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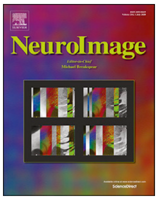

The function of the hippocampus and middle temporal gyrus in forming new associations and concepts during the processing of novelty and usefulness features in creative designs

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ABSTRACT

Creative thought relies on the reorganization of existing knowledge to generate novel and useful concepts. However, how these new concepts are formed, especially through the processing of novelty and usefulness (which are usually regarded as the key properties of creativity), is not clear. Taking familiar and useful (FU) objects/designs as the starting point or fundamental baseline, we modified them into novel and useless (NS) objects/designs or novel and useful (NU) ones (i.e., truly creative ones) to investigate how the features of novelty and usefulness are processed (processing of novelty: NU minus FU; processing of usefulness: NU minus NS). Specifically, we predicted that the creative integration of novelty and usefulness entails not only the formation of new associations, which could be critically mediated by the hippocampus and adjacent medial temporal lobe (MTL) areas, but also the formation of new concepts or categories, which is supported by the middle temporal gyrus (MTG). We found that both the MTL and the MTG were involved in the processing of novelty and usefulness. The MTG showed distinctive patterns of information processing, reflected by strengthened functional connectivity with the hippocampus to construct new concepts and strengthened functional connectivity with the executive control system to break the boundaries of old concepts. Additionally, participants' subjective evaluations of concept distance showed that the distance between the familiar concept (FU) and the successfully constructed concept (NU) was larger than that between the FU and the unsuccessfully constructed concept (NS), and this pattern was found to correspond to the patterns of their neural representations in the MTG. These findings demonstrate the critical mechanism by which new associations and concepts are formed during novelty and usefulness processing in creative design; this mechanism may be critically mediated by the hippocampus-MTG connection.

1. Introduction

Creativity is conceptualized as the generation of novel and useful thoughts (Barron, 1955; Runco and Charles, 1993; Sternberg and Lubart, 1996; Hennessey and Amabile, 2010; Runco and Jaeger, 2012). Several subsequent studies have also sought to identify additional features of creativity (Storme and Lubart, 2012); these expansions have been domain-specific and selectively applicable to specific real-world fields. Thus, the notion that creativity requires both novelty and usefulness is still widely accepted as the "standard definition" of creativity (Runco, 2004; Hennessey and Amabile, 2010; Runco and Jaeger, 2012). Although researchers have studied the mechanisms of creative thinking for more than a dozen years (Arden et al., 2010; Dietrich and Kanso, 2010; Takeuchi and Kawashima, 2019), the neural mechanisms that underlie novelty and usefulness information construction during the creative cognitive process remain elusive. The aim of studying novelty and

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usefulness information construction is to determine how the information constructs of novelty and usefulness are processed separately and how they combine to form creativity.

Notably, studying the neural mechanisms that underlie novelty and usefulness information construction during the creative cognitive process is essential. In fact, some studies have demonstrated that novelty and usefulness features are closely related to the process of creative concept formation produced by creative thinking, which refers to destruction of the familiar concept category and the formation of a new, reasonable concept that is different from the familiar concept during the creative process. For instance, the novelty feature requires thinking outside the box and mental exploration of remotely connected concepts while suppressing dominant concepts and inhibiting the obvious associations to form novel associations (Luft et al., 2018). Additionally, usefulness features require new concepts to be formed in appropriate ways based on novel associations (Runco and Charles, 1993). In this way, the neural basis of "novelty" and "usefulness" features in innovative design may be the same mechanism used for new categorical processing and updating. For example, the invention of digital cameras subverts the understanding that the essential attribute of a camera is that it must capture images with film, and the invention of electric vehicles overturns the fundamental thought that cars must be driven by fuel, illustrating that novelty in innovation can update the critical features of traditional categories. On the other hand, the invention of the tank led to a brand new category of strong weapons that differed from traditional pillboxes, vehicles, and cannons, and the invention of smartphones integrating a good user experience created a new category of electronics that was different from traditional mobile phones, computers, and other products such as the Walkman and cameras. These examples illustrate that the usefulness of innovations can also lead to the formation of new categories. Therefore, investigating the neural bases of the two features of creativity could enrich the understanding of the neural mechanisms of creativity concept representation.

Thus far, the neural mechanisms of novelty and usefulness feature representation are widely considered the critical part of creativity; however, few creativity studies refer to the neural basis of the two features. Behavioral studies devoted to investigating the novelty and usefulness features of creativity are also rare (Diedrich et al., 2015). One multivariate analysis of creativity ratings of advertisements found that the features of "originality" and "logic" (White et al., 2002) were closely associated with creativity, and another study discovered that "originality" and "value" (Sullivan and Ford, 2005) were. Well-controlled experiments investigating how ratings of novelty/originality and usefulness/appropriateness contributed to judgments of creativity have shown that the novelty feature was strongly positively related to creativity, while the useful feature was negatively related to both creativity and novelty (Runco and Charles, 1993). A later study found that usefulness could predict creativity only when the novelty of an idea was high (Diedrich et al., 2015). Although these behavioral studies confirmed the "novel and useful" account of creativity and revealed that novelty rather than usefulness might play an essential role in determining the holistic evaluation of creativity, they did not answer the more fundamental question of how these basic features of creativity are mentally represented.

The only two studies devoted to systematically dissociating the cognitive brain mechanisms for representing novelty and usefulness in creativity were carried out in the context of a specific type of insight problem solving. The first study used the chunk decomposition (CD) task, which involves decomposing familiar patterns into their constituent elements so that they can be recombined in a meaningful way, and adopted Chinese characters (an ideal kind of perceptual chunk) as materials (Luo et al., 2006; Luo and Knoblich, 2007). The study found that the procedural memory system (caudate) is involved in novelty processing, while the episodic memory system (hippocampus) is involved in appropriateness processing (Huang et al., 2015). The second study used the riddle task, adopting brain teasers as materials. The results indicated that novelty processing is completed by the executive system (dorsolateral prefrontal cortex [DLPFC]), whereas appropriateness processing is completed by the episodic memory (hippocampus), emotion (amygdala), and reward systems (orbitofrontal cortex [OFC]). Additionally, both novelty and appropriateness processing are mediated by the temporoparietal junction (TPJ) (Huang et al., 2018). Although these studies revealed some of the information constructed in novelty and usefulness processing, the research results from CD and riddle insight tasks still have limitations. The most obvious limitation is related to how well the two tasks can represent the whole field of creativity. As a less common example of insight problem solving, the CD task is characterized by its perceptual nature - the difficulty or constraint of CD tasks occurs in the very early stage of problem perception and encoding (Knoblich et al. 1999, 2001; Luo et al., 2006). The research results on CD are difficult to generalize to other types of insight, such as constraint relaxation (Knoblich et al., 1999), let alone other types of creativity. Moreover, both CD and riddle tasks apparently differ from typical creative thinking, such as divergent thinking and real-life creativity. A recent study found that people's performance in solving insight problems could not predict their real-life creativity (Beaty et al., 2014), thus implying a potential difference between insight and other types of creative thinking. Therefore, more representative types of creativity are still needed to answer the key question of how the features of novelty and usefulness are mentally represented.

In this study, we take a typical example of creativity, creative designs or products as materials to investigate novelty and usefulness processing. We utilized everyday objects or designs ("familiar and useful," FU) as prototypes or a starting point, and these designs were then further modified to create two kinds of new objects or designs. The first type of new object was a novel but inappropriate adaptation that caused the familiar design to lose its essential function and resulted in an inappropriate/useless new object or design ("novel and useless," NS). The second type of new object was a novel and appropriate adaptation that could reasonably extend the function of the familiar design and make it an innovative object ("novel and useful," NU). This condition represents the construction of a new concept with both usefulness and novelty features (Fig. 1a). We could then define the neural correlates of novelty processing by contrasting NU and FU and the neural correlates of usefulness on the basis of novelty (theoretically, we did not consider the usefulness feature in the FU condition because it was not a new form of usefulness produced by the innovative design or products) by contrasting NU and NS. This experimental design not only enabled us to identify the distinct neural correlates of "novel" and "useful" processing but also helped us elucidate the processing of creativity construction based on novelty and usefulness features; thus, the degree of representational change could be easily evaluated according to changes in these features. However, we could not find a familiar useless (FS) design, which means that the FS design does not exist in the real product (Supplemental Material Fig. S1). Thus, we retain a 2 × 2 full factorial design instead of the three-level design. Additionally, it was impossible for participants to generate a creative design in the different conditions during the limited scanning time. Here, we used the design-induced paradigm, which displays each design directly to induce the participant's creativity processing; this paradigm has been widely used in studies of creative problem solving (Luo and Knoblich, 2007; Kroger et al., 2012; Huang et al., 2015; Huang et al., 2018). This method of passive comprehension is not identical to generating a creative design; it mostly involves the evaluation of creativity when participants try to comprehend the utility of a given creative product, yet also requires an initial stage of constructing the presented idea through a generative process. The two-fold model of creativity suggests that creativity involves both idea generation and idea evaluation, cycling between the two phases (Ellamil et al., 2012; Kleinmintz et al., 2019). Previous research has shown that the evaluation process is extremely important because intervention in this process can lead to significant changes in the quality of creative products (Kroger et al., 2012; Runco and Jaeger, 2012; Rutter et al., 2012a,b; Abraham, 2014;

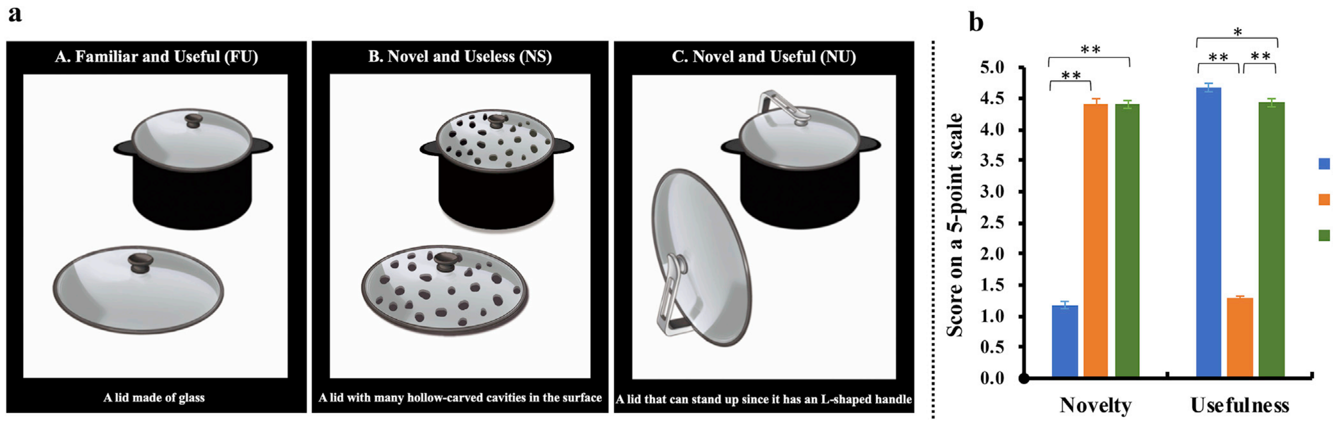


Fig. 1. | Experimental material and behavioral results. (a) Examples of the three creativity object conditions. A pot lid, i.e., a familiar object, was adapted by hollowing out the center such that its main function as a cover disappeared, which was a "novel and useless" adaptation. Likewise, the traditional round handle of the pot was adapted to a long L-shaped handle (this improvement conveniently allowed the pot lid to stand on the table and protected the pot or table from being contaminated), which was considered a "novel and useful" adaptation. (b) Behavioral results. The picture shows the mean scores of the novelty and usefulness evaluation for the three conditions. *FU, familiar and useful; NS, novel and useless; NU, novel and useful. Error bars represent the standard error of the mean. The asterisks indicate significant differences between conditions.* $^{*}p < 0.01$, $^{**}p < 0.001$.

Mayseless et al., 2014; Kleinmintz et al., 2018). The design-induced paradigm that we used for the passive comprehension of creative products focuses primarily on the creative evaluation phase, which is usually accompanied by the "generation process" in the two-process model (Ellamil et al., 2012). In the current study, the passive comprehension of creative products involves restructuring a concept to include new functions or seeing it as related to a new category, which requires a phase of imagination and generation of the concept, as well as an initial stage of constructing the presented idea through a generative process. Additionally, the involvement of brain regions such as the hippocampus and other medial temporal lobe (MTL) regions, which are critically involved in the "generation process" (Ellamil et al., 2012; Beaty et al., 2016b), has been observed in the solution-induced paradigm (Luo and Niki, 2003). Therefore, the passive comprehension of creative products belongs to creative evaluation processes, but also requires a generative process to construct a concept from a presented idea.

A key hypothesis of this study is that the creative idea or design may result in the formation not only of novel associations but also of new concepts. First, creativity is related to inhibiting obvious associations and forming novel ones. A long-standing theory of creativity postulates that creative cognition requires mental exploration of remotely connected concepts (novel association) while suppressing dominant ones (Shen et al., 2017; Takeuchi and Kawashima, 2019). Recent advances in cognitive neuroscience also suggest that right temporal alpha oscillations may support creativity by acting as a neural mechanism for the active inhibition of obvious semantic associations (Luft et al., 2018). Suppressing old semantic associations to search for a novel association, can also cause old information to be reorganized. Thus, there is an opportunity for new information to be generated. Second, in the hippocampus-neocortex system, the hippocampus is a fast-learning structure that captures episodic memories, and the neocortex is a slow-learning structure that stores semanticized knowledge (Mcclelland et al., 1995; Kumaran et al., 2016). Creative thinking, which is often accompanied by insight, is a special form of memory encoding, combining "episodic memory" and "semantic memory" (Luo and Niki, 2003; Huang et al., 2015). Creativity-related memory can be acquired quickly, sometimes even in a single trial, which is very different from learning and memory in the general sense. The previous study also showed that insight leads to reconfiguration of representational neural networks within a memory space and has implications for knowledge acquisition in educational settings (Milivojevic et al., 2015). Therefore, creative thinking may be a direct change in the semantic and conceptual system. This processing may induce the destruction of old concepts and detach the familiar category to construct a new concept.

More concretely, we predicted that two key functional areas would be involved in the formation of new associations and concepts, which is essentially achieved via novelty and usefulness feature processing. The first area is the hippocampus and adjacent areas in the MTL. The hippocampus plays a critical role in forming useful novel associations (Luo and Niki, 2003; Hassabis and Maguire, 2007; Duff et al., 2013; Backus et al., 2016) and in integrating the goal-relevant features of new concept representations in the process of concept learning (Schapiro et al., 2012; Mack et al., 2016), which are then incorporated into existing knowledge neocortical representations (Liu et al., 2016). The second area is the posterior middle temporal gyrus (pMTG). Although the medial prefrontal cortex (mPFC) has more frequently been reported to be involved in new information integration (Takashima et al., 2006; Takashima et al., 2009; Bonnici et al., 2012; Sheth et al., 2012; Zeithamova et al., 2012; Schlichting and Preston, 2016; Tompary and Davachi, 2017), the middle temporal gyrus (MTG) may be highly involved in the construction of creative concept-related novelty and usefulness information. The MTG not only plays critical roles in the processing of novel associations in creativity-related tasks (Shen et al., 2017) but also participates in semantic and conceptual associations (Martin et al., 1996; Chao et al., 1999; Tranel et al., 2003; Brambati et al., 2006; Wei et al., 2012; Bi et al., 2016; Kersey et al., 2016). Moreover, as part of the neocortical region, the MTG may provide the conceptual updating that integrates the useful novel concept with existing knowledge.

We hypothesize that the neural mechanisms of novelty and usefulness information construction, e.g., the functions of the hippocampus and surrounding MTL cortices coupled with the MTG, play vital and distinct roles during the creative cognitive process. Moreover, we suggest that hippocampus-MTG mechanisms are involved in successful creative concept formation. Additionally, beyond the MTL, the MTG is involved in integrating the creative concept and updating the memory system by forming different representational patterns of neural population codes. We also closely focus on the emotion and reward regions, including the midbrain and amygdala, which are important in the processing of novel information (Blackford et al., 2010; Kafkas and Montaldi, 2014).

2. Materials and methods

2.1. Experimental design

Participants. Twenty-one healthy subjects (11 males, mean age ± s.d., 22.10 ± 2.05) were recruited from an agricultural university as paid volunteers. All twenty-one participants were right-handed with normal or corrected-to-normal vision and no history of neurological or psychiatric disease. Data from two participants (2 males) were excluded from further fMRI analysis because of headache during scanning in one case and excessive head motion during scanning (the root mean squared head motion exceeding 3 mm) in the other case. Another twenty-seven healthy subjects (11 males, mean age ± s.d., 24.5 ± 2.72) were recruited as paid volunteers to participate in the additional behavioral experiment. All twenty-seven participants were right-handed, had normal or corrected-to-normal vision and had no history of neurological or psychiatric disease. Informed consent was obtained from each subject recruited for fMRI scanning under a protocol approved by the ethics committee of the Center for Biomedical Imaging Research, Tsinghua University. All the participants in the behavioral experiment (including stimulus design, the stimulus screening phase, and the additional behavioral experiment) signed written informed consent forms before the experiment. Additionally, all the behavioral experimental protocols were approved by the ethics committee of the Beijing Key Laboratory of Learning and Cognition, Capital Normal University.

Stimuli. A total of 153 pictures of objects were used as stimuli in this experiment. These were further divided into three categories or conditions (51 items in each condition). The “familiar and useful” condition (FU) included typical objects that individuals often encounter and use in their daily lives. The “novel and useful” condition (NU) included objects with novel and appropriate changes that reasonably extended the function of the familiar designs of their FU counterparts, thus making them creative objects. The “novel and useless” condition (NS) included objects with an inappropriate change in the familiar design, resulting in the loss of essential functions and making the new objects novel but useless. For instance, for the FU object of a pot lid, the “NU” change exchanged the traditional round-button handle for a long L-shaped handle (this improvement made the object more convenient by allowing the pot lid to stand stably on the table while protecting the pot and table from being contaminated). The “NS” change corresponded to a pot lid with a hollowed-out center; thus, the main function of the lid no longer existed, and the lid became a useless object (Fig. 1a).

The 153 objects (or the stimuli) used in the experiment were selected from a broader set of pictures depicting more than 300 objects. We assembled the pool of pictures by searching for the FU materials on the Internet and designing their corresponding NU and NS stimuli ourselves. Three people familiar with this experiment (including two authors) were involved in the NU and NS design process: 1. With reference to the FU object, we used brainstorming to generate several example NU and NS designs. 2. We recruited more than 100 people to provide excellent NU and NS designs for a $1-3 reward. 3. We conducted a preliminary screening of the collected NU and NS ideas, removing complex or difficult-to-understand items to form an object idea pool. 4. We wrote a detailed description of the ideas for each design and gave these ideas to three professional graphic designers with more than five years of design experience. 5. We evaluated the pictures drawn by the design experts to see if they matched the ideas we wanted to express and then returned them to the experts, who modified them until they met our requirements (average of three revisions for each picture). To help participants understand, perceive, and evaluate the object pictures, 11 to 12 words of description, which included the object’s name and critical function, were presented at the bottom of each picture. In terms of image quality, we used Photoshop to create images with a uniform 600 × 450 resolution and strove to select the products that were most consistent in terms of visual characteristics.

Notably, fMRI research requires many objects to serve as stimuli. As some products are difficult to design corresponding NU or NS products for, the stimuli selected used in our experiments may not completely guarantee that all objects have three conditions; in other words, the stimuli for the three conditions may not be the same object. We attempted to standardize the stimuli and to minimize potential confounding factors. We controlled the key attributes of the selected stimuli in terms of novelty, usefulness, complexity, and understandability based on a pilot study of an independent group of participants (N = 20, mean age ± s.d., 22.1 ± 2.13). The subjects were asked to rate these four attributes of each picture on a 7-point scale (e.g., for the novelty factor, "1" = extremely ordinary; "7" = extremely novel. A similar rating scale was used for usefulness and complexity. For the understandability attribute, "1" = extremely hard to understand; "7" = extremely easy to understand). The results of the novelty attribute showed a main effect across the three conditions ($F(2, 38)_{\text{novelty}} = 349.95$, $p < 0.001$, $\eta_p^2 = 0.95$). The novelty scores for the two novel conditions (NS, NU) were higher (above 5 points) than the novelty score for the FU condition (below 2 points). Post hoc comparisons (multiple comparisons performed with the Bonferroni test) showed that the novelty scores for the NU and NS conditions were significantly higher than the novelty score for the FU condition ($p < 0.001$), and the novelty score for the NU condition was higher than that for the NS condition ($p = 0.012$, $\text{Mean}_{\text{NU}} \pm \text{s.d.} = 5.81 \pm 0.49$; $\text{Mean}_{\text{NS}} \pm \text{s.d.} = 5.36 \pm 0.86$). The results suggested that the novel objects (NS, NU) and the familiar objects (FU) we selected could be distinguished by the novelty score. For the usefulness factor, the main effect was significant across the three conditions ($F(2, 38)_{\text{usefulness}} = 426.60$, $p < 0.001$, $\eta_p^2 = 0.96$). The usefulness scores for the two useful conditions (FU, NU) were higher (above 5 points) than that for the NS condition (below 2 points). Post hoc comparisons showed that the FU and NU conditions had significantly higher usefulness scores than the NS condition ($p < 0.001$), and the FU condition had a higher usefulness score than the NU condition ($p = 0.001$, $\text{Mean}_{\text{FU}} \pm \text{s.d.} = 6.37 \pm 0.56$; $\text{Mean}_{\text{NU}} \pm \text{s.d.} = 5.70 \pm 0.45$). This result indicated that the useful objects (FU, NU) and the useless objects (NS) we selected could be distinguished by the usefulness score. For complexity scores, the main effect was significant ($F(2,38)_{\text{complexity}} = 25.01$, $p < 0.001$, $\eta_p^2 = 0.57$), but the mean of all three conditions was low (below 3.5 points). Post hoc comparisons showed that the complexity score was higher in the NU condition than the NS condition ($p = 0.013$) and in the NS condition than the FU condition ($p = 0.005$). The main effect of the understandability score was also significant ($F(2, 38)_{\text{understandability}} = 13.92$, $p < 0.001$, $\eta_p^2 = 0.42$), but the mean scores of all three conditions exceeded 5.5 points. Post hoc comparisons showed that the FU condition had a higher understandability score than the NU condition ($p = 0.003$), and the NU condition had a higher understandability score than the NS condition ($p = 0.04$). In conclusion, the results showed that the objects we selected could be effectively distinguished by novelty and usefulness, and they all had low complexity and high understandability (Table 1). In addition, we also performed the stimulus control for the low-level features (Supplemental Material Table S6).

General fMRI experimental procedures. Every subject performed the entire experiment, which consisted of three phases: the practice phase, the fMRI scanning phase, and the post-scan test phase. The practice phase comprised 15 trials and took approximately 5 min. This phase allowed participants to become familiarized with the experimental procedures before entering the scanner (Fig. 2a). The procedures for this phase were the same as those used in the fMRI scanning phase. During the practice and fMRI phases, participants were given detailed instructions about the experimental procedures and the experimental task. For the core task, the participants were instructed at the beginning of the task to gain a complete understanding of the displayed object by studying it for the entire 6 s period. They were also asked to evaluate the usefulness of the object during the presentation by pressing a button (1-Yes; 2-No). Participants

Table 1
Mean scores of the stimulus behavioral assessments.

	Familiar and Useful		Novel and Useless		Novel and Useful	
	Mean	SD	Mean	SD	Mean	SD
Novelty	1.52	0.53	5.36	0.86	5.81	0.49
Usefulness	6.37	0.56	2.25	0.41	5.7	0.45
Complexity	1.68	0.56	2.53	0.93	3.11	1.05
Understandability	6.8	0.29	5.87	1.18	6.24	0.73

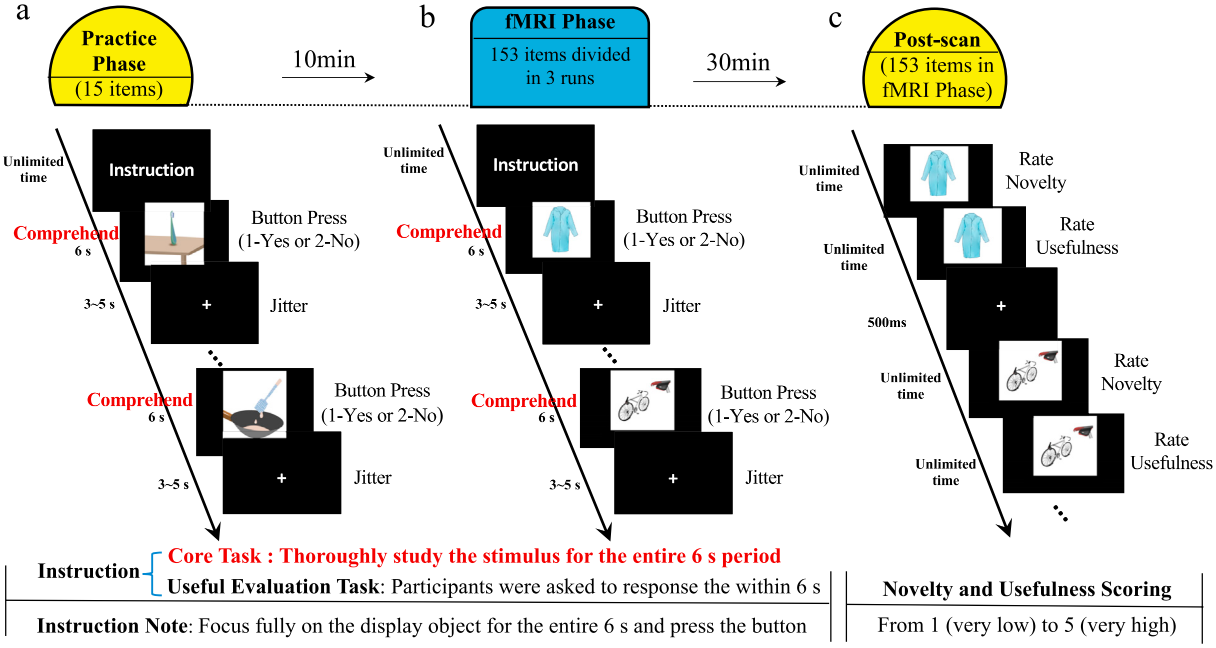


Fig. 2. | Experimental design and procedure. The experimental design consisted of three phases: (a) the practice phase, (b) the fMRI scanning phase, and (c) the post-scan test phase. The procedures in the practice phase were the same as those in the fMRI scanning phase. During (a) and (b), participants were given detailed instructions about the experimental procedures and the experimental task. The core task was for the participants to thoroughly study the displayed object for an entire 6 s period, which they were told at the beginning of this task. They were also asked to evaluate the usefulness of the object during the presentation by pressing a button (1-Yes; 2-No). The detailed procedure was as follows: the item was presented for 6 s, followed by a variable delay period (Jitter: 3–5 s), and the second item was presented again for 6 s. Participants were expected to evaluate whether the item was useful within 6 s and press the button (see the task procedures for more details). During (c), the post-scan test phase, participants were asked to rate the degree of novelty and usefulness of each of the 153 items (fMRI scanning phase items) on a 5-point scale ranging from 1 (very low) to 5 (very high). The time interval between (a) and (b) was 10 min, and that between (b) and (c) was 30 min.

could press the button whenever they were ready within the 6 s display period. However, they were also asked to keep understanding, feeling, or imagining the object, even after they pressed the button, until the image disappeared (core task). The usefulness evaluation task was an additional task to keep participants' attention focused on the core task, and their performance could also be regarded as an index of their concentration. In addition, task performance not only ensured that the participants were focused on fully comprehending each object but was also indicative of whether the subjects were genuinely engaged in the task. We chose the usefulness evaluation as an additional task during the experimental procedures because this evaluation is a more natural task and overlaps with the object comprehension process better than novelty evaluation, which means that participants do not need to use many attention resources during the object comprehension process. The usefulness evaluation task was designed to ensure that participants performed the core task.

During the fMRI scanning phase, participants performed a total of 153 trials, which were equally divided into three runs, with 17 trials per condition each run. The order of the trials was pseudorandomized with the constraint that the same condition could not appear more than three times (to ensure that the subjects focused on the task) in each run, and the sequence of the three runs was balanced across all participants. During scanning, each picture, with its descriptive text, appeared for 6 s, and the subject was instructed to evaluate whether the object or design was useful by pressing a button using the index or middle finger of the right hand within this timeframe. The subject was expected to follow the instructions given in the practice phase to focus on understanding the object for the entire display period. The length of the resting interval between trials varied randomly from 3 to 5 s (Fig. 2b). The duration of each run was 9 min 35 s, and the entire functional MRI session took 28 min 45 s. There was a 1 min rest interval between the two runs.

After scanning, the participants completed a post-test phase in which they were asked to rate the degree of novelty and usefulness of each of the 153 items (fMRI scanning phase items) on a 5-point scale ranging from 1 (very low) to 5 (very high) (Fig. 2c). To screen out inappropriate trials, we conducted an evaluation based on the participant's online (i.e., during MRI scanning) and offline (i.e., after MRI scanning) task performance. For the online task, we excluded items for which the participant made a different judgment than the definition. For the offline evaluation, we excluded pictures with novelty scores above 3 points or usefulness scores below 3 for the FU condition, novelty scores below 3 points or usefulness scores above 3 for the NS condition, and novelty scores below 3 points or usefulness scores below 3 for the NU condition. This procedure was performed for each participant separately.

Additional behavior experimental procedures. One hundred and two object pictures from the fMRI experiment were used in this experiment, which employed two types of novel objects or designs (51 items each for the NU condition and NS conditions, the same as in the fMRI experiment). Participants were asked to make three judgments: Q1. To evaluate the concept dissimilarity between the novel object and the prototype object. Subjects were asked to rate the difference on a 6-point scale ("1" = extremely small, "2" = very small, "3" = small, "4" = large, "5" = very large, "6" = extremely large). Q2. To evaluate whether the object has generated a new concept. The subjects were asked to answer Yes or No. Q3. According to the second question, the subject was asked to evaluate the degree of the new concept generated by the object on a 6-point scale in two novel conditions (NS and NU; "1" = extremely small, "2" = very small, "3" = small, "4" = large, "5" = very large, "6" = extremely large) (scale reliability control in the Supplemental Materials, Table S7). Before the behavioral experiment began, we gave the participants instructions on how to answer the three questions. They followed three guidelines in evaluating the new concept; 1. Evaluate whether the displayed object belongs to the familiar category, with reference to the familiar object's concept; 2. Evaluate whether the displayed object redefines the familiar concept, with reference to the familiar concept's novelty; and 3. Evaluate whether the displayed object redefines the familiar concept, with reference to the familiar object's utility. Participants need to follow these points to make the three judgments. Regarding the question scale, Q2 and Q3 ask the same question, the only difference being that Q2 is a binary question, while Q3 has 6 response options. We designed Q3 because we wanted to know the degree to which the new object represented a new concept. After being given the detailed evaluation instructions, each subject performed the entire behavioral experiment, which consisted of three evaluations of each object. Fixation crosses ("+") appeared before the next stimuli's display; the two kinds of objects were randomly displayed (Fig. 6a).

Imaging data acquisition. All subjects were scanned on a 3T Philips Achieva 3.0T TX MRI scanner with a 32-channel head coil at the Center for Biomedical Imaging Research, Tsinghua University. To restrict head movement, sandbags and foam padding were placed around the subject's head during the entire experiment. Functional images were acquired using an echo-planar imaging (EPI) sequence based on blood oxygenation level-dependent (BOLD) contrast. T2*-weighted function images parallel to the anterior-posterior commissure and covering the whole brain were imaged with the following parameters: repetition time (TR) = 2000 ms, echo time (TE) = 35 ms, flip angle (FA) = 90°, field of view (FOV) = 200 mm × 200 mm, 64 × 64 matrix, voxel size = 3.12 mm × 3.12 mm × 4 mm, 30 slices, 4 mm thickness, and no-gap slices. High-resolution structural T1*-weighted anatomical images of the whole-brain images were acquired using a 3D gradient-echo pulse sequence (180 slices, TR = 7.65 ms, TE = 3.73 ms, FA = 8°, FOV = 230 mm × 230 mm, voxel size = 1 mm × 1 mm × 1 mm, 1 mm thickness). Visual stimuli were presented using E-prime 2.0 software (Psychology Software Tools, INC), and the display was projected onto a screen that was visible from the scanner via a mirror.

Behavioral data analysis for the fMRI experiment. We computed the stimulus novelty scores and usefulness scores (the scores were tested in the post-scan test) for the three conditions, which were separately submitted to one-way repeated measures ANOVAs to test for differences among the experimental conditions. The post hoc comparisons were performed with the Bonferroni correction. Individual participants' novelty scores or usefulness scores for each stimulus were averaged in each condition and then used for further brain-behavioral prediction analyses.

Behavioral data analysis for the behavioral experiment. A paired samples *t*-test was used to test the difference between the NS objects and the NU objects according to their concept dissimilarity with the prototype object. The chi-squared (χ^2) test showed that the difference between the NS and NU objects was reflective of the new concept. Additionally, a paired samples *t*-test was used to test the difference between the degrees of the new concepts represented by the NS and NU objects.

2.2. Statistical analysis of fMRI data

Imaging data preprocessing. Brain images were preprocessed and analyzed using custom scripts combined with core functions from the Statistical Parametric Mapping software package (SPM8; http://www.fil.ion.ucl.ac.uk/spm) implemented within MATLAB 2015a (MathWorks; http://ch.mathworks.com, Natick, MA, USA). The images for each subject were realigned for head motion correction, slice-time corrected, spatially normalized to the standard Montreal Neurological Institute (MNI) template and resampled into 2 mm isotropic voxels. Finally, images were spatially smoothed by convolving them with an isotropic three-dimensional 6 mm full width at half maximum (FWHM) Gaussian kernel. Additionally, the data were statistically analyzed under the framework of a general linear model (GLM) (Friston et al., 1995).

Univariate GLM analysis. To dissociate the neural activity associated with the novelty and usefulness processing of creative objects, a univariate GLM composed of three separate regressors of interest (see below) was modeled and convolved with the canonical hemodynamic response function (HRF) for each subject in the first-level analysis. The three regressors were defined as the experimental conditions (FU, NS, NU) in which we individually screened the trials for each participant. An additional regressor was modeled for no interest conditions, including inaccurate (inconsistent with the common definition) or missed response trials. Additionally, each subject's six motion parameters (three rigid-body translations and three rotations from the realignment procedure) were included to regress out effects related to head movement-related variability. All events were time locked to the onset of the 6-s image display period. Regionally specific condition effects were tested using linear contrasts for each key event relative to the baseline and each subject. We used a high-pass filter cutoff of 1/128 Hz to remove the slow signal drifts with a longer period, and a first-order autoregressive model (AR (1)) was used for serial correlations with the classical restricted maximum likelihood (REML) parameter.

The resulting contrast parameter estimates from the individual-subject level were entered into a random effects model for a second-level analysis. First, we used a one-way within-subjects ANOVA with T contrast of "NU vs. FU" to examine the novelty effect and a one-way within-subjects ANOVA with T contrast of "NU vs. NS" to examine the usefulness effect. Second, to investigate the neural activity associated with both novelty and usefulness, we performed a conjunction analysis between the novelty effect (NU-FU) and the usefulness effect (NU-NS). Significant clusters were determined from the group analysis using a well-accepted statistical criterion including a threshold of $P < 0.05$ with family-wise error (FWE) corrections by random-field theory for multiple comparisons and activation clusters that involved more than 30 voxels, as reported. Additionally, the threshold of uncorrected $P < 0.001$ was also used to detect activation of the amygdala where no superthreshold activation was found after FWE correction.

Within the defined peak coordinates, we transferred the MNI coordinate to Talairach atlas coordinates and used the Talairach Daemon (http://www.talairach.org, University of Texas Health Science Center San Antonio, UTHSCSA) software for the daemon, which includes graphical overlays and nearest gray matter searches (Lancaster et al., 1997; Lancaster et al., 2000); the labeled anatomical location was the peak nearest the gray matter. Thus, the labeled anatomical region may not be exactly within the peak coordinates when the peak is in the boundary between different regions or in the white matter (we searched the nearest gray matter).

Region-of-interest (ROI) analysis. To display the activation differences in novelty and usefulness processing, we performed a complementary ROI analysis including the regions of the bilateral amygdala, the left midbrain, the bilateral MTL and the bilateral MTG, which are critical regions in novelty detection and mental reward in novelty processing (NU-FU). Additionally, the regions of the left MFG, the left precuneus, the bilateral MTL and the bilateral MTG were analyzed for usefulness processing (NU-NS). To display the signal change during the two types of processing, we chose a 4 mm sphere centered at the peak of the clusters after small volume correction (SVC) showing significant activation for novelty and usefulness. Our aim was to display the signal changes in those regions in novelty processing (with the contrast of NU-FU) and usefulness processing (with the contrast of NU-NS). Because these regions were defined based on the NU-FU and NU-NS comparison, we did not use inferential statistics to compare the extracted signals across conditions. The MTL and the MTG are critical for both novelty and usefulness processing. We performed a conjunction analysis of (NU-FU)∩(NU-NS) and performed an ROI analysis of the two regions to investigate the activation across the three conditions. The ROIs were defined as 4 mm spheres centered at the peaks of the clusters showing significant activation after the anatomical templates were applied as an inclusive mask with SVC in the conjunction analysis. Here, we sought to compare the signal changes in those among in the three conditions, which all contain the novelty and usefulness features we focus on. To balance the activation level of the ROI in terms of novelty and usefulness, we chose the peak coordinates of the ROI with activation related to both novelty processing and usefulness processing (conjunction analysis). Parameter estimates (percentage signal changes) associated with the conditions of interest were extracted from the previously defined ROIs at the individual level using MarsBar (http://marsbar.sourceforge.net/), averaged across voxels within each ROI, and then plotted in bar graphs for visualization purposes only. For the brain activation visualization, the activated regions were defined using structurally defined templates as an inclusive mask, and functionally activated regions derived from the specific comparison (e.g., the NU-NS comparison) were obtained within these regions. Structural templates including automated anatomical labeling (AAL) templates were defined on the anatomical mask using the WFU PickAtlas toolbox (Maldjian et al., 2003) (Version 3.0, http://fmri.wfubmc.edu/software/PickAtlas).

Task-dependent functional connectivity analysis. We examined the bMTG functional connectivity changes in the NU and NS conditions via psychophysiological interaction (PPI) analysis (Friston et al., 1997). We separated the MTG region into left and right subregions and defined each ROI as a 6 mm sphere centered at the peak of the clusters showing significant activation in the conjunction analysis (Conjunction SVC, MNI, left MTG peak $x = -42$, $y = -66$, $z = 18$; right MTG peak $x = 44$, $y = -72$, $z = 22$). We performed a generalized form of task-dependent PPI (gPPI) (McLaren et al., 2012). The physiological activity of the given two seed regions (bMTGs) was computed in all voxels as the mean time series and was then deconvolved to estimate the neural activity. Next, the three PPI regressors were modeled and convolved similarly to each task regressor from the individual level in the univariate GLM analysis. The neuronal activity was estimated from the seed region multiplied by a vector encoding the effects of each condition, resulting in three PPI vectors. We further convolved a canonical HRF with the interaction vector to form three PPI regressors of interest.

The individual-level PPI effects corresponding to contrast images were then submitted to one-way within-subjects ANOVA for the second-level group analysis. First, we investigated ROI-seeded functional connectivity with the NU object (compared to the NS object). Additionally, we investigated ROI-seeded functional connectivity with the NS object (compared to the NU object). The next setting was similar to the univariate GLM analysis above. The PPI effects were then determined using the threshold of uncorrected $p < 0.001$ (cluster size >30) in the PPI comparison.

Multivoxel pattern similarity analysis. To assess multivoxel pattern similarity in novelty and usefulness processing, we modeled each item with a duration of 6 s as a separate regressor and convolved it with a canonical HRF implemented in SPM8. This resulted in 17 regressors for each condition and 51 regressors in total (averaged from three runs). Contrast images for each item versus fixation generated by the individual-level analysis between conditions (FU-NU, FU-NS, NU-NS) (Supplemental Material Fig. S2) or within conditions (FU-FU, NS-NS, NU-NU) were then submitted to subsequent between-conditions or within-conditions multivariate pattern similarity analysis for the bMTGs and bMTLs that include the bilateral hippocampal and the bilateral parahippocampal gyrus (PHG) ROIs and for the whole brain.

ROI-based pattern dissimilarity analysis. We determined the ROI masks of the bMTGs and the bMTLs using the AAL atlas. To further our understanding of how the brain represents the differences among the three conditions, we implemented a multivariate pattern analysis measuring the dissimilarity between neural patterns, and we focused on the dissimilarity between FU and NS stimuli and the dissimilarity between FU and NU stimuli. We considered the FU condition as a baseline and computed the dissimilarity between NU and FU and between NS and FU (Fig. 6b). Then, we compared the difference between the NU-FU dissimilarity and the NS-FU dissimilarity. We determined the dissimilarity score using Fisher's Z transformation of 1 minus the correlation coefficient extracted from the whole-brain pattern similarity analysis separately for each participant (Kriegeskorte et al., 2008; Kriegeskorte and Kievit, 2013; Haxby et al., 2014).

Whole-brain pattern similarity analysis and prediction analysis. We performed both whole-brain pattern similarity analysis and prediction analysis to confirm that the MTG specifically represents new concept knowledge. First, we used a 6 mm spherical ROI (Etzel et al., 2013) to implement a searchlight method to measure interitem multivoxel pattern similarity at the whole-brain level (Kriegeskorte et al., 2006; Kriegeskorte et al., 2008) with the NU-NS (usefulness processing) contrast to confirm whether the MTG specifically represents the new meaning concept (Supplemental Material Table S3). Based on the whole-brain pattern similarity analysis, we inferred that the MTG has a unique function in both usefulness and novelty representation. Second, we also used a machine learning approach with balanced four-fold cross-validation to investigate the relationship of similarity changes and individual changes in novelty and usefulness scores (post-scan test scores) within conditions in the bMTGs (Supplemental Material Fig. S3).

Estimates of effect size and post hoc statistical correction. We used the partial eta squared (η_p^2) values for the ANOVA effect sizes. For the paired *t*-test effect sizes, we used Cohen's d, referred to as d_{as} in the text, which takes the mean difference score as the numerator and the pooled standard deviation from both repeated measures as the denominator (Lakens, 2013). The Bonferroni post hoc test was used for statistical correction in this study.

Data and code availability statement. The data and code used in the study are available upon direct request and can be shared or re-used with permission from the authors and a formal data sharing agreement. These data and code sharing policies comply with the requirements of the funding bodies and the Beijing Key Laboratory of Learning and Cognition, Capital Normal University. Direct URL to the dataset: https://osf.io/n9cy7.

3. Results

3.1. Behavioral data of the fMRI experiment

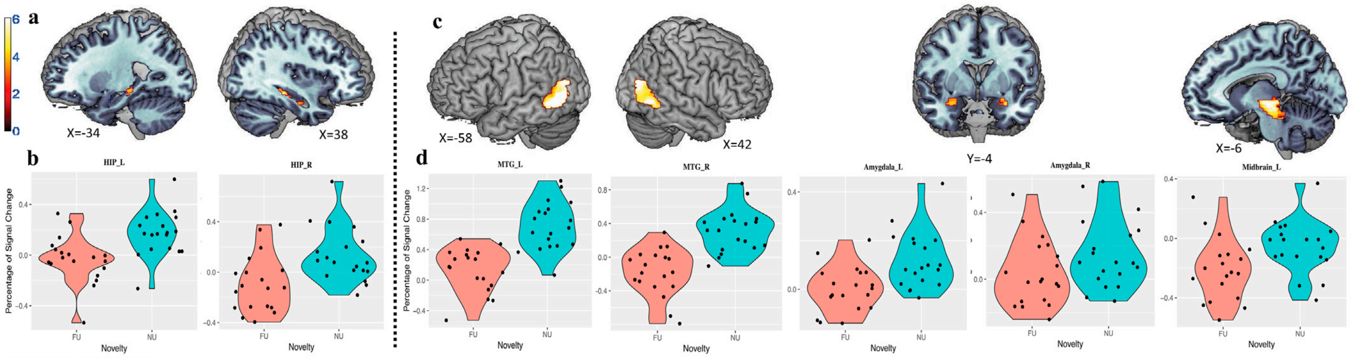
We compared the post-scan test scores of novelty and usefulness, which were evaluated by the participants on a 5-point scale in the post-scan test. First, we used repeated measures ANOVA to examine the difference in the novelty score across the three conditions. The results showed that the main effect of novelty was significant ($F_{\text{novelty}}(2, 36) = 910.61$, $P < 0.001$, $\eta_p^2 = 0.98$). *Post hoc* comparisons showed that the novelty scores in the NS condition ($\text{Mean}_{\text{NS}} = 4.42$, $P < 0.001$) and NU condition ($\text{Mean}_{\text{NU}} = 4.41$, $P < 0.001$) were significantly higher than that in the FU condition ($\text{Mean}_{\text{FU}} = 1.18$). However, there was no significant difference between the NS and NU ($\text{Mean}_{\text{NS}} = 4.42$, $\text{Mean}_{\text{NU}} = 4.41$, $P = 1$) conditions. Second, repeated measures ANOVA revealed that the main effect of usefulness was significant ($F_{\text{usefulness}}(2, 36) = 1053.65$, $P < 0.001$, $\eta_p^2 = 0.98$). *Post hoc* comparisons showed that the usefulness scores in the FU ($\text{Mean}_{\text{FU}} = 4.68$, $P < 0.001$) and NU ($\text{Mean}_{\text{NU}} = 4.48$, $P < 0.001$) conditions were significantly higher than that in the NS ($\text{Mean}_{\text{NS}} = 1.28$) condition, and the FU condition score was also significantly higher than the NU condition score ($\text{Mean}_{\text{FU}} = 4.68$; $\text{Mean}_{\text{NU}} = 4.43$, $P = 0.001$) (Fig. 1b). Together, these results indicate that the rating scores can differentiate the three conditions.

4. Image analyses

4.1. The neural basis of the novelty and usefulness processing of creative objects

4.1.1. The whole-brain activation basis of novelty processing

To detect the brain regions relevant to novelty processing, we compared the NU condition and the FU condition (NU minus FU). The results revealed the involvement of the following brain regions: the MTL, the posterior MTG, the middle occipital gyrus (MOG), the amygdala, the midbrain (substantia nigra, SN), the thalamus, the fusiform gyrus, the perceptual motion system (pre/postcentral gyrus), the precuneus and several frontal regions (Fig. 3, Table 2). The results showed that novelty processing involves many novel detection regions and reward-related regions.



Up (Novelty Processing)

Down (Usefulness Processing)

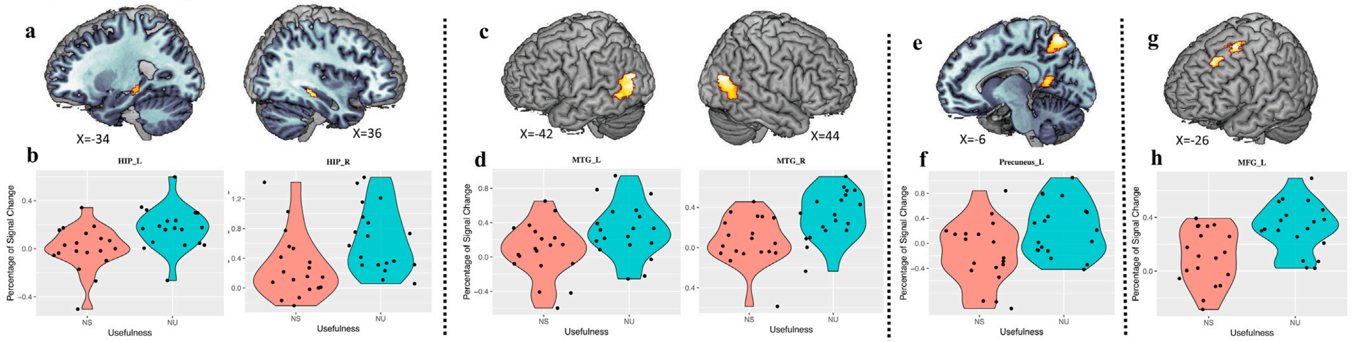


Fig. 3. | Distinct brain regions involved in novelty and usefulness processing. (up) Novelty processing. (a, c) HIP [left (MNI, peak at -34 -32 -12, SVC), right (MNI, peak at 38 -32 -12, SVC)] and bilateral posterior MTG [left (MNI, peak at (−58, −56, −2), SVC), right (MNI, peak at (42, −72, 22), SVC)], bilateral amygdala and left midbrain are involved in novelty detection in comparisons of the novel and useful and familiar and useful objects (NU > FU) (b, d) Violin graphs represent functional activation in the regions showing higher engagement during novelty feature processing. (down) Usefulness processing. (a, c, e, g) HIP [left (MNI, peak at (−34, −32, −12), SVC) and right (MNI, peak at (36, −34, −10), SVC)] and several cortical regions are involved in usefulness feature processing in comparisons of the novel and useful and novel and useless objects (NU > NS), including the bilateral MTG [left (MNI, peak at (−42, −66, −18), SVC), right (MNI, peak at (44, −72, 22), SVC)], left precuneus and left MFG. (b, d, f, h) Violin graphs represent functional activation in the HIP and these cortical regions, with higher engagement during usefulness feature processing. Color bars represent T values. *MFG, middle frontal gyrus; MTG, middle temporal gyrus; HIP, hippocampus; L, left; R, right. MNI, Montreal Neurological Institute coordinate system; SVC, small volume correction.*

4.1.2. *The whole-brain activation basis of usefulness processing*

To examine the neural correlates of the usefulness processing of novel objects, we compared the NU condition and the NS condition (NU minus NS). Again, we observed the involvement of the MTL and the posterior MTG. We also detected the involvement of the superior/middle occipital gyrus, the precuneus, and several frontal regions, such as the superior/middle frontal gyrus (Fig. 3, Table 3).

4.2. *The shared neural basis of novelty and usefulness found in the MTL and the MTG*

4.2.1. *The whole-brain activation basis of both novelty and usefulness processing*

Since we identified the involvement of both the MTL and the MTG in novelty and usefulness processing, we conducted a further investigation to refine these results. We performed a conjunction analysis between novelty (novel and useful minus familiar and useful [NU-FU]) and usefulness (novel and useful minus novel and useless [NU-NS]), which revealed significant clusters in the MTL, the MTG and several other brain regions (Table 4). This result supports our hypothesis that the MTL and the MTG are both involved in novelty and usefulness processing. Further, we sought to determine whether the MTL and the MTG played different roles in the two types of processing. To investigate the primary functions of the MTL and the MTG, we conducted an ROI analysis and a time-course analysis.

4.2.2. *The ROI analysis of the MTL and the MTG*

To detect whether the neural activity of the MTL and the MTG varied across the three conditions, we chose the bilateral regions of the MTG (bMTGs) and the MTL (bMTLs) from the conjunction analysis and applied a GLM to compute the signal change within the MTG and the MTL across the FU, NS, and NU conditions. The results showed increased signal changes across the FU, NS, and NU conditions. However, the most consistent signal change pattern between the MTL and the MTG was observed in the NU condition, which induced the highest activation in both the bMTGs and the bMTLs among the three conditions. In contrast, the signal change in the FU condition showed the greatest deactivation, and the NS condition showed weaker activation than the NU condition (Fig. 4). Our results indicate that both the MTG and the MTL participate in novelty and usefulness processing, and their involvement, according to the signal changes in the three conditions, is most consistent in the NU condition.

4.3. *Distinct functional pathways in MTG representing the useful or useless concept*

Next, as we hypothesized that the MTG plays a critical role in semantic concept processing. Thus, we sought to determine whether there was stronger functional connectivity between the MTL and the MTG when the usefulness of novel stimuli was being processed. Hence, we conducted a PPI analysis to identify functional coupling of the MTG from each hemisphere with every other voxel of the brain for the comparison of the NU minus NS conditions. For the left MTG, the results revealed significantly higher functional coupling with brain regions such as the PHG, the hippocampus (HIP) and the caudate. A similar result was observed for the right MTG, with significantly higher functional coupling with the PHG and the HIP. These results showed that instead of working separately, the MTG and the MTL cooperate to process the usefulness

Table 2
Brain regions associated with novel and useful objects (NU) and familiar and useful objects (FU).

Brain Region	Hemisphere	Brodmann's Area	MNI Coordinates x	y	z	t (18)	k
Novel and Useful > Familiar and Useful							
Fusiform Gyrus	Left	37	−40	−46	−14	12.69	5661
Middle Temporal Gyrus	Right	39	42	−72	22	12.47	3853
Parahippocampal Gyrus	Right	36	34	−40	−12	11.87	
Middle Temporal/Occipital Gyrus	Right	19	38	−82	22	11.84	
Midbrain	Left	–	−4	−28	−4	7.76	94
Substantia Nigra	Left	–	−12	−16	−4	6.06	
Midbrain	Left	–	−6	−28	−12	6.01	
Amygdala*	Left	–	−28	−4	−16	5.86	140
Amygdala*	Right	–	28	−2	−18	4.64	62
Precuneus	Left	7	−24	−70	46	11.73	
Middle Temporal/Occipital Gyrus	Left	19	−38	−80	22	11.64	
Middle Frontal Gyrus	Right	6	30	0	58	6.9	103
Precentral Gyrus	Left	6	−52	8	34	11.04	1770
Middle Frontal Gyrus	Left	6	−28	8	60	10.38	
Precentral Gyrus	Left	6	−48	6	24	10.04	
Precentral Gyrus	Right	6	50	6	32	7.26	176
Precentral Gyrus	Right	6	42	0	38	5.99	
Postcentral Gyrus	Right	2	64	−24	46	7.22	43
Thalamus	Left	–	−20	−30	2	7.03	32
Culmen	Right	–	28	−68	−26	6.85	137
Dentate	Right	–	20	−72	−26	6.66	
Familiar and Useful > Novel and Useful							
Precuneus	Left	31	−14	−68	28	10.21	4682
Cuneus	Left	18	−10	−78	32	9.29	
Precuneus	Right	31	10	−66	32	9.03	
Superior Frontal Gyrus	Right	9	22	54	24	7.55	400
Medial Frontal Gyrus	Right	10	16	56	6	6.97	
Superior Frontal Gyrus	Right	10	26	58	18	6.86	
Inferior Parietal Lobule	Right	40	52	−60	44	7.17	36
Lentiform Nucleus	Left	30	−32	−52	4	6.94	60

Note: Activation was considered significant at $p < 0.05$, FWE corrected unless otherwise specified, * means threshold was set at $p < 0.001$ (uncorrected). Statistics in the t column show values at the peak coordinates. The cluster size is represented by k ($k > 30$). MNI = Montreal Neurological Institute.

feature of novel stimuli, which indicates that more information is transferred between the MTG and the MTL (PHG, HIP) when processing NU stimuli than when processing NS stimuli. However, the opposite comparison (NS minus NU) showed significantly higher functional coupling of both the left and right MTG with brain regions such as the anterior cingulate gyrus (ACC) and several other frontal/parietal regions (Fig. 5, Table S1 and Table S2).

4.4. The neural-based pattern representation of new concept formation in the MTG

4.4.1. Distinct concept distance of the NU and NS objects and new concept formation in the NU condition

To investigate the degree of new concept construction achieved by increasing the novelty and usefulness features and whether the NU object represented a new or creative concept, we conducted an experiment with an independent cohort of 27 participants to evaluate the concept dissimilarity between NU and NS objects and the corresponding familiar object (FU) at the behavioral level. The behavioral results showed that the concept dissimilarity distance between the NU and FU conditions was larger than that between the NS and FU conditions ($t\ (26) = 19.13$, $P < 0.001$, $d_{as} = 3.68$) (Fig. 6 d1). Moreover, the percentage of NU objects representing a meaningful new concept was significantly higher than that in the NS condition ($\chi^2 = 2067.178$, phi (ϕ) = 0.866, $P < 0.001$), and the degree of meaningful new concept construction in the NU condition was significantly higher than that in the NS condition ($t\ (26) = 24.23$, $P < 0.001$, $d_{as} = 4.66$) (Fig. 6c). The results indicated that concept distance is increased by adding the usefulness feature, which might lead to the meaningful new concept creation in the NU condition.

4.4.2. Distinct representation pattern distance among the three conditions in the MTG

In a further analysis, we computed the dissimilarity or representation distances as in the behavior experiment to investigate how the concept of novel information is represented in the MTG and the MTL. The distance between two conditions reveals the degree of representational change from one condition to the other, and greater distances indicate greater dissimilarity between the two conditions (Fig. 6b).

Regarding the MTG, which was anatomically defined, comparison of the dissimilarity between the FU and NU conditions ($disS_{NU\text{-}FU}$) with the dissimilarity between the FU and NS conditions ($disS_{NS\text{-}FU}$) revealed a significant difference in the left ($t_{LMTG}\ (18) = 2.20$, $P = 0.042$, $d_{as} = 0.50$) and right MTG ($t_{RMTG}\ (18) = 3.33$, $P = 0.004$, $d_{as} = 0.76$). For the anatomically defined MTL, no significant difference between the $disS_{NS\text{-}FU}$ and $disS_{NU\text{-}FU}$ was found in the left HIP ($t_{LHIP}\ (18) = 1.84$, $P = 0.083$), the left PHG ($t_{LPHG}\ (18) = 1.56$, $P = 0.137$), the right HIP ($t_{RHIP}\ (18) = 1.75$, $P = 0.097$), or the right PHG ($t_{RPHG}\ (18) = 1.93$, $P = 0.069$) (Fig. 6 d2).

Together, the more significant concept dissimilarity between the NU and FU than between the NS and FU conditions observed in the behavior experiments conducted with the independent sample of 27 participants, consistent with the neural pattern representation distance in the MTG, may reflect new meaningful concept formation in the MTG induced by the NU stimuli.

5. Discussion

We investigated the neural basis of novelty and usefulness processing, which inevitably results in the formation of new associations and new

Table 3
Brain regions associated with novel and useful objects (NU) and novel and useless objects (NS).

Brain Region	Hemisphere	Brodmann's	MNI Coordinates			t (18)	k
		Area	x	y	z		
Novel and Useful>Novel and Useless							
Parahippocampal Gyrus	Left	36	−30	−32	−16	10.62	364
Parahippocampal Gyrus	Left	37	−32	−40	−10	9.96	
Parahippocampal Gyrus	Right	37	36	−40	−10	9.26	141
Hippocampus	Right	–	38	−32	−14	6.79	
Middle Temporal Gyrus	Right	39	44	−72	22	9.11	278
Superior/Middle Occipital Gyrus	Left	19	−38	−80	24	8.5	892
Middle Temporal/Occipital Gyrus	Left	19	−40	−70	16	7.86	
Middle Occipital Gyrus	Left	19	−40	−80	34	7.82	
Middle Frontal Gyrus	Left	6	−26	6	58	7.5	238
Middle Frontal Gyrus	Left	6	−22	8	50	7.2	
Superior Frontal Gyrus	Left	8	−24	22	44	6.71	
Precuneus	Left	7	−6	−66	58	7.27	80
Precuneus	Left	7	−22	−72	46	6.65	75
Novel and Useless > Novel and Useful							
Superior Temporal Gyrus	Right	–	50	−22	−2	8.28	314
Superior Temporal Gyrus	Right	22	64	−24	−4	6.48	
Inferior Frontal Gyrus	Left	47	−32	22	−12	8.14	177
Insula	Left	13	−42	20	−4	6.74	
Inferior Parietal Lobule	Right	40	52	−60	44	8.02	272
Supramarginal Gyrus	Right	40	60	−52	34	7.45	
Inferior Parietal Lobule	Right	40	52	−52	52	6.87	
Inferior Frontal Gyrus	Right	47	46	36	−8	7.94	261
Inferior Frontal Gyrus	Right	–	52	18	−6	6.32	
Inferior Frontal Gyrus	Right	13	46	30	4	6.14	
Medial Frontal Gyrus	Right	6	4	46	32	7.74	402
Superior Frontal Gyrus	Right	6	6	32	52	7.27	
Medial Frontal Gyrus	Left	9	2	54	28	7.21	
Superior Frontal Gyrus	Right	9	22	54	24	7.55	116
Insula	Left	13	−38	6	12	6.56	34
Claustrum	Right	–	34	12	4	6.26	30
Lentiform Nucleus	Right	–	32	14	−8	6.26	31

Note: Activation was considered significant at $p < 0.05$, FWE corrected unless otherwise specified. Statistics in the t column show values at the peak coordinates. The cluster size is represented by k ($k > 30$). MNI = Montreal Neurological Institute.

Table 4
Brain regions associated with the conjunction of novelty and usefulness.

Brain Region	Hemisphere	Brodmann's	MNI Coordinates			t (18)	k
		Area	x	y	z		
(Novel and Useful>Familiar and Useful) ∩ (Novel and Useful>Novel and Useless)							
Parahippocampal Gyrus	Left	36	−30	−32	−18	10.2	289
Parahippocampal Gyrus	Left	37	−32	−40	−10	9.96	
Parahippocampal Gyrus	Right	37	36	−40	−10	9.26	132
Hippocampus	Right	–	38	−32	−14	6.79	
Middle Temporal Gyrus	Right	39	44	−72	22	9.11	268
Superior/Middle Occipital Gyrus	Left	19	−38	−80	24	8.5	785
Middle Temporal/Occipital Gyrus	Left	19	−40	−70	16	7.86	
Superior Occipital Gyrus	Left	19	−36	−72	28	7.43	
Middle Frontal Gyrus	Left	6	−26	6	58	7.5	159
Middle Frontal Gyrus	Left	6	−22	8	50	7.2	
Precuneus	Left	7	−22	−72	46	6.65	74

Note: Activation was considered significant at $p < 0.05$, FWE corrected. Statistics in the t column show values at the peak coordinates. The cluster size is represented by k ($k > 30$). MNI = Montreal Neurological Institute.

concepts. Our results showed that the hippocampus and the MTG are critical in both novelty and usefulness processing during concept construction. The MTG distinguished information transfer via functional connectivity with the MTL to construct a new concept from that with the executive control system to detect the destruction of a useless concept during the updating of the usefulness concept. Additionally, the behavioral concept distance evaluation in an independent cohort of 27 participants showed that the representation distance was larger between successful concept construction and the familiar concept than that between unsuccessful concept construction and the familiar concept; this finding was consistent with the neural pattern representation in the MTG, possibly reflecting new meaningful concept formation in the MTG. Our findings suggest the critical role of the hippocampus-MTG during the creative concept construction process, which involves detecting novelty features to create new associations in novelty processing and evaluating the new associations in usefulness processing, thereby leading to new concept formation through the MTG.

First, we observed significant activation in the MTL, amygdala, midbrain (substantia nigra, SN) and MTG during novelty processing. Most of these regions appear to be involved in novelty detection circuits (Blackford et al., 2010; Kafkas and Montaldi, 2014) and the dopamine reward loop (Gruber et al., 2014). Previous studies have shown that the MTL is critical in processing novelty-related stimuli, especially in novelty detection processing (Blackford et al., 2010; Kafkas and Montaldi, 2014).

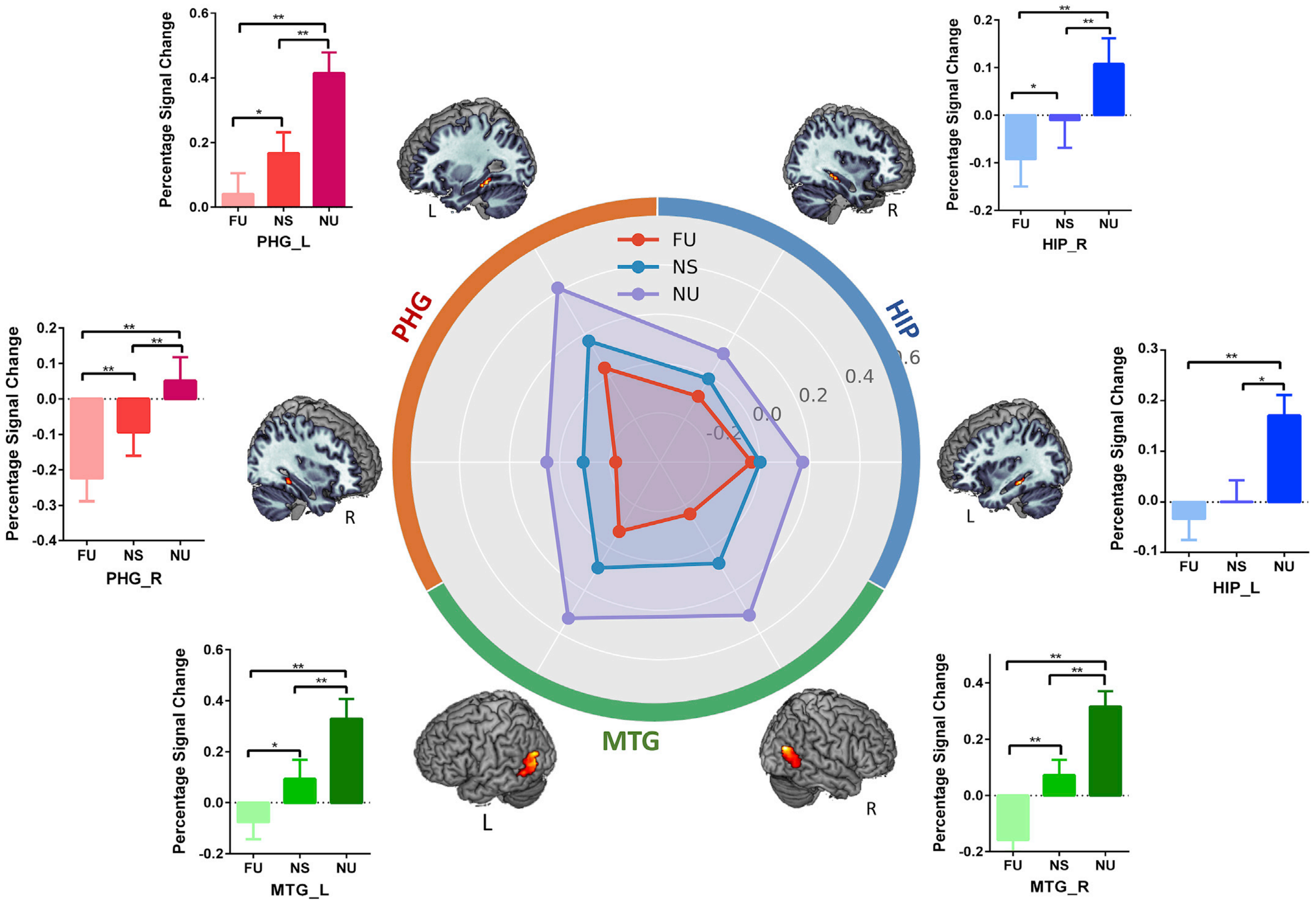


Fig. 4. The signal activity between the MTL and the MTG across the three conditions. Schematic polar plot illustrating the signal change in the three conditions distributed across the MTG [left (MNI, peak at (−42, −66, −18), SVC), right (MNI, peak at (44, −72, 22), SVC)], HIP [left (MNI, peak at (−34, −32, −12), SVC), right (MNI, peak at (36, −34, −10), SVC)], and PHG [left (MNI, peak at (−32, −40, −10), SVC), right (MNI, peak at (36, −40, −10), SVC)] regions separated into the left and right sides. The graphs show that the percent signal changes increased across the FU, NS, and NU conditions. Error bars represent the standard error of the mean. The asterisks indicate significant differences between conditions. *FU, familiar and useful; NU, novel and useful; NS, novel and useless; MTG, middle temporal gyrus; HIP, hippocampus; PHG, parahippocampal gyrus; L, left; R, right. MNI, Montreal Neurological Institute coordinate system; SVC, small volume correction.* *$p < 0.05$, **$p < 0.005$, ***$p < 0.001$.

The amygdala is a critical brain area for emotional arousal (McGaugh, 2004; Phelps and LeDoux, 2005), and the activation level of the amygdala reflects the intensity of emotional arousal for both positive and negative emotions (Löw et al., 2008; Shabel and Janak, 2009; Costa et al., 2010; Fastenrath et al., 2014). The amygdala responds to novel stimuli (Schwartz et al., 2003; Wright et al., 2003; Kiehl et al., 2005) and unknown or ambiguous stimuli (Whalen, 1998; Hsu et al., 2005; Whalen et al., 2005). Neural activity in the SN is beneficial to reward-related memory (Adcock et al., 2006; Wolosin et al., 2012) and curiosity-driven reward learning (Gruber et al., 2014). Surprisingly, while most of the brain regions identified seem reasonable, as we discussed above, our results also revealed that the MTG, which was rarely mentioned in previous studies, was also related to novelty detection processing. Several pieces of evidence suggest that the MTG promotes the novel semantic associations of novel stimuli involved in inhibiting/ignoring the default task-relevant semantic concept meaning (Jung-Beeman, 2005) and seeking remote semantic associations (novel semantic associations) (Whitney et al., 2011a,b; Davey et al., 2016). Therefore, the MTG activation here may facilitate the ability of the MTL to detect novel stimuli by novel semantic associations. In addition, the fusiform gyrus, thalamus, perceptual motion system (pre/postcentral gyrus), precuneus and several frontal regions were also found to be involved in novelty processing. A previous study showed that the fusiform gyrus is involved in high-level visual processing, specifically object recognition and category identification (Weiner et al., 2018). Additionally, as part of the olfactory and visual system, the thalamus has an important role in mediating sensory information to cortical areas (Muller et al., 2019). The perceptual motion system is most likely involved in action-related information processing (Binkofski et al., 1999; Johnson-Frey, 2004; Rumiati et al., 2005), such as the mental manipulation of the spatial representation of tools or other objects (Johnson-Frey, 2004), especially in the case of the use of the right hand (Martin et al., 1996). Our results are consistent with those of previous studies, which may indicate that visual object category identification and mental manipulation of spatial representation are involved in the process of novel detection. Moreover, the precuneus is part of the default mode network (DMN), and the frontal regions, which are critical in the executive control network, are both activated in novelty detection as well in usefulness processing. This finding is consistent with previous studies showing that default and executive control networks, which can exhibit an antagonistic relation, tend to cooperate during creative cognition and artistic performance (Takeuchi et al., 2012; Beaty et al., 2016a; Beaty et al., 2017; Beaty et al., 2018).

Second, we also found activation of the MTL and MTG regions and several left frontal regions and the left precuneus in usefulness processing. According to previous studies, the middle/superior frontal regions

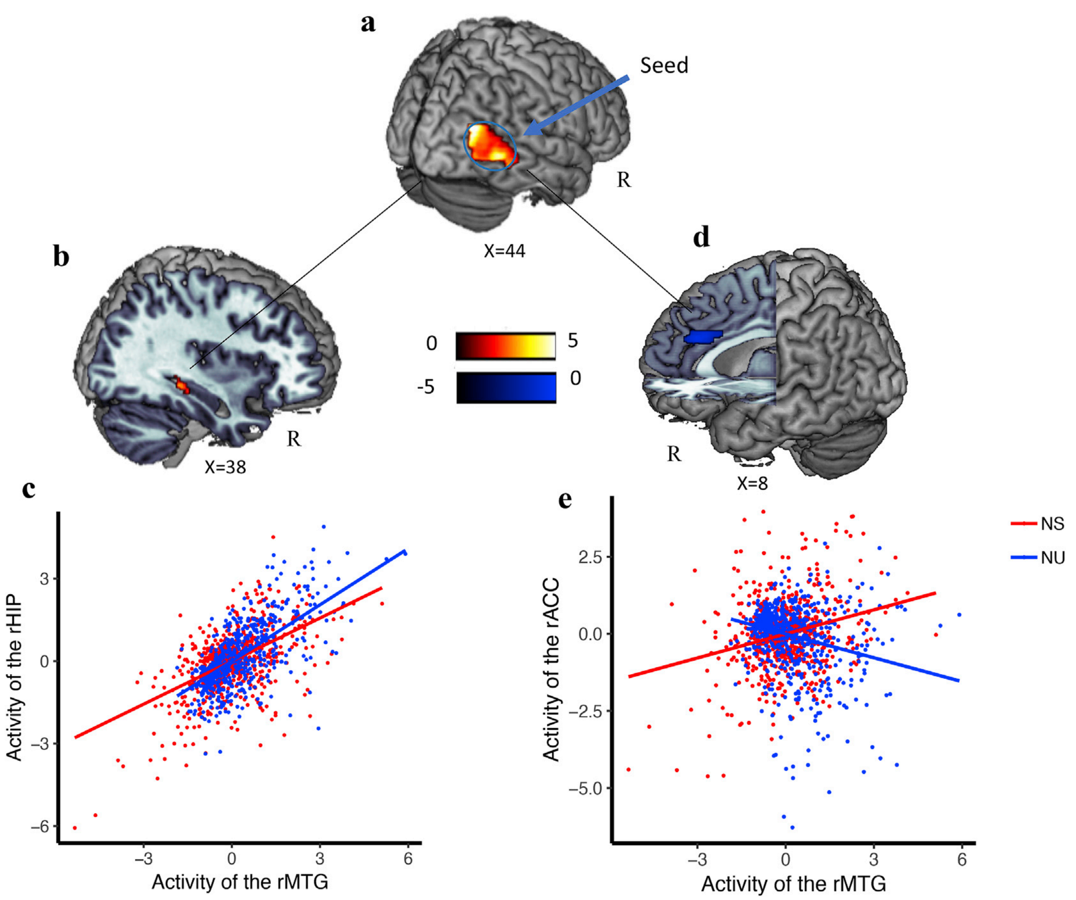


Fig. 5. Distinct functional connectivity pathways for different novel object representations. (a) The right MTG seed (MNI, peak at (44, −72, 22), SVC) used in the gPPI analysis of task-based functional connectivity. (b, d) Regions showing positive (red) and negative (blue) associations with right MTG activation modulated by a novel and useful object relative to a novel and useless object (NU vs. NS). (c, e) An increase in activation in the right MTG was associated with an increase in activation in the HIP and a decrease in activation in the ACC under the condition of NU compared with NS. The color bar represents *T* values; *MTG, middle temporal gyrus; HIP, hippocampus; PHG, parahippocampal gyrus; ACC, anterior cingulate cortex; NU, novel and useful; NS, novel and useless; MNI, Montreal Neurological Institute coordinate system; SVC, small volume correction.*

are involved in the storage of prior existing knowledge (Liu et al., 2016), and the precuneus, together with the left prefrontal cortex, is involved in the recall of episodic memories (Lundstrom et al., 2003). We speculated that usefulness processing might be related to the retrieval of prior information from the left prefrontal cortex and the precuneus. The hippocampus and the surrounding MTL are well known to be involved in the acquisition of novel associations and the formation of new memories (Squire et al., 2004). A recent study suggested that the hippocampus plays an essential role in the formation of new concepts (Mack et al., 2016). Here, MTL and neocortical region activation may reflect that usefulness processing requires the hippocampus to form and update the new concept in the presence of novel stimuli (Davachi et al., 2003; Komorowski et al., 2009), and this process may require the retrieval of prior information from various cortical regions (Squire and Alvarez, 1995; Nadel and Moscovitch, 1997). The MTG is another region that we speculated could be involved in new concept processing. Previous studies also showed that the MTG plays crucial roles in novel associations, semantic categorization and tool processing (Chao et al., 1999). Our results showed that the MTG exhibits differential functional connectivity in the processing of NS and NU concepts. The functional connectivity between the MTG and the MTL indicates information transformation in the MTG and the MTL during useful information processing. Thus, the MTG plays a crucial role in interpreting the novel associations of novel useful information. The data lead us to speculate that communication between the MTL and the MTG is critical in interpreting the meaning of novel stimuli during usefulness processing. However, functional connectivity between the MTG and the ACC and other frontal regions was found during useless information processing. Previous studies have shown that the dorsal ACC (dACC) and the frontal regions are the critical hubs in a domain-general executive function network (Shenhav et al., 2016). Some evidence suggests that the function of the dACC in cognitive control corresponds to error detection (Ito et al., 2003; Narayanan et al., 2013; Shen et al., 2015), explicit negative feedback (Quilodran et al., 2008), and conflict (Sheth et al., 2012; Oehrn et al., 2014; Michelet et al., 2016; Tang et al., 2016). Moreover, the cingulo-opercular network, which contains the dACC, and the bilateral anterior insula play critical roles in the task control signal (Neta et al., 2017). Additionally, previous studies revealed the role of the frontal regions in inhibitory control: enhanced activation of the left inferior frontal gyrus (IFG) was associated with lower originality scores (Mayseless et al., 2014; Mayseless and Shamay-Tsoory, 2015; Ivancovsky et al., 2018). Therefore, the functional connectivity between the MTG and the executive function network may suggest that greater effort is necessary to process the mismatch created by the inappropriateness of novel but useless objects. Overall, the difference in functional connectivity in the processing of NU and NS objects may reflect the ease of assigning a new existing category to NU objects. Finding a suitable category for objects after they lose their obvious functionality (NS object) is comparatively difficult.

It is worth noting that the MTL and the MTG are involved in both novelty and usefulness processing, but we believe that they are engaged in different functional roles in representing the two features. With the involvement of other novel detection regions, novelty processing may

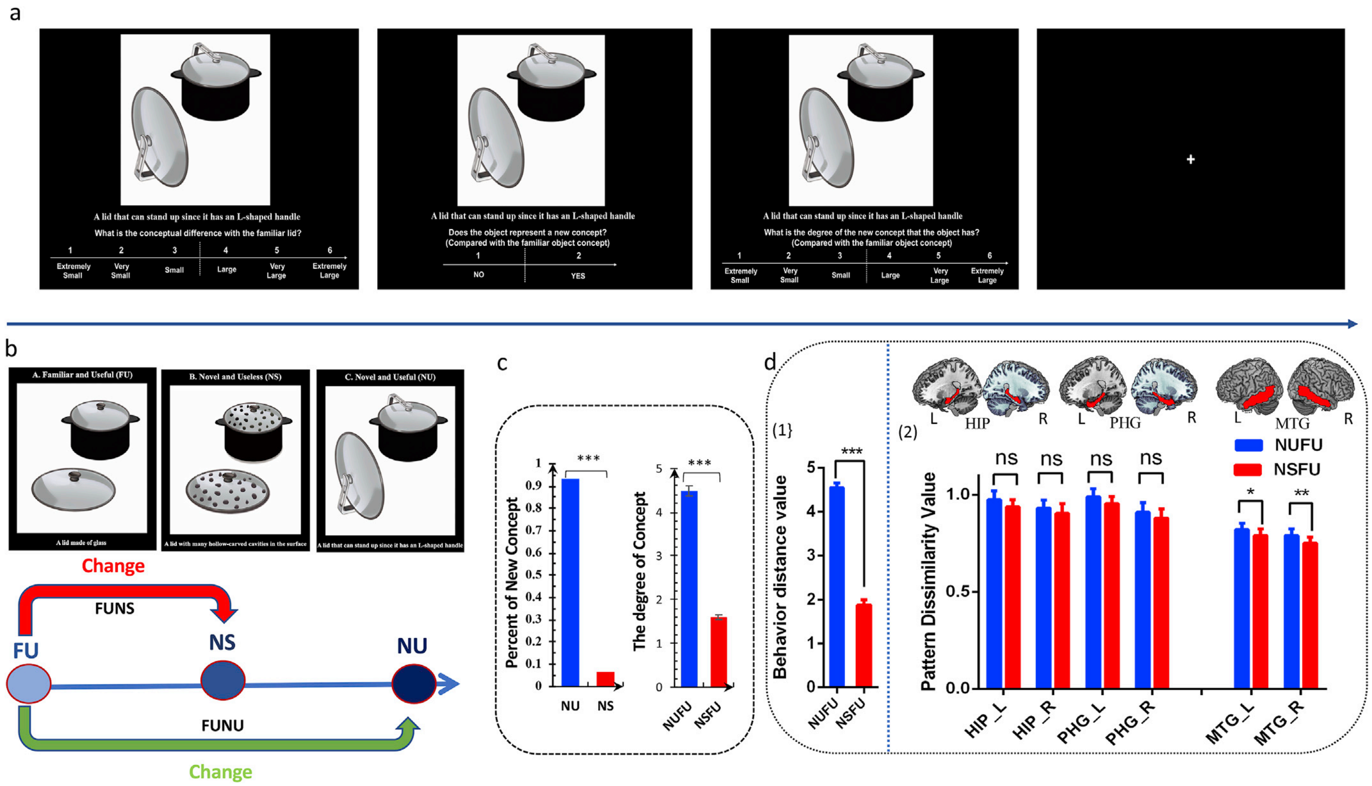


Fig. 6. | Distinct behavioral and multivoxel representational concept patterns in new concept processing. (a) Procedure of the evaluation experiment. Participants were asked to make three judgments: Q1. To evaluate the concept dissimilarity between the novel product and the prototype product. Subjects were asked to provide respond on 1–6 point scale ("1" = extremely small, "2" = very small, "3" = small, "4" = large, "5" = very large, "6" = extremely large). Q2. To evaluate whether the product has generated a new concept. The subjects were asked to answer Yes or No. Q3. As a follow-up to the second question, the subject was asked to evaluate on a 6-point scale the degree of the new concept generated by the object in the two novel conditions (NS and NU; "1" = extremely small, "2" = very small, "3" = small, "4" = large, "5" = very large, "6" = extremely large). (b) The representational change in the two novel conditions. The distance between FU and NS represents the degree of change for the NS condition (with the novelty feature); the distance between FU and NU represents the degree of change for the NU condition (with both novelty and usefulness features). (c) The new concept percentage contained in the NS and NU products (left); the degree of new concept contained in NS and NU products (right). (d1) Mental conceptual distance behavioral experiment results ($\text{dissimilarity}_{\text{NU-FU}} > \text{dissimilarity}_{\text{NS-FU}}$). The mental conceptual distance was evaluated as the conceptual distance between the novel object and its familiar object (FU) by participants. (d2) The MTG neural pattern represents the difference between the NU-FU distance and the NS-FU distance ($\text{dissimilarity}_{\text{NU-FU}} > \text{dissimilarity}_{\text{NS-FU}}$), but the MTL neural pattern represents the distance between NU-FU and NS-FU, with no significant difference. Error bars represent the standard error of the mean (SEM). The asterisks indicate significant differences between conditions. *$^{*}p < 0.05$, $^{**}p < 0.005$, $^{***}p < 0.001$; FU, familiar and useful; NS, novel and useless, NU, novel and useful; NS-FU, the dissimilarity values between FU and NS; NU-FU, the dissimilarity values between FU and NU; MTG, middle temporal gyrus; HIP, hippocampus; PHG, parahippocampal gyrus; L, left; R, right.*

depend on the MTL to detect novel features, and the MTG, which is involved in novelty processing, may play a role in facilitating the ability of the MTL to detect novelty features through novel semantic association. In usefulness processing, functional connectivity was found between the MTG and MTL, and signal changes in the MTL and MTG were both enhanced when the stimuli were both novel and useful. These results reflect that communication between the MTL and the MTG may reflect critical information transfer during usefulness processing.

Third, the results of the additional behavioral concept distance evaluation experiment with 27 independent participants showed that a new concept was formed in the NU condition based on the participants' direct evaluation and that the conceptual distance was larger between the NU and FU than between the NS and FU objects. This may indicate that conceptual distance is based on appropriate functionality and that positive change in appropriate functionality creates conceptual distance. The objects can either gain an additional function (novel function), expand their mental conceptual perception (NU) or lose functionality (NS). In the expanding conceptual perception condition (NU), the object gains a new function that refines the familiar object. For example, the NU object of "a lid that can stand up since it has an L-shaped handle", the improvement made the lid handle more convenient by allowing the pot lid to stand stably on the table while protecting the pot and table from being contaminated. This prompted the participants to refine the object and put it into a new concept category. However, in the loss of familiar functionality (NS) condition, the object may gain an unexpected functionality and thus creative value. For example, useless objects such as "a pot lid with many hollowed-carved cavities in the center" or "a wooden writing desk covered with dead wood cracks" could elicit the following thoughts: "the pot lid is a steamer or humidity creator" and "the table can now be seen as a sculpture". Therefore, a shorter distance exists between FU and NS than that between FU and NU demonstrating the difficulty of detaching oneself from the familiar use of an object and that once objects are made "useless" by removing their familiar functionality, more effort is required to see these useless objects as valuable, not only in functional terms but also in creative terms. This result is consistent with PPI results showing that the stronger the functional connectivity was between the MTG and the executive function network in the NS condition, the more effort was required to process the mismatch created by the inappropriateness of these novel but useless objects.

In addition, considering that the multivoxel pattern similarity analysis showed a pattern distance similar to the behavior concept distance in the MTG, the MTG may play a critical role in representing new meaning concept formation. Most neuroscience studies have suggested that new knowledge acquisition supported by the hippocampus-neocortex is related to the subsequent integration of partially overlapping events (Daphna and Wagner, 2008; Dagmar and Preston, 2010; Kuhl et al., 2011; Schlichting and Preston, 2014; Tompary and Davachi, 2017). From this perspective, as a special type of new knowledge processing, creative concept formation through creative thinking needs to associate the basic familiar concept with novel information through the hippocampus-MTG system. We believe that both the hippocampus and MTG are associated with new concept in terms of both novelty and usefulness features. Our signal change results showed that the signal increased both in the MTL and MTG as the features increased. However, the novel association, supported by a well-established associative memory network, needs to pass the usefulness association evaluation, which integrates the new concept with the existing memory system that can be accepted. Therefore, the MTG may act as a classifier to stop further useless information concept construction through functional connectivity with the executive system. It is different to assign meaning to NS objects. Finally, only the new meaning information can be further constructed in the MTG. Previous studies indicate that the posterior MTG is the core of conceptual processing (Karalyn et al., 2007). It contributes to the retrieval of conceptual knowledge (Tranel et al., 2003; James et al., 2015; Davey et al., 2016) and allows semantic retrieval to be ‘shaped’ to suit the current context to understand actions and nondominant semantic associations (Tranel et al., 2003).

The additional behavioral and functional connectivity data together indicate that the designs in the NU condition were more likely to be perceived as a new category of objects than the designs in the NS condition. Overall, we believe that the MTG integrates novel and useful conceptual knowledge ‘shaped’ by prior semantic knowledge, representing creative conceptual knowledge.

6. Limitations and future directions

There were several limitations to this study. Primarily, although creativity is generally considered an active process of both generation and evaluation, the current task merely requires participants to engage in a relatively passive form of evaluation. Although the evaluation process has an important influence on the quality of creative products and the passive comprehension of creative products process may reflect a form of creativity evaluation processing, yet also requires an initial stage of constructing the presented idea through a generative process, these processes are also unlikely to be completely equivalent to full creativity processing. Further experiments are recommended to focus on spontaneously generated creativity design processing (Dietrich and Kanso, 2010; Gonen-Yaacovi et al., 2013). The generation phase combines remote associations in a novel way (Mednick, 1962) based on a search of semantic memory and autobiographical memory (Milivojevic et al., 2015; Christensen et al., 2018; Madore et al., 2019), which is also critical for creativity concept reconstruction. In addition, our experimental design lacks an FS condition. It should be noted that there are no FS objects exist in real life. The current study from our previous two studies on insight problem solving, in which we used insight problems with possible FS answers as the materials (Huang et al., 2015; Huang et al., 2018). Moreover, considering the better representation of creativity in the real world, we made the creative object the material in this experiment. Although this made for better material than in previous studies, the objects still could not represent all types of creativity. Future studies could find other materials to represent creativity more comprehensively. Furthermore, the total number of scanned participants was somewhat low in this study. The previous study showed that although the power was very poor in the range of most conventional fMRI studies (10–20 subjects), most activated areas were true positives (Murphy and Garavan, 2004); we hope that future studies will include larger fMRI-scanned samples.

7. Conclusion

In conclusion, our study provides behavioral and neuronal evidence demonstrating the neural mechanisms of novelty and usefulness representation during creative cognitive processing. The hippocampus-MTG connection is involved in both novelty and usefulness concept processing and is associated with the interpretation of new conceptual knowledge. Moreover, the MTG is involved in integrating the creative concept and updating the memory system by forming different representational patterns of neural population codes. Our study provides new evidence for understanding the critical mechanism of new association formation and concept formation during novelty and usefulness processing and reveals the critical role of the new concept and new category processing mechanism in creativity formation.

Declarations of competing interest

The authors declare no competing financial interests.

CRediT authorship contribution statement

Jingyuan Ren: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Furong Huang:** Conceptualization, Writing - review & editing. **Ying Zhou:** Conceptualization, Writing - original draft, Writing - review & editing. **Liping Zhuang:** Conceptualization, Writing - review & editing. **Jiahua Xu:** Conceptualization, Writing - review & editing. **Chuanji Gao:** Conceptualization, Writing - review & editing. **Shaozheng Qin:** Conceptualization, Software, Writing - original draft, Writing - review & editing. **Jing Luo:** Conceptualization, Methodology, Resources, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.116751.

References

Abraham, A., 2014. Creative thinking as orchestrated by semantic processing vs. cognitive control brain networks. Front. Hum. Neurosci. 8 (95) https://doi.org/10.3389/fnhum.2014.00095.

Adcock, R.A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., Gabrieli, J.D., 2006. Reward-motivated learning: mesolimbic activation precedes memory formation. Neuron 50 (3), 507–517. https://doi.org/10.1016/j.neuron.2006.03.036.

Arden, R., Chavez, R.S., Grazioplene, R., Jung, R.E., 2010. Neuroimaging creativity: a psychometric view. Behav. Brain Res. 214 (2), 143–156. https://doi.org/10.1016/j.bbr.2010.05.015.

Backus, A.R., Bosch, S.E., Ekman, M., Grabovetsky, A.V., Doeller, C.F., 2016. Mnemonic convergence in the human hippocampus. Nat. Commun. 7, 11991. https://doi.org/10.1038/ncomms11991.

Barron, F., 1955. The disposition toward originality. J. Abnorm. Psychol. 51 (3), 478–485. https://doi.org/10.1037/h0048073.

Beaty, R.E., Benedek, M., Silvia, P.J., Schacter, D.L., 2016a. Creative cognition and brain network dynamics. Trends Cognit. Sci. 20 (2), 87–95. https://doi.org/10.1016/j.tics.2015.10.004.

Beaty, R.E., Benedek, M., Wilkins, R.W., Jauk, E., Fink, A., Silvia, P.J., Hodges, D.A., Koschutnig, K., Neubauer, A.C., 2014. Creativity and the default network: a functional connectivity analysis of the creative brain at rest. Neuropsychologia 64, 92–98. https://doi.org/10.1016/j.neuropsychologia.2014.09.019.

Beaty, R.E., Chen, Q., Christensen, A.P., Qiu, J., Silvia, P.J., Schacter, D.L., 2018. Brain networks of the imaginative mind: dynamic functional connectivity of default and cognitive control networks relates to openness to experience. Hum. Brain Mapp. 39 (2), 811–821. https://doi.org/10.1002/hbm.23884.

Beaty, R.E., Christensen, A.P., Benedek, M., Silvia, P.J., Schacter, D.L., 2017. Creative constraints: brain activity and network dynamics underlying semantic interference during idea production. Neuroimage 148, 189–196. https://doi.org/10.1016/j.neuroimage.2017.01.012.

Beaty, R.E., Kaufman, S.B., Benedek, M., Jung, R.E., Kenett, Y.N., Jauk, E., Neubauer, A.C., Silvia, P.J., 2016b. Personality and complex brain networks: the role of openness to experience in default network efficiency. Hum. Brain Mapp. 37 (2), 773–779. https://doi.org/10.1002/hbm.23065.

Bi, Y., Wang, X., Caramazza, A., 2016. Object domain and modality in the ventral visual pathway. Trends Cognit. Sci. 20 (4), 282–290. https://doi.org/10.1016/j.tics.2016.02.002.

Binkofski, F., Buccino, G., Posse, S., Seitz, R.J., Freund, H.J., 1999. A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. Eur. J. Neurosci. 11 (9), 3276–3286. https://doi.org/10.1046/j.1460-9568.1999.00753.x.

Blackford, J.U., Buckholtz, J.W., Avery, S.N., Zald, D.H., 2010. A unique role for the human amygdala in novelty detection. Neuroimage 50 (3), 1188–1193. https://doi.org/10.1016/j.neuroimage.2009.12.083.

Bonnici, H.M., Chadwick, M.J., Antoine, L., Demis, H., Nikolaus, W., Maguire, E.A., 2012. Detecting representations of recent and remote autobiographical memories in vmPFC and hippocampus. J. Neurosci. 32 (47), 16982–16991. https://doi.org/10.1523/JNEUROSCI.2475-12.2012.

Brambati, S.M., Myers, D., Wilson, A., Rankin, K.P., Allison, S.C., Rosen, H.J., Miller, B.L., Gornotempini, M.L., 2006. The anatomy of category-specific object naming in neurodegenerative diseases. J. Cognit. Neurosci. 18 (10), 1644–1653. https://doi.org/10.1162/jocn.2006.18.10.1644.

Chao, L.L., Haxby, J.V., Martin, A., 1999. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. Nat. Neurosci. 2 (10), 913–919. https://doi.org/10.1038/13217.

Christensen, A.P., Kenett, Y.N., Cotter, K.N., Beaty, R.E., Silvia, P.J., 2018. Remotely close associations: openness to experience and semantic memory structure. Eur. J. Pers. 32 (4), 480–492. https://doi.org/10.1002/per.2157.

Costa, V.D., Lang, P.J., Sabatinelli, D., Versace, F., Bradley, M.M., 2010. Emotional imagery: assessing pleasure and arousal in the brain's reward circuitry. Hum. Brain Mapp. 31 (9), 1446–1457. https://doi.org/10.1002/hbm.20948.

Dagmar, Z., Preston, A.R., 2010. Flexible memories: differential roles for medial temporal lobe and prefrontal cortex in cross-episode binding. J. Neurosci. 30 (44), 14676–14684. https://doi.org/10.1523/JNEUROSCI.3250-10.2010.

Daphna, S., Wagner, A.D., 2008. Integrating memories in the human brain: hippocampal-midbrain encoding of overlapping events. Neuron 60 (2), 378–389. https://doi.org/10.1016/j.neuron.2008.09.023.

Davachi, L., Mitchell, J.P., Wagner, A.D., 2003. Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. Proc. Natl. Acad. Sci. Unit. States Am. 100 (4), 2157–2162. https://doi.org/10.1073/pnas.0337195100.

Davey, J., Thompson, H.E., Hallam, G., Karapanagiotidis, T., Murphy, C., De Caso, I., Krieger-Redwood, K., Bernhardt, B.C., Smallwood, J., Jefferies, E., 2016. Exploring the role of the posterior middle temporal gyrus in semantic cognition: integration of anterior temporal lobe with executive processes. Neuroimage 137, 165–177. https://doi.org/10.1016/j.neuroimage.2016.05.051.

Diedrich, J., Benedek, M., Jauk, E., Neubauer, A.C., 2015. Are creative ideas novel and useful? Psychol. Aesthet. Creativ. Arts 9 (1), 35–40. https://doi.org/10.1037/a0038688.

Dietrich, A., Kanso, R., 2010. A review of EEG, ERP, and neuroimaging studies of creativity and insight. Psychol. Bull. 136 (5), 822–848. https://doi.org/10.1037/a0019749.

Duff, M.C., Kurczek, J., Rubin, R., Cohen, N.J., Tranel, D., 2013. Hippocampal amnesia disrupts creative thinking. Hippocampus 23 (12), 1143–1149. https://doi.org/10.1002/hipo.22208.

Ellamil, M., Dobson, C., Beeman, M., Christoff, K., 2012. Evaluative and generative modes of thought during the creative process. Neuroimage 59 (2), 1783–1794. https://doi.org/10.1016/j.neuroimage.2011.08.008.

Etzel, J.A., Zacks, J.M., Braver, T.S., 2013. Searchlight analysis: promise, pitfalls, and potential. Neuroimage 78, 261–269. https://doi.org/10.1016/j.neuroimage.2013.03.041.

Fastenrath, M., Coynel, D., Spalek, K., Milnik, A., Gschwind, L., Roozendaal, B., Papassotiropoulos, A., de Quervain, D.J., 2014. Dynamic modulation of amygdala-hippocampal connectivity by emotional arousal. J. Neurosci. 34 (42), 13935–13947. https://doi.org/10.1523/JNEUROSCI.0786-14.2014.

Friston, K., Buechel, C., Fink, G., Morris, J., Rolls, E., Dolan, R., 1997. Psychophysiological and modulatory interactions in neuroimaging. Neuroimage 6 (3), 218–229. https://doi.org/10.1006/nimg.1997.0291.

Friston, K.J., Holmes, A.P., Poline, J., Grasby, P., Williams, S., Frackowiak, R.S., Turner, R., 1995. Analysis of fMRI time-series revisited. Neuroimage 2 (1), 45–53. https://doi.org/10.1006/nimg.1995.1023.

Gonen-Yaacovi, G., de Souza, L.C., Levy, R., Urbanski, M., Josse, G., Volle, E., 2013. Rostral and caudal prefrontal contribution to creativity: a meta-analysis of functional imaging data. Front. Hum. Neurosci. 7, 465. https://doi.org/10.3389/fnhum.2013.00465.

Gruber, M.J., Gelman, B.D., Ranganath, C., 2014. States of curiosity modulate hippocampus-dependent learning via the dopaminergic circuit. Neuron 84 (2), 486–496. https://doi.org/10.1016/j.neuron.2014.08.060.

Hassabis, D., Maguire, E.A., 2007. Deconstructing episodic memory with construction. Trends Cognit. Sci. 11 (7), 299–306. https://doi.org/10.1016/j.tics.2007.05.001.

Haxby, J.V., Connolly, A.C., Guntupalli, J.S., 2014. Decoding neural representational spaces using multivariate pattern analysis. Annu. Rev. Neurosci. 37, 435–456. https://doi.org/10.1146/annurev-neuro-062012-170325.

Hennessey, B.A., Amabile, T.M., 2010. Creativity. Annu. Rev. Psychol. 61, 569–598. https://doi.org/10.1146/annurev.psych.093008.100416.

Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., Camerer, C.F., 2005. Neural systems responding to degrees of uncertainty in human decision-making. Science 310 (5754), 1680–1683. https://doi.org/10.1126/science.1115327.

Huang, F., Fan, J., Luo, J., 2015. The neural basis of novelty and appropriateness in processing of creative chunk decomposition. Neuroimage 113, 122–132. https://doi.org/10.1016/j.neuroimage.2015.03.030.

Huang, F., Tang, S., Sun, P., Luo, J., 2018. Neural correlates of novelty and appropriateness processing in externally induced constraint relaxation. Neuroimage 172, 381–389. https://doi.org/10.1016/j.neuroimage.2018.01.070.

Ito, S., Stuphorn, V., Brown, J.W., Schall, J.D., 2003. Performance monitoring by the anterior cingulate cortex during saccade countermanding. Science 302 (5642), 120–122. https://doi.org/10.1126/science.1087847.

Ivancovsky, T., Kleinmintz, O., Lee, J., Kurman, J., Shamay-Tsoory, S.G., 2018. The neural underpinnings of cross-cultural differences in creativity. Hum. Brain Mapp. 39 (11), 4493–4508. https://doi.org/10.1002/hbm.24288.

James, D., Cornelissen, P.L., Thompson, H.E., Saurabh, S., Glyn, H., Jonathan, S., Elizabeth, J., 2015. Automatic and controlled semantic retrieval: TMS reveals distinct contributions of posterior middle temporal gyrus and angular gyrus. J. Neurosci. 35 (46), 15230–15239. https://doi.org/10.1523/JNEUROSCI.4705-14.2015.

Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. Trends Cognit. Sci. 8 (2), 71–78. https://doi.org/10.1016/j.tics.2003.12.002.

Jung-Beeman, M., 2005. Bilateral brain processes for comprehending natural language. Trends Cognit. Sci. 9 (11), 512–518. https://doi.org/10.1016/j.tics.2005.09.009.

Kafkas, A., Montaldi, D., 2014. Two separate, but interacting, neural systems for familiarity and novelty detection: a dual-route mechanism. Hippocampus 24 (5), 516–527. https://doi.org/10.1002/hipo.22241.

Karalyn, P., Nestor, P.J., Rogers, T.T., 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. Nat. Rev. Neurosci. 8 (12), 976–987. https://doi.org/10.1038/nrn2277.

Kersey, A.J., Clark, T.S., Lussier, C.A., Mahon, B.Z., Cantlon, J.F., 2016. Development of tool representations in the dorsal and ventral visual object processing pathways. Cerebr. Cortex 26 (7). https://doi.org/10.1093/cercor/bhv140.

Kiehl, K.A., Stevens, M.C., Laurens, K.R., Pearlson, G., Calhoun, V.D., Liddle, P.F., 2005. An adaptive reflexive processing model of neurocognitive function: supporting evidence from a large scale (n = 100) fMRI study of an auditory oddball task. Neuroimage 25 (3), 899–915. https://doi.org/10.1016/j.neuroimage.2004.12.035.

Kleinmintz, O.M., Abecasis, D., Tauber, A., Geva, A., Chistyakov, A.V., Kreinin, I., Klein, E., Shamay-Tsoory, S.G., 2018. Participation of the left inferior frontal gyrus in human originality. Brain Struct. Funct. 223 (1), 329–341. https://doi.org/10.1007/s00429-017-1500-5.

Kleinmintz, O.M., Ivancovsky, T., Shamay-Tsoory, S.G., 2019. The two-fold model of creativity: the neural underpinnings of the generation and evaluation of creative ideas. Curr. Opin. Behav. Sci. 27, 131–138. https://doi.org/10.1016/j.cobeha.2018.11.004.

Knoblich, G., Ohlsson, S., Haider, H., Rhenius, D., 1999. Constraint relaxation and chunk decomposition in insight problem solving. J. Exp. Psychol. Learn. Mem. Cognit. 25 (6), 1534–1555. https://doi.org/10.1037/0278-7393.25.6.1534.

Knoblich, G., Ohlsson, S., Raney, G.E., 2001. An eye movement study of insight problem solving. Mem. Cognit. 29 (7), 1000–1009. https://doi.org/10.3758/BF03195762.

Komorowski, R.W., Manns, J.R., Eichenbaum, H., 2009. Robust conjunctive item-place coding by hippocampal neurons parallels learning what happens where. J. Neurosci. 29 (31), 9918–9929. https://doi.org/10.1523/JNEUROSCI.1378-09.2009.

Kriegeskorte, N., Goebel, R., Bandettini, P., 2006. Information-based functional brain mapping. Proc. Natl. Acad. Sci. Unit. States Am. 103 (10), 3863–3868. https://doi.org/10.1073/pnas.0600244103.

Kriegeskorte, N., Kievit, R.A., 2013. Representational geometry: integrating cognition, computation, and the brain. Trends Cognit. Sci. 17 (8), 401–412. https://doi.org/10.1016/j.tics.2013.06.007.

Kriegeskorte, N., Mur, M., Bandettini, P., 2008. Representational similarity analysis - connecting the branches of systems neuroscience. Front. Syst. Neurosci. 2, 4. https://doi.org/10.3389/neuro.06.004.2008.

Kroger, S., Rutter, B., Stark, R., Windmann, S., Hermann, C., Abraham, A., 2012. Using a shoe as a plant pot: neural correlates of passive conceptual expansion. Brain Res. 1430, 52–61. https://doi.org/10.1016/j.brainres.2011.10.031.

Kuhl, B.A., Jesse, R., Chun, M.M., Wagner, A.D., 2011. Fidelity of neural reactivation reveals competition between memories. Proc. Natl. Acad. Sci. Unit. States Am. 108 (14), 5903–5908. https://doi.org/10.2307/41125423.

Kumaran, D., Hassabis, D., McClelland, J.L., 2016. What learning systems do intelligent agents need? Complementary learning systems theory updated. Trends Cognit. Sci. 20 (7), 512–534. https://doi.org/10.1016/j.tics.2016.05.004.

Lakens, D., 2013. Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for t-tests and ANOVAs. Front. Psychol. 4 https://doi.org/10.3389/fpsyg.2013.00863.

Lancaster, J.L., Rainey, L.H., Summerlin, J.L., Freitas, C.S., Fox, P.T., Evans, A.C., Toga, A.W., Mazziotta, J.C., 1997. Automated labeling of the human brain: a preliminary report on the development and evaluation of a forward-transform method. Hum. Brain Mapp. 5 (4), 238–242. https://doi.org/10.1002/(SICI)1097-0193(1997)5:4<238::AID-HBM6>3.0.CO;2-4.

Lancaster, J.L., Woldorff, M.G., Parsons, L.M., Liotti, M., Freitas, C.S., Rainey, L., Kochunov, P.V., Nickerson, D., Mikiten, S.A., Fox, P.T., 2000. Automated Talairach atlas labels for functional brain mapping. Hum. Brain Mapp. 10 (3), 120–131. https://doi.org/10.1002/1097-0193(200007)10:3<120::aid-hbm30>3.0.co;2-8.

Liu, Z.X., Grady, C., Moscovitch, M., 2016. Effects of prior-knowledge on brain activation and connectivity during associative memory encoding. Cerebr. Cortex 27 (3), 1991–2009. https://doi.org/10.1093/cercor/bhw047.

Löw, A., Lang, P.J., Smith, J.C., Bradley, M.M., 2008. Both predator and prey: emotional arousal in threat and reward. Psychol. Sci. 19 (9), 865–873. https://doi.org/10.1111/j.1467-9280.2008.02170.x.

Luft, C.D.B., Zioga, I., Thompson, N.M., Banissy, M.J., Bhattacharya, J., 2018. Right temporal alpha oscillations as a neural mechanism for inhibiting obvious associations. Proc. Natl. Acad. Sci. Unit. States Am. 115 (52), E12144–E12152. https://doi.org/10.1073/pnas.1811465115.

Lundstrom, B.N., Petersson, K.M., Andersson, J., Johansson, M., Fransson, P., Ingvar, M., 2003. Isolating the retrieval of imagined pictures during episodic memory: activation of the left precuneus and left prefrontal cortex. Neuroimage 20 (4), 1934–1943. https://doi.org/10.1016/j.neuroimage.2003.07.017.

Luo, J., Knoblich, G., 2007. Studying insight problem solving with neuroscientific methods. Methods 42 (1), 77–86. https://doi.org/10.1016/j.ymeth.2006.12.005.

Luo, J., Niki, K., 2003. Function of hippocampus in "insight" of problem solving. Hippocampus 13 (3), 316–323. https://doi.org/10.1002/hipo.10069.

Luo, J., Niki, K., Knoblich, G., 2006. Perceptual contributions to problem solving: chunk decomposition of Chinese characters. Brain Res. Bull. 70 (4), 430–443. https://doi.org/10.1016/j.brainresbull.2006.07.005.

Mack, M.L., Love, B.C., Preston, A.R., 2016. Dynamic updating of hippocampal object representations reflects new conceptual knowledge. Proc. Natl. Acad. Sci. Unit. States Am. 113 (46), 13203–13208. https://doi.org/10.1073/pnas.1614048113.

Madore, K.P., Thakral, P.P., Beaty, R.E., Addis, D.R., Schacter, D.L., 2019. Neural mechanisms of episodic retrieval support divergent creative thinking. Cerebr. Cortex 29 (1), 150–166. https://doi.org/10.1093/cercor/bhx312.

Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19 (3), 1233–1239. https://doi.org/10.1016/S1053-8119(03)00169-1.

Martin, A., Wiggs, C.L., Ungerleider, L.G., Haxby, J.V., 1996. Neural correlates of category-specific knowledge. Nature 379 (6566), 649–652. https://doi.org/10.1038/379649a0.

Mayseless, N., Aharon-Peretz, J., Shamay-Tsoory, S., 2014. Unleashing creativity: the role of left temporoparietal regions in evaluating and inhibiting the generation of creative ideas. Neuropsychologia 64, 157–168. https://doi.org/10.1016/j.neuropsychologia.2014.09.022.

Mayseless, N., Shamay-Tsoory, S.G., 2015. Enhancing verbal creativity: modulating creativity by altering the balance between right and left inferior frontal gyrus with tDCS. Neuroscience 291, 167–176. https://doi.org/10.1016/j.neuroscience.2015.01.061.

Mcclelland, J.L., Mcnaughton, B.L., Oreilly, R.C., 1995. Why there are complementary learning-systems in the Hippocampus and neocortex - insights from the successes and failures of connectionist models of learning and memory. Psychol. Rev. 102 (3), 419–457. https://doi.org/10.1037/0033-295x.102.3.419.

McGaugh, J.L., 2004. The amygdala modulates the consolidation of memories of emotionally arousing experiences. Annu. Rev. Neurosci. 27, 1–28. https://doi.org/10.1146/annurev.neuro.27.070203.144157.

McLaren, D.G., Ries, M.L., Xu, G., Johnson, S.C., 2012. A generalized form of context-dependent psychophysiological interactions (gPPI): a comparison to standard approaches. Neuroimage 61 (4), 1277–1286. https://doi.org/10.1016/j.neuroimage.2012.03.068.

Mednick, S.A., 1962. The associative basis of the creative process. Psychol. Rev. 69 (3), 220–232. https://doi.org/10.1037/h0048850.

Michelet, T., Bioulac, B., Langbour, N., Goillandeau, M., Guehl, D., Burbaud, P., 2016. Electrophysiological correlates of a versatile executive control system in the monkey anterior cingulate cortex. Cerebr. Cortex 26 (4), 1684–1697. https://doi.org/10.1093/cercor/bhv004.

Milivojevic, B., Vicente-Grabovetsky, A., Doeller, C.F., 2015. Insight reconfigures hippocampal-prefrontal memories. Curr. Biol. 25 (7), 821–830. https://doi.org/10.1016/j.cub.2015.01.033.

Muller, F., Niso, G., Samiee, S., Ptito, M., Baillet, S., Kupers, R., 2019. A thalamocortical pathway for fast rerouting of tactile information to occipital cortex in congenital blindness. Nat. Commun. 10 (1), 5154. https://doi.org/10.1038/s41467-019-13173-7.

Murphy, K., Garavan, H., 2004. An empirical investigation into the number of subjects required for an event-related fMRI study. Neuroimage 22 (2), 879–885. https://doi.org/10.1016/j.neuroimage.2004.02.005.

Nadel, L., Moscovitch, M., 1997. Memory consolidation, retrograde amnesia and the hippocampal complex. Curr. Opin. Neurobiol. 7 (2), 217–227. https://doi.org/10.1016/S0959-4388(97)80010-4.

Narayanan, N.S., Cavanagh, J.F., Frank, M.J., Laubach, M., 2013. Common medial frontal mechanisms of adaptive control in humans and rodents. Nat. Neurosci. 16 (12), 1888–1895. https://doi.org/10.1038/nn.3549.

Neta, M., Nelson, S.M., Petersen, S.E., 2017. Dorsal anterior cingulate, medial superior frontal cortex, and anterior insula show performance reporting-related late task control signals. Cerebr. Cortex 27 (3), 2154–2165. https://doi.org/10.1093/cercor/bhw053.

Oehrn, C.R., Hanslmayr, S., Fell, J., Deuker, L., Kremers, N.A., Do Lam, A.T., Elger, C.E., Axmacher, N., 2014. Neural communication patterns underlying conflict detection, resolution, and adaptation. J. Neurosci. 34 (31), 10438–10452. https://doi.org/10.1523/JNEUROSCI.3099-13.2014.

Phelps, E.A., LeDoux, J.E., 2005. Contributions of the amygdala to emotion processing: from animal models to human behavior. Neuron 48 (2), 175–187. https://doi.org/10.1016/j.neuron.2005.09.025.

Quilodran, R., Rothe, M., Procyk, E., 2008. Behavioral shifts and action valuation in the anterior cingulate cortex. Neuron 57 (2), 314–325. https://doi.org/10.1016/j.neuron.2007.11.031.

Rumiati, R.I., Weiss, P.H., Tessari, A., Assmus, A., Zilles, K., Herzog, H., Fink, G.R., 2005. Common and differential neural mechanisms supporting imitation of meaningful and meaningless actions. J. Cognit. Neurosci. 17 (9), 1420–1431. https://doi.org/10.1162/0898929054985374.

Runco, M.A., 2004. Creativity. Annu. Rev. Psychol. 55 (1), 657–687. https://doi.org/10.1146/annurev.psych.55.090902.141502.

Runco, M.A., Charles, R.E., 1993. Judgments of originality and appropriateness as predictors of creativity. Pers. Indiv. Differ. 15 (5), 537–546. https://doi.org/10.1016/0191-8869(93)90337-3.

Runco, M.A., Jaeger, G.J., 2012. The standard definition of creativity. Creativ. Res. J. 24 (1), 92–96. https://doi.org/10.1080/10400419.2012.650092.

Rutter, B., Kroger, S., Hill, H., Windmann, S., Hermann, C., Abraham, A., 2012a. Can clouds dance? Part 2: an ERP investigation of passive conceptual expansion. Brain Cognit. 80 (3), 301–310. https://doi.org/10.1016/j.bandc.2012.08.003.

Rutter, B., Kroger, S., Stark, R., Schweckendiek, J., Windmann, S., Hermann, C., Abraham, A., 2012b. Can clouds dance? Neural correlates of passive conceptual expansion using a metaphor processing task: implications for creative cognition. Brain Cognit. 78 (2), 114–122. https://doi.org/10.1016/j.bandc.2011.11.002.

Schapiro, A.C., Kustner, L.V., Turk-Browne, N.B., 2012. Shaping of object representations in the human medial temporal lobe based on temporal regularities. Curr. Biol. 22 (17), 1622–1627. https://doi.org/10.1016/j.cub.2012.06.056.

Schlichting, M.L., Preston, A.R., 2014. Memory reactivation during rest supports upcoming learning of related content. Proc. Natl. Acad. Sci. Unit. States Am. 111 (44), 15845–15850. https://doi.org/10.1073/pnas.1404396111.

Schlichting, M.L., Preston, A.R., 2016. Hippocampal-medial prefrontal circuit supports memory updating during learning and post-encoding rest. Neurobiol. Learn. Mem. 134, 91–106. https://doi.org/10.1016/j.nlm.2015.11.005.

Schwartz, C.E., Wright, C.I., Shin, L.M., Kagan, J., Whalen, P.J., Mcmullin, K.G., Rauch, S.L., 2003. Differential amygdalar response to novel versus newly familiar neutral faces: a functional MRI probe developed for studying inhibited temperament. Biol. Psychiatr. 53 (10), 854–862. https://doi.org/10.1016/s0006-3223(02)01906-6.

Shabel, S.J., Janak, P.H., 2009. Substantial similarity in amygdala neuronal activity during conditioned appetitive and aversive emotional arousal. Proc. Natl. Acad. Sci. Unit. States Am. 106 (35), 15031–15036. https://doi.org/10.1073/pnas.0905580106.

Shen, C., Ardid, S., Kaping, D., Westendorff, S., Everling, S., Womelsdorf, T., 2015. Anterior cingulate cortex cells identify process-specific errors of attentional control prior to transient prefrontal-cingulate inhibition. Cerebr. Cortex 25 (8), 2213–2228. https://doi.org/10.1093/cercor/bhu028.

Shen, W., Yuan, Y., Liu, C., Luo, J., Shen, W., Yuan, Y., Liu, C., Luo, J., 2017. The roles of the temporal lobe in creative insight: an integrated review. Think. Reas. 23 (4), 321–375. https://doi.org/10.1080/13546783.2017.1308885.

Shenhav, A., Cohen, J.D., Botvinick, M.M., 2016. Dorsal anterior cingulate cortex and the value of control. Nat. Neurosci. 19 (10), 1286–1291. https://doi.org/10.1038/Nn.4384.

Sheth, S.A., Mian, M.K., Patel, S.R., Asaad, W.F., Williams, Z.M., Dougherty, D.D., Bush, G., Eskandar, E.N., 2012. Human dorsal anterior cingulate cortex neurons mediate ongoing behavioural adaptation. Nature 488 (7410), 218–221. https://doi.org/10.1038/nature11239.

Squire, L.R., Alvarez, P., 1995. Retrograde-Amnesia and memory consolidation - a neurobiological perspective. Curr. Opin. Neurobiol. 5 (2), 169–177. https://doi.org/10.1016/0959-4388(95)80023-9.

Squire, L.R., Stark, C.E., Clark, R.E., 2004. The medial temporal lobe. Annu. Rev. Neurosci. 27, 279–306. https://doi.org/10.1146/annurev.neuro.27.070203.144130.

Sternberg, R.J., Lubart, T.I., 1996. Investing in creativity. Am. Psychol. 51 (7), 677–688. https://doi.org/10.1037/0003-066x.51.7.677.

Storme, M., Lubart, T., 2012. Conceptions of creativity and relations with judges' intelligence and personality. J. Creativ. Behav. 46 (2), 138–149. https://doi.org/10.1002/jocb.10.

Sullivan, D.M., Ford, C.M., 2005. The relationship between novelty and value in the assessment of organizational creativity. Korean J. Think. Probl. Solving 15 (2), 117–131.

Takashima, A., Nieuwenhuis, I.L., Jensen, O., Talamini, L.M., Rijpkema, M., Fernández, G., 2009. Shift from hippocampal to neocortical centered retrieval network with consolidation. J. Neurosci. 29 (32), 10087–10093. https://doi.org/10.1523/JNEUROSCI.0799-09.2009.

Takashima, A., Petersson, K.M., Rutters, F., Tendolkar, I., Jensen, O., Zwarts, M.J., McNaughton, B.L., Fernández, G., 2006. Declarative memory consolidation in humans: a prospective functional magnetic resonance imaging study. Proc. Natl. Acad. Sci. Unit. States Am. 103 (3), 756–761. https://doi.org/10.1073/pnas.0507774103.

Takeuchi, H., Kawashima, R., 2019. Implications of large-sample neuroimaging studies of creativity measured by divergent thinking. Curr. Opin. Behav. Sci. 27, 139–145. https://doi.org/10.1016/j.cobeha.2018.12.009.

Takeuchi, H., Taki, Y., Hashizume, H., Sassa, Y., Nagase, T., Nouchi, R., Kawashima, R., 2012. The association between resting functional connectivity and creativity. Cerebr. Cortex 22 (12), 2921–2929. https://doi.org/10.1093/cercor/bhr371.

Tang, H.L., Yu, H.Y., Chou, C.C., Crone, N.E., Madsen, J.R., Anderson, W.S., Kreiman, G., 2016. Cascade of neural processing orchestrates cognitive control in human frontal cortex. eLife 5. https://doi.org/10.7554/eLife.12352.

Tompary, A., Davachi, L., 2017. Consolidation promotes the emergence of representational overlap in the Hippocampus and medial prefrontal cortex. Neuron 96 (1), 228–241. https://doi.org/10.1016/j.neuron.2017.09.005 e225.

Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H., Damasio, A.R., 2003. Neural correlates of conceptual knowledge for actions. Cogn. Neuropsychol. 20 (3), 409–432. https://doi.org/10.1080/02643290244000248.

Wei, T., Liang, X., He, Y., Zang, Y.F., Han, Z.Z., Caramazza, A., Bi, Y.C., 2012. Predicting conceptual processing capacity from spontaneous neuronal activity of the left middle temporal gyrus. J. Neurosci. 32 (2), 481–489. https://doi.org/10.1523/Jneurosci.1953-11.2012.

Weiner, K.S., Natu, V.S., Grill-Spector, K., 2018. On object selectivity and the anatomy of the human fusiform gyrus. Neuroimage 173, 604–609. https://doi.org/10.1016/j.neuroimage.2018.02.040.

Whalen, P.J., 1998. Fear, vigilance, and ambiguity: initial neuroimaging studies of the human amygdala. Curr. Dir. Psychol. Sci. 7 (6), 177–188. https://doi.org/10.1111/1467-8721.ep10836912.

Whalen, P.J., Rauch, S.L., Etcoff, N.L., Mcinerney, S.C., Lee, M.B., Jenike, M.A., 2005. Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. J. Neurosci. 18 (1), 411–418. https://doi.org/10.1523/JNEUROSCI.18-01-00411.1998.

White, A., Shen, F., Smith, B.L., 2002. Judging advertising creativity using the creative product semantic scale. J. Creativ. Behav. 36 (4), 241–253. https://doi.org/10.1002/j.2162-6057.2002.tb01067.x.

Whitney, C., Jefferies, E., Kircher, T., 2011a. Heterogeneity of the left temporal lobe in semantic representation and control: priming multiple versus single meanings of ambiguous words. Cerebr. Cortex 21 (4), 831–844. https://doi.org/10.1093/cercor/bhq148.

Whitney, C., Kirk, M., O'Sullivan, J., Ralph, M.A.L., Jefferies, E., 2011b. The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. Cerebr. Cortex 21 (5), 1066–1075. https://doi.org/10.1093/cercor/bhq180.

Wolosin, S.M., Zeithamova, D., Preston, A.R., 2012. Reward modulation of hippocampal subfield activation during successful associative encoding and retrieval. J. Cognit. Neurosci. 24 (7), 1532–1547. https://doi.org/10.1162/jocn_a_00237.

Wright, C.I., Martis, B., Schwartz, C.E., Shin, L.M., Fischer, H.Å., Mcmullin, K., Rauch, S.L., 2003. Novelty responses and differential effects of order in the amygdala, substantia innominata, and inferior temporal cortex. Neuroimage 18 (3), 660–669. https://doi.org/10.1016/s1053-8119(02)00037-x.

Zeithamova, D., Dominick, A., Preston, A., 2012. Hippocampal and ventral medial prefrontal activation during retrieval-mediated learning supports novel inference. Neuron 75 (1), 168–179. https://doi.org/10.1016/j.neuron.2012.05.010.