantic on one end and most episodic on the other. Combination refers to trials drawing on both episodic and semantic memory. The values in these 2 plots are based on an item analysis of each word-pair (the x-axis shows the engagement of semantic to episodic memory, as a proportion or responses for each trial that engaged that memory-type).

(5 point scale). The exact wording of these questions and an example of the format can be found in the supplementary materials (see Supplementary materials: Task information). There was a high degree of overlap between: participants' in-scanner ratings of the link they made and word2vec (Pearson $r = 0.83$, $P < 0.001$); word2vec and post-scan ratings (Pearson $r = 0.82$, $P < 0.001$); and in-scanner and post-scan ratings (Pearson $r = 0.98$, $P < 0.001$).

After these questions, participants also performed a standard 3 alternative-forced-choice semantic association task (e.g. carrot—dinner, celebrity, and television). This consisted of 120 trials (60 strong associations and 60 weak associations), presented in 4 mini-blocks. The task started with an instruction screen, which had no deadline and participants could initiate the start of the task at their own pace. Each trial remained on screen until an answer was given (maximum duration 3 s), after which the next item was presented. The target and distractors were presented first, and then after 900 ms the probe appeared and participants could make their response. Responses were not recorded for 4 participants; therefore, this task was not included in any data analysis.

fMRI task procedure

Before entering the scanner, participants re-practiced the link formation task for 2 trials, stating their retrieved associations aloud, with feedback from the experimenter. They then completed 25 practice trials on a computer using the same presentation format as the task in the scanner, with 4.5 s for each word-pair followed by the link rating question, and chevron trials.

The MRI session included a localizer scan, 3 functional runs (11 min and 45 s each), and a structural T1 scan following completion of the 3 functional runs. We used a slow-event-related design, with 7.5 s between trials; 6 s were filled with the chevron task—participants indicated whether the chevron faced left or right, with 10 chevrons presented across this 6-s block). There was then 1.5-s of fixation to alert the participant to the upcoming trial (Fig. 2). Halfway through each run participants had 30 s of rest to help maintain focus.

FMRI acquisition

Whole brain structural and functional MRI data were acquired using a 3T Siemens MRI scanner utilizing a 64-channel head coil, tuned to 123 MHz at York Neuroimaging Centre, University of York. A Localizer scan and 3 whole brain functional runs were acquired using a multiband multi-echo (MBME) EPI sequence, each 11.45-min long (time repetition [TR] = 1.5 s; time echo [TEs] = 12, 24.83, and 37.66 ms; 48 interleaved slices per volume with slice thickness of 3 mm (no slice gap); Field-of-view, FoV = 24 cm (resolution matrix = 3 × 3 × 3; 80 × 80); 75° flip angle; 455 volumes per run; 7/8 partial Fourier encoding and GRAPPA (acceleration factor = 3, 36 ref. lines); and multiband acceleration factor = 2). Structural T1-weighted images were acquired using an MPRAGE sequence (TR = 2.3 s, TE = 2.26 s; voxel size = 1 × 1 × 1 isotropic; 176 slices; flip angle = 8°; FoV = 256 mm; interleaved slice ordering).

Multi-echo data preprocessing

This study used a multiband multi-echo (MBME) scanning sequence to optimize signal from medial temporal regions (e.g. ATL and MTL) while also maintaining optimal signal across the whole brain. We used TEDANA (version 0.0.7) to combine the images (https://tedana.readthedocs.io/en/latest/outputs.html; Kundu et al. 2013; Posse et al. 1999). Before images were combined, some preprocessing was performed. FSL_anat (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/fsl_anat) was used to process the anatomical images, including re-orientation to standard (MNI) space (fslreorient2std), automatic cropping (robustfov), bias-field correction (RF/B1—inhomogeneity-correction, using FAST), linear and nonlinear registration to standard-space (using FLIRT and FNIRT), brain extraction (using FNIRT, BET), tissue-type segmentation (using FAST), and subcortical structure segmentation (FAST). The multi-echo data were preprocessed using AFNI (https://afni.nimh.nih.gov/), including de-spiking (3dDespike), slice timing correction (3dTshift; heptic interpolation), and motion correction (3dvolreg applied to echo 1 to realign all images to the first volume; these transformation parameters were then applied to echoes 2 and 3; and cubic interpolation). The script used to implement the preprocessing TEDANA pipeline is available at OSF (https://osf.io/ydmt4).

fMRI data analysis

First, second and group-level analyses were conducted using FSL-FEAT version 6 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl; Jenkinson et al. 2002; Smith et al. 2004; Woolrich et al. 2009). The TEDANA outputs (denoised optimally combined time-series) registered to the participants' native space were submitted to FSL, and preprocessing included high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 50s), linear co-registration to the corresponding T1-weighted image followed by linear co-registration to MNI152 standard-space (Jenkinson and Smith 2001), spatial smoothing using a Gaussian kernel with full-width-half-maximum (FWHM) of 6 mm, and grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor.

Preprocessed time series data were modeled using a general linear model correcting for local autocorrelation (Woolrich et al. 2001). We used an event-related parametric design—the linear model included 3 experimental conditions as parametric variables (start time, duration, and a mean-centered parametric regressor for each trial). Our analysis focused on the effect of (i) word2vec (i.e. a measure of semantic control based on the degree of preexisting semantic relatedness between the 2 words); (ii) unusualness (i.e. the degree to which each participant's response was unusual/creative (see behavioral results); and (iii) the degree to which the participant used episodic memory to form the link. Other EVs were: (iv) mean activation for the trial (start, duration, and weighting of 1), (v) participant judgment of link made (1.5 s), (vi) rest (30 s of rest, occurring mid-way through each run), (vii) fixation, and (viii) the first 2 chevron trials. We modeled the first 2 trials of the implicit baseline (chevron task) in order to account for the switch cost (i.e. moving from link formation to fast-paced chevrons). We did not include any motion parameters in the model as the data submitted to these first level analyses had already been denoised as part of the TEDANA pipeline (Kundu et al. 2012). All group-level analyses were cluster corrected using a z-statistic threshold of 3.1 to define contiguous clusters (Worsley 2001) and then cluster corrected for multiple comparisons at $P < 0.05$ FWE; the group-analyses were run within a liberal gray-matter mask (40% probability of GM). Conjunction analyses were run using FSL's "easythresh_conj" tool across all of the task conditions (weak association, strong association, episodic, and unusual). All maps generated are freely available at Neurovault (https://identifiers.org/neurovault.collection:8799).

Any trials where no link was made were not included in any of the parametric regressors. The average (across participants) number of trials where no link was made was 8 (out of 144 trials). About 76% of recall was self-rated as highly confident (3 or 4 on a 0–4 scale), whereas only 12% of recall was rated as low confidence (0 or 1 on 0–4 scale); Supplementary materials section: Behavioral data). The average number of "low confidence" trials was 15 (out of 144) and these remained in the model due to the low number of low-confidence trials per run and the unchanged behavioral correlation of association strength and diversity of responses (Supplementary materials section: Behavioral data).

Behavioral data analysis

Using participants' post-scan recall of the links that they formed, we analyzed the unusualness of each response. These values were expressed as a proportion of the total sample who gave that particular response, ranging from 0.03 (a minimum of 1/31 participants) to 1 (a maximum of 31/31 participants). Participants made the links covertly in the scanner, and then reproduced those links outside of the scanner. Given participants had already been in the scanner for 1 h, and needed to recall 144 word-pairs, we instructed them to be brief in their recall to ensure that all 144 word-pairs were completed. Participants typically provided a short sentence to describe the link they made. For example, for the word-pair "flask-gin," participant responses such as, "a hip flask full of gin" or "gin in a flask" were scored as the same; whereas a response such as "you can sneak gin into a festival using a flask," the gist of which is different to "using a flask as a storage container," was scored as a different category of response for that item. The number of similar responses within a "response category" for a word-pair was counted and assigned a score. For example, the gist of 24 of the 31 participants' links between flask and gin was "use it to carry gin"—all of these responses were given a score of 0.78 (24/31), whereas 3 people said you could use a flask to sneak alcohol, so these responses each received a score of 0.1 (3/31). Therefore, each participant received a score for each word-pair, rather than an overall rating of "unusualness" across all trials (i.e. for the "gin-flask" trial: 24 participants each had a score of 0.78 and 3 participants each received a score of 0.1). This scoring method is akin to "relative frequency of occurrence" scoring, where relative frequencies are directly used for scoring (as in our study), which is less problematic than other frequency-based scoring methods based on thresholds (e.g. 5% and 10% thresholds; Reiter-Palmon et al. 2019; Forthmann et al. 2020). Furthermore, required sample sizes may be lower for tasks with a constrained solution space, as was the case in our experimental task where participants produce one response, linking 2 words together (Forthmann et al. 2020). However, it is important to acknowledge that there are limitations associated with frequency-based scoring methods and a larger sample size would of course be optimal to increase the reliability of our scores (Reiter-Palmon et al. 2019), but this was not possible for our study. Further studies could seek to replicate these findings, both at the behavioral and neural level with a larger sample; and using a variety of scoring methods. Although there are limitations to frequency-based scoring, for example, the requirement for larger sample sizes for precision of frequency-based scores, it does still help to capture how similar or different response types were between participants for each trial in our study. These frequency-based scores do correlate with the preexisting strength of relationship between the 2 words (i.e. participants are more likely to produce responses that diverge from one another when the preexisting semantic relationship is low; $r = -.6$, $P < 0.001$). Given the large number of trials (144), the correlation of the word-pair scores with semantic association strength, and the neural correlates (consistent with previous creativity literature), we can be confident that the scoring method employed is appropriate, but may also need replication with larger sample sizes in the future. Unfortunately, we were not able to analyze each response for the "cleverness" of the idea, and chose to use frequency as a more "objective" measure, to localize parts of the brain that activate when more divergent responses are generated.

Results

Behavioral results

Participants relied most on semantic memory to make links between the 2 words ($F(2, 60) = 25$, $P < 0.001$; response breakdown = semantic 53%, combination 27%, and episodic 20%). Using a linear mixed effects model, we characterized the relationship between unusualness of response and the engagement of semantic-to-episodic memory, as well as preexisting semantic association strength (determined by word2vec; all 3 variables were grand-mean-centered), and their interaction; including by subject random intercepts for each trial and subject specific random intercepts and slopes. This model confirmed a significant relationship between the unusualness of the response and the engagement of semantic-to-episodic memory ($t = 5.02$, $P < 0.001$), as well as the preexisting semantic association strength of the 2 words (as indicated by word2vec; $t = -11.99$, $P < 0.001$) and their interaction ($t = 4.3$, $P < 0.001$); when words share little-to-no semantic relationship, the engagement of semantic memory is more likely to produce an unusual response, whereas when words are semantically highly associated—semantic responses are more heterogenous, and episodic responses are more unusual.

fMRI results

Our fMRI model included 3 parametric regressors of interest (all entered simultaneously into the same model). The first regressor provided a measure of semantic cognition, based on the degree of preexisting semantic relatedness between the 2 words: from controlled (low associative strength) in one direction to uncontrolled (high associative strength) in the other. This first regressor captured the neural response for semantic memory, and a second regressor captured neural activation for more episodic responses. This regressor used the self-reported engagement of semantic-to-episodic memory during link generation; only the episodic end of the scale revealed significant neural activation (after thresholding), as any engagement of semantic memory was already captured by the first regressor. A final regressor captured the generation of more unusual responses (i.e. the degree to which each participant's response was unusual/creative).

There were clear differences in the neurocognitive processes that underpinned the retrieval of links between words, depending on their associative strength. Strongly related word-pairs (with high word2vec values) were often linked in a stereotypical way, which was common across participants. The parametric effect of strongly linked items was associated with greater activation in swathes of medial parietal and medial occipital cortex (Fig. 3). Peak responses were observed in right inferior lateral occipital cortex, left postcentral gyrus extending into precentral and superior parietal lobule, right and left parietal operculum and right and left central operculum. These effects overlapped with visual, motor, and ventral attention networks (VAN; Supplementary Fig. S2, see online supplementary material for a color version of this figure; Yeo et al. 2011). Decoding this map using Neurosynth identified terms consistent with a role in less constrained, more stereotypical cognition, such as "sensorimotor," and "resting" (Supplementary Fig. S3, see online supplementary material for a color version of this figure). In contrast, as participants retrieved links between words that were more distantly related, activation increased in semantic control and MDN regions, with a stronger response in left IFG, dmPFC, bilateral insula, and left posterior middle and inferior temporal gyri (Figs. 3 and 4). There were also increases in activation beyond control networks, in posterior fusiform gyrus, right occipital pole and cerebellum. Functions associated with this map, decoded using Neurosynth, encompass executive terms such as "working memory" and "demands" and language terms such as "semantic," "language" and "reading" (Supplementary Fig. S3, see online supplementary material for a color version of this figure).

Our behavioral analysis showed that trials of different associative strengths elicit responses that vary in their degree of unusualness across individuals. Weakly associated word-pairs tend to elicit more diverse associations across participants, suggesting this pattern of retrieval places higher demands on processes that support creativity. A regressor examining changes in activation as participants' responses became more unusual revealed greater activation in left IFG and dmPFC. Both of these clusters overlapped with areas of the SCN that showed more activation for weak associations (Figs. 3 and 4A). A formal conjunction analysis confirmed this pattern of overlap (Fig. 3). Cognitive decoding using Neurosynth revealed an overlap with both semantic and executive responses—identifying terms such as "semantic," "demands," etc. (Fig. 4E). Since greater activation within the SCN for more unusual responses was identified in a model that also included word2vec as a regressor, this analysis suggests that activation within the SCN can be observed in response to more creative responses. There was also greater activation in temporal fusiform cortex for more unusual responses, which did not overlap with the effect of presenting weaker associations (reported above). This finding additionally suggests that anterior parts of the medial temporal lobe support the ability to generate a novel connection between 2 words.

A final regressor examined how the neural response during link generation varied as a function of reliance on episodic memory. On trials in which participants indicated that they were drawing more on episodic memory, stronger left-lateralized activation was seen in AG, ventral and dorsal clusters within anterior cingulate cortex extending into frontal pole and superior frontal gyrus, and in posterior cingulate cortex extending into retrosplenial cortex (Fig. 3). These regions were largely overlapping with the DMN (Fig. 4B) and included sites implicated in episodic memory. Cognitive decoding of the map in Neurosynth elicited terms such as "autobiographical," "retrieval" and "episodic" (Fig. 4E). The unusualness of the response (see above) did not overlap with this effect of reliance on episodic memory: more creative links, generated by only a few participants, elicited activation in anterior aspects of the medial temporal lobes, whereas the episodic memory regressor was associated with greater posterior medial temporal and parietal activation. However, the reliance on episodic memory did overlap with the effects of strong associative strength (captured by word2vec), particularly in medial parietal regions. A formal conjunction analysis confirmed this pattern of overlap (Fig. 3).

We identified DMN activation when participants generated both more episodic and more unusual responses, yet there was an absence of overlap between these 2 regressors. We therefore assessed the contribution of 3 previously-described DMN subsystems (medial, core, and dorsomedial; Yeo et al. 2011) to link formation. Greater availability of episodic information during the generation of verbal associations primarily activated the core DMN, while also eliciting activation in the dorsomedial and medial DMN subsystems (Fig. 4D). In contrast, when links were formed for weakly associated words, and when responses were more unusual, DMN activation fell within the dmDMN, with little or no activation in the other subsystems (Fig. 4D

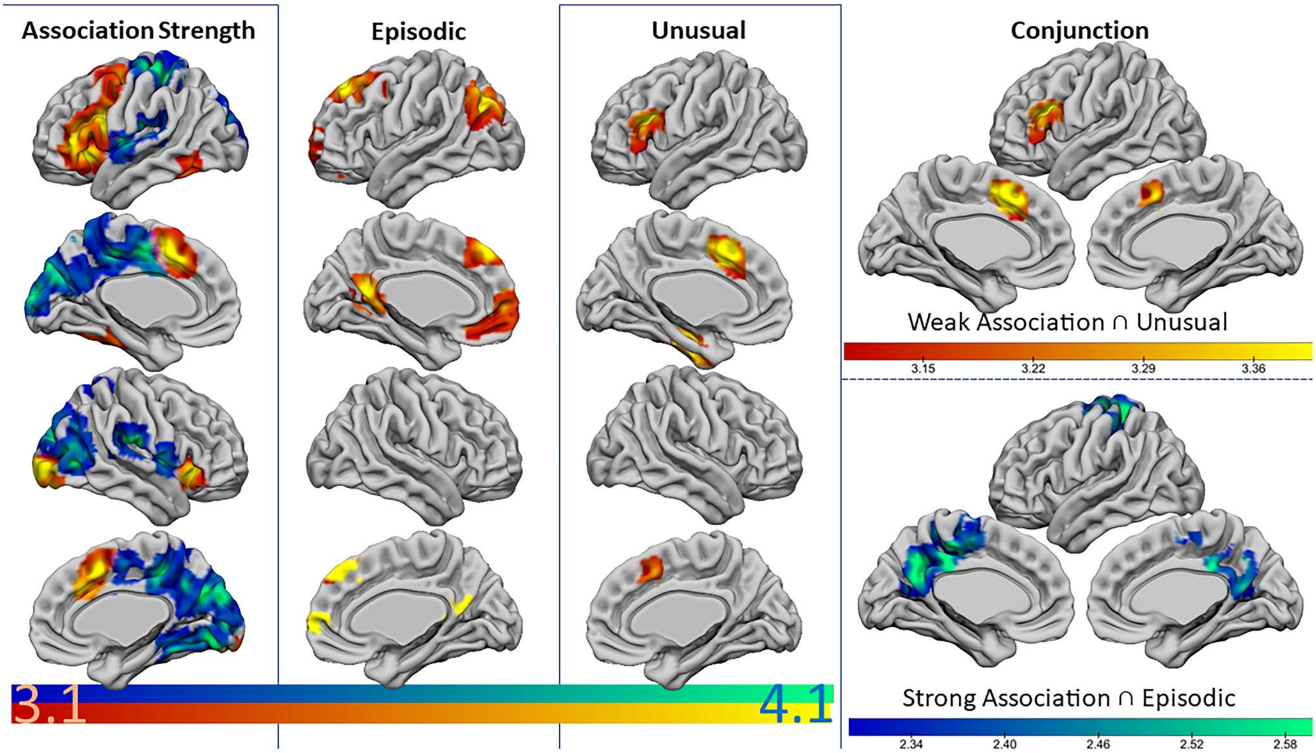

Fig. 3. fMRI activation for the parametric effects ($z \geq 3.1$, $P \leq 0.05$). The first column shows thresholded activation for weak (red-yellow) to strong (blue-green) association strength as measured by word2vec ratings. The second column shows areas in which activation increased as participants became more reliant on episodic memory. The third column displays activation associated with more unusual responses. The fourth column shows the activation across pairs of regressors, with conjunctions observed for weak associations and unusual responses, as well as for strong associations and more episodic retrieval. There were no conjunctions when these conditions were recombined (i.e. no conjunction of weak associations and episodic retrieval, or strong associations and unusual responses). Even a more lenient analysis ($z > 2.3$, $P < 0.05$) designed to minimize type II errors confirmed this pattern of selective conjunctions between (i) weak association ∩ unusualness and (ii) strong association ∩ episodic (and not the reverse).

and Supplementary Fig. S3, see online supplementary material for a color version of this figure). In order to assess whether activation within these DMN subsystems was significantly different across our regressors, we extracted the percentage of each participant's activation map (thresholded at $z = 2.3$) that fell within each DMN subsystem (dorsomedial, medial, and core) for each regressor (word2vec, unusualness, and episodic). Episodically-mediated trials overlapped with significantly more of the core DMN than unusual ($t(30) = -2.481$, $P = 0.019$) and weak-associate ($t(30) = 3.551$, $P = 0.001$) responses. The percentage of voxels within each map falling within the dmDMN subsystem did not significantly differ across episodic, weakly associated, or unusual link generation regressors ($F(2, 60) < 1$). There was also no difference between these regressors within the medial subsystem ($F(2, 60) = 2.1$, $P = 0.13$).

Correlation with UUT

Our analyses revealed activation in left IFG, dmPFC, and temporal fusiform cortex for more unusual word-pair link formation. In order to assess whether the activation during link formation related to individual differences in generating more unusual ideas (a component of creativity) on a more standard assessment, we determined whether the strength of the unusualness effects in these regions was associated with performance on the UUT. It should be noted that, due to time constraints, we were unable to assess all aspects of creativity; therefore, this analysis reflects at least one aspect of creative thought (i.e. the fluent generation of unusual ideas), but does not represent all forms of creativity or DT (Reiter-Palmon et al. 2019). In a regression analysis predicting Unusual Uses performance from the activation in each of these clusters simultaneously, we found that increased activation in dmPFC during the generation of unusual links correlated with better performance on UUT ($F(1, 27) = 6.95$, $P = 0.014$; Fig. 4C). Activation within the other clusters did not make a unique contribution to UUT (IFG: $F(1,27) = 2.545$, $P = 0.12$; temporal fusiform: $F(1, 27) = 2.2$, $P = 0.15$).

As a control, we also confirmed that activation in a cluster adjacent to dmPFC (elicited by the episodic regressor) did not correlate with Unusual Uses performance ($F(1, 26) = 1.3$, $P = 0.3$; see supplementary materials: Correlations with Unusual Uses Task Performance).

Discussion

This study investigated the contribution of brain networks supporting semantic and episodic retrieval as participants generated links between words that varied in their degree of association along a continuum from strongly related (lowest creativity) to unrelated (highest creativity). In this way, we were able to test hypotheses about the contribution of different long-term memory processes and neural networks related to creative and stereotypical verbal behavior. Participants largely relied on semantic information to identify links between words, although episodic memory contributed to more unusual link generation for strongly associated trials. Creative connections were generated through flexible and controlled retrieval of less dominant semantic information—with greater recruitment of the SCN in left IFG and dmPFC when unusual links were generated. The functional

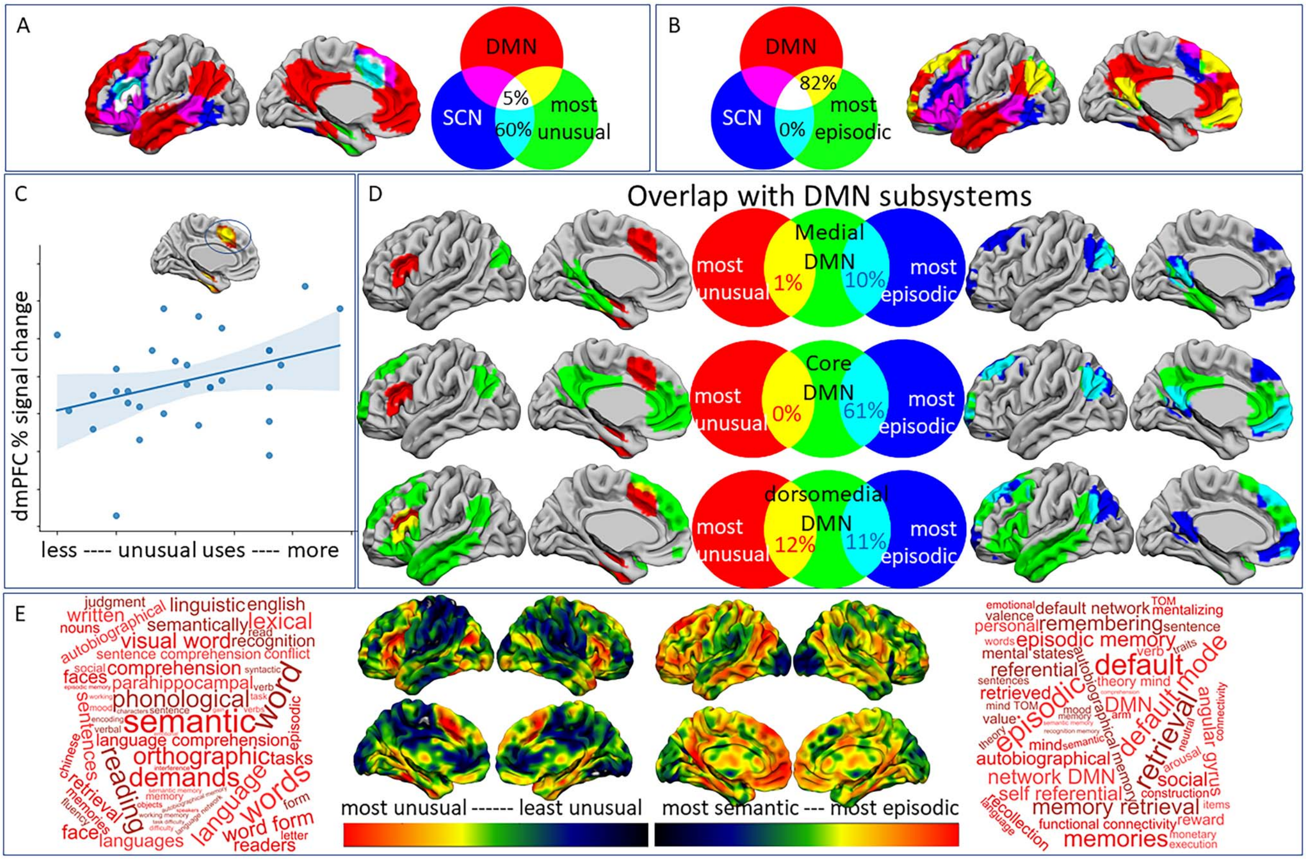

Fig. 4. Top row: Overlap of activation for parametric effects for most unusual and most episodic responses with the following 2 networks: Semantic Control (SCN from a meta-analysis of semantic control; Jackson 2021) and Default Mode (DMN from the 7-network parcellation of resting state data; Yeo et al. 2011). The Venn diagrams show the percentage of voxels for each effect that overlapped with these established networks, both (A) unusual and (B) episodic responses fall within nonoverlapping parts of the DMN. Middle panel: (C) The relationship between increased activitation in dmPFC for more unusual link generation and greater DT on the UUT outside of the scanner. (D) Overlap of activation for parametric effects, with the DMN subsystems: Medial (Yeo 15), core (Yeo 16), and dorsomedial (Yeo17). The Venn diagrams show the percentage of overlapping voxels for each effect with these established networks. Bottom panel (E): Unthresholded activation maps showing the continuous response associated with the parametric regressors. The word-clouds are derived from a Neurosynth meta-analysis of these maps.

network supporting verbal creativity partially overlapped with the dmDMN subsystem and novel responses generated activation in this subsystem. In contrast, strong associations aligned across both episodic and semantic aspects of long-term memory and supported by relatively uncontrolled patterns of retrieval were associated with activation in core DMN. These results support the notion that creativity emerges from an interaction of memory and control processes (Zhuang et al. 2021)—and help to elucidate the specific neurocognitive processes that drive activation in control and DMN networks.

When 2 items are strongly associated, people are more likely to have episodic memories of their interaction or relationship—and therefore they can generate links relying on both episodic and semantic memory. This fits with the emerging literature demonstrating that these 2 memory systems draw on distinct yet interacting long-term stores, and share common automatic and controlled retrieval pathways (Rajah and McIntosh 2005; Burianova and Grady 2007; Burianova et al. 2010; Irish and Vatansever 2020; Vatansever et al. 2021). The activation associated with the use of episodic memory to generate links between items in the current study overlapped with regions previously implicated in more uncontrolled aspects of episodic retrieval, including in left AG, ventromedial prefrontal cortex, posterior cingulate/precuneus, and middle and superior frontal gyri, largely within core DMN. The AG, and other regions of DMN, are purported to play a role in binding and integrating information, in both episodic and semantic memory (Seghier 2012; Bonnici et al. 2016; Ramanan et al. 2017) and the activation seen for our task may have reflected the integration of semantic and episodic contributions to link generation. Moreover, this situation involving information integration may promote a pattern of "ecphory"—i.e. strong uncontrolled retrieval driven by highly-constrained circumstances (Renoult and Rugg 2020).

Although it might be assumed that semantic knowledge is broadly shared across participants (despite individual differences that reflect interests and expertise), we observed considerable variability in the links that participants formed between words, especially with greater semantic distance. The accompanying neural activation was spread across control networks and dmDMN—this activation profile was also seen when responses were more unusual. The SCN sits at the intersection of dorsomedial DMN and MDN regions in the left hemisphere (Wang et al. 2021), with both structural and functional connectivity to regions within both networks (Davey et al. 2016), and is therefore well positioned to leverage these networks in support of link formation for distantly related concepts. Activation in 2 key SCN nodes, left inferior frontal cortex, and dmPFC, was common to weak-associate word-pairs and when the link generated was unusual. We also saw activation in other parts of the SCN for weakly associated concepts, including in inferior pMTG/ITG—a site commonly recruited by more difficult semantic judgments (Whitney et al. 2011, 2012; Davey et al. 2015, 2016).

There was also a functional dissociation within the DMN. The core DMN subsystem, encompassing posterior and anterior cingulate cortex plus AG, showed more activation when participants relied on episodic memory, primarily when the word-pairs had a strong preexisting semantic relationship. In contrast, the dmDMN subsystem, which encompasses anterior ventral parts of IFG as well as temporal and parietal regions, responded during the retrieval of weaker and unusual associations, with no activation in the core DMN. Large-scale meta-analyses have implicated dmDMN in conceptual processing (Andrews-Hanna et al. 2010, 2014), whereas the core and medial DMN subsystems show greater recruitment during episodic memory (Huijbers et al. 2011; Sestieri et al. 2011), past and future autobiographical thought and self-referential processing (Andrews-Hanna et al. 2010, 2014; Chiou et al. 2020; Zhang et al. 2021). In addition, the dmDMN but not the core DMN (as defined by a parcellation of resting-state fMRI of 1,000 brains) overlaps with the functionally-defined SCN; this provides further evidence that dmDMN supports both uncontrolled and controlled aspects of semantic cognition.

The activation pattern across DMN and control regions is consistent with resting-state and task-based functional studies of creativity: these networks play a complementary role in the generation and evaluation of ideas (Beaty et al. 2016, 2019; Frith et al. 2021; Xie et al. 2021; Zhuang et al. 2021). The increased activation in key nodes of the SCN during unusual responses might reflect the way that creativity emerges from core cognitive processes involving memory, attention, and executive control (Abraham et al. 2012; Abraham and Bubic 2015; Benedek and Fink 2019; Frith et al. 2021; Zhuang et al. 2021). For example, Zhuang et al. (2021) suggest that coupling of DMN and executive networks is critical for creativity; and more efficient connectivity between default, control, salience, motor, and visual networks during semantic relatedness judgments predicts a less modular semantic memory structure, and higher "real-life" creativity (Ovando-Tellez et al. 2022). The SCN is ideally situated to support this network interaction, as it is physically located between aspects of DMN and MDN on the cortical surface. This account can therefore explain why key SCN regions, in left inferior frontal cortex and dmPFC, showed greater activation during the generation of unusual responses. Leveraging the SCN may allow activation to be directed towards unusual and nondominant features and associations of concepts, so that a novel link can be identified. Furthermore, the observation that dmPFC activation was linked to better performance on the UUT outside the scanner, corroborates previous studies demonstrating dmPFC as a key player in creative cognition (future studies would benefit from using a wider range of creativity measures, especially since the UUT only captures one aspect of creative thought (DT); and we only measured DT with a single task; Gonen-Yaacovi et al. 2013; Boccia et al. 2015).

Participants also recruited LIFG and dmPFC, in a recent study (Benedek et al. 2020), when generating more original associations to a single-adjective (e.g. red = "ketchup"); as well as recruiting vmPFC (a site associated with episodic memory in our study), and calcarine and superior temporal gyrus (both activated for strong-associates in our study). Neural activation when generating links between 2 adjectives (e.g. red-round = "clown's nose") overlapped with 2 results in our study: AG (recruited for episodic memory in our study) and bilateral lingual gyri (activated by strong-associates and restricted to right hemisphere in our study). These activation overlaps help elucidate some of the component processes underlying previously reported activation—e.g. the engagement of different memory systems, and the ease with which participants can generate a link between items (preexisting semantic relationship between stimuli). Benedek et al.'s (2020) task necessitates a feature-based strategy (akin to some feature-based selection studies of semantic control; Davey et al. 2016; Wang et al. 2020, 2021): participants may have engaged more visually mediated processes to hone in on features that link the adjectives, whereas in our study, participants could leverage the concept as a whole to generate links between nouns—this highlights the wide array of strategies available to participants when generating creative ideas, and how neural activation may change as a consequence.

A limitation of this study is that we cannot model the emergence of creative idea generation in a dynamic way: we used a slow-event-related design to maximally separate activation across trials, and are unable to model activation at different time-points in the generative process—for example, to investigate whether aspects of DMN couple with ventral attention versus control networks during initial retrieval and later elaboration (cf. Beaty et al. 2015). Our results revealed activation in executive and DMN, but little activation in the VAN, for both weak associations and more unusual links (only strong association word-pairs elicited VAN activation, consistent with the detection of salient associations between items in long-term memory that were sufficient for performing the task; Supplementary Fig. S2, see online supplementary material for a color version of this figure). Secondly, although 2 of the clusters associated with more unusual responses fell within the SCN (left IFG and dmPFC), one did not, in temporal fusiform cortex. However, this site is often associated with semantic processing (Mion et al. 2010; Chrysikou and Thompson-Schill 2011; Ellamil et al. 2012; Ding et al. 2016; Shen et al. 2017). Fusiform gyrus, alongside left inferior frontal cortex, is reported to show maximal activity for unrelated word-pairs, and least activity when identical words are repeated (Wheatley et al. 2005), similar to our study, where more disparately related concepts elicited greater fusiform activation (posterior for weak associations, and anterior for more unusual generation). Fusiform cortex has also been implicated in the formation of new associations, when participants are required to generate uncommon uses for objects (Chrysikou and Thompson-Schill 2011). Shen et al. (2017) propose that the fusiform gyrus has at least 2 roles in creative problem solving: (i) "gestalt-like" processing of feature conjunctions and (ii) perspective taking (i.e. taking a different/new perspective other than the most salient meaning of a word, for example, by thinking of a shoe as a flower pot rather than an item of clothing).

Finally, previous studies have increased creativity using episodic induction prior to creative idea generation (Madore et al. 2015, 2016a, 2016b, 2019; Beaty et al. 2020), and in our study, episodic memory was linked to more unusual responses when the preexisting link between the 2 words was strong. This suggests that the neurocognitive basis of creative idea generation may vary with the task: here, participants were required to generate a link between 2 words, which required semantic processing on every trial (e.g. to access the meanings of the individual words). Consequently, in our paradigm, the retrieval of less homogenous episodic information was more likely on strongly associated trials where episodic and semantic sources of information were likely to be coherent. This allows for the 2 items to have been encountered together in numerous ways, thereby permitting variability in the episodic memory used across individuals (whereas semantic information for strong-associates is more likely to be the same across participants). Future studies could continue to unpick the psychological processes that contribute to different types of creative behavior, for example, by examining which aspects of semantic control (e.g. flexible retrieval, selection from amongst competing alternatives, conceptual combination, etc.) correspond with convergent and divergent verbal creativity.

In conclusion, this study asked participants to produce links between 2 words to establish the contribution of semantic and episodic memory to our capacity to creatively link ideas, and also examined the neurocognitive processes that underpin more unusual compared with more stereotypical responses. We found that participants engaged semantic memory for more creative generation, with accompanying recruitment of the SCN. When semantic and episodic memory stores were well-aligned, activation was dominated by the DMN. Furthermore, we uncovered a dissociation within DMN during link generation. The core DMN was recruited when information from episodic and semantic memory systems was likely to be coherent, supporting information integration. In contrast, the core DMN was not implicated in the semantic control processes required for more unusual ideas, but, areas within the dmDMN were; these trials were more reliant on semantic information to generate a link and were less constrained by experiences in episodic memory.

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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