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Review

Tracking the neurodynamics of insight: A meta-analysis of neuroimaging studies

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ABSTRACT

The nature of insight has been the interdisciplinary focus of scientific inquiry for over 100 years. Behavioral studies and biographical data suggest that insight, as a form of creative cognition, consists of at least four separate but intercorrelated stages as described by Wallas (1926). Yet no quantitative evidence was available for insight- or insight-stage-specific brain mechanisms that generalize across various insight tasks. The present work attempted, for one, to present an integrated and comprehensive description of the neural networks underlying insight and, for another, to identify dynamic brain mechanisms related to the four hypothetical stages of insight. To this end, we performed two quantitative meta-analyses: one for all available studies that used neuroimaging techniques to investigate insight, and the other for the phasic brain activation of insight drawn from task characteristics, using the activation likelihood estimation (ALE) approach. One key finding was evidence of an integrated network of insight-activated regions, including the right medial frontal gyrus, the left inferior frontal gyrus, the left amygdala and the right hippocampus. Importantly, various brain areas were variably recruited during the four stages. Based on the ALE results, the general and stage-specific neural correlates of insight were determined and potential implications are discussed.

1. Introduction

As one key aspect of human wisdom, creative insight is a phenomenon that is generally considered sporadic, unpredictable and transient (Luo & Knoblich, 2007). Different from the *illumination* of Wallas' four-stage model, *insight* is often conceptualized as a process by which a problem solver suddenly and abruptly moves from a state of not knowing how to solve a problem to a state of knowing how to solve it (Schooler, Fallshore, & Fiore, 1995; Sheth, Sandkühler, & Bhattacharya, 2009). Although it has been traditionally regarded to be an unconscious process (Siegler, 2000), an increasing number of studies (e.g., Sandkühler & Bhattacharya, 2008; Weisberg, 2013; Shen, Luo, Liu, & Yuan, 2013) have shown that insight is actually a multi-stage process involving both conscious and unconscious aspects, components, or stages.

Despite considerable progress in uncovering the essence of insight, the available evidence remains inconclusive. Accompanying the rapid development of neuroimaging techniques such as functional magnetic resonance imaging (fMRI), a growing number of neuroimaging studies have attempted to reveal brain mechanisms underlying insight. Previous efforts to seek a consistent pattern integrating neuroscientific findings across studies on insight have been limited to narrative (e.g., Kounios & Beeman, 2014) and/or table-based literature reviews (e.g., Dietrich & Kanso, 2010). Those avenues are qualitative rather than quantitative in nature and must be interpreted with caution due to their high dependence on self-supplied anatomical labels that might be unduly broad or, under some circumstances, inaccurate. Additionally, comparison of reported focus coordinates across studies has proven challenging in that localization of a given set of coordinates to a

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particular neuroanatomical location is over-reliant on the target brain atlas and corresponding stereotaxic space in which the data set was registered (Christ, Van Essen, Watson, Brubaker, & McDermott, 2009; Laird et al., 2005). That is, an integrated understanding (e.g., Martinsen, Furnham, & Hærem, 2016) of the neurocognitive substrates of insight is difficult to achieve for the various stages of insight focused in existing studies, though three influential reviews (Dietrich & Kanso, 2010; Kounios & Beeman, 2014; Shen et al., 2013) have summarized brain patterns correlated with insight.

In contrast to the above-mentioned methods, the foci-based activation likelihood estimate (ALE) method is a quantitative voxel-wise meta-analysis technique that can precisely integrate findings from multiple studies by aligning the activation results of neuroimaging studies using reported coordinates in a standardized 3D atlas space (van der Laan, De Ridder, Viergever, & Smeets, 2011). This meta-analytical method has been fully validated (see Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012) and widely used in the meta-analysis of neuroimaging studies across a broad range of psychological processes, such as working memory in non-creative domains (e.g., Nee et al., 2013) and divergent thinking in creative domains (e.g., Wu et al., 2015), due to its apparent superiority in quantification. As discussed by Laird et al. (2005), the ALE, which was originally developed by Turkeltaub, Eden, Jones, and Zeffiro, (2002), is a novel, effective, and quantitative method of function-location meta-analysis that does not rely on the traditional tabular technique of establishing agreement across studies.

In the present study, the ALE meta-analytical method was utilized to identify possible insight-related brain networks across independent studies and, in particular, brain regions consistently exhibiting insight-related activity across various studies. More specifically, the objectives of the present study were twofold. The first objective was to identify potential brain activation patterns of key regions commonly engaged in insight irrespective of the specific experimental tasks. Considering that insight processes are unlikely to appear without any involvement of memory subsystems, isolating insight processes would involve dissociating different memory sub-processes such as memory retrieval, memory search and long-term memory activation. However, the isolated insights (insight process that is purely endogenous) obtained by using the cognitive subtraction design (Shen, Yuan, Liu & Zhang et al., 2016; Weisberg, 2013) do not necessarily involve kinds of memory sub-processes, which is because brain activation of memory sub-processes engaged in the cognitive tasks of triggering creative insight (not insight process only) has been masked by those activations elicited by the corresponding (at least theoretically) well-matched baseline tasks. On the basis of previous studies, we hypothesized that brain networks of insight might encompass widespread regions within the prefrontal cortex, such as inferior frontal gyrus (IFG; Anderson, Anderson, Ferris, Fincham, & Jung, 2009; Aziz-Zadeh, Kaplan, & Iacoboni, 2009) and middle frontal gyrus (MFG; e.g., Huang, Fan, & Luo, 2015), and other regions including anterior cingulate cortex (ACC; Luo & Niki, 2003; Luo, Niki, & Phillips, 2004), hippocampal gyri (Jung-Beeman et al., 2004; Luo & Niki, 2003), superior temporal gyri (STG; Jung-Beeman et al., 2004), and occipital regions (Luo, Niki, & Knoblich, 2006; Wu, Knoblich, & Luo, 2013).

The second goal was to identify possible stage-specific neural networks involved in insight. As a heuristic working model, we adopted the four-stage approach of Wallas (1926), which was also used by the EEG-based stage analysis of Martindale and Hasenfus (1978), and which is still considered to provide a useful categorization of insight-related processing stages (Sadler-Smith, 2015; for a review, see Runco et al., 1994). According to Wallas' four-stage account, derived from Helmholtz's ideas on thought process for insightful ideas (Rhodes, 1961; Sadler-Smith, 2015), the creative process can be divided into the stages of preparation, incubation, illumination, and verification. This framework has recently been used to describe the insightful process as a four-phase sequence consisting of mental preparation, set-triggered/impasse-related restructuring, forming novel associations, and solution verification (cf., Sandkühler & Bhattacharya, 2008; Luo & Niki, 2003; Jung-Beeman et al., 2004; Weisberg, 2013). The appropriateness of Wallas' approach in insight problem solving is due to the close similarity between creativity and insight in conceptualization, measures and processes. One typical support is that most insight tasks (e.g., the remote associate problems) are also used to study creativity (for details, see Shen, Yuan, Liu, & Luo, 2017). From the four-stage perspective, the stage of mental preparation of insight is similar to Wallas' preparation process, although the authors conceptualized mental preparation as not fully identical to the preparation referred in Wallas' model. During Wallas' (1926) stage of preparation, the solver often confronts an important problematic situation, conceptualizes the problem's core aspects, and makes exerted tentative unsuccessful attempts (Terai, Miwa, & Asami, 2014). However, the stage of mental preparation during insight or insight problem solving, mainly refers to, in laboratory settings, the time interval between the starting of a problem-solving trial (mostly manifesting as the presentation of a cross-fixation) and the presentation of the given problem or the timespan prior to the presentation of the given problem during which participants can prepare for the next problem-solving trial. In this regard, it seems impossible for the solver to initiate any preparation in information processing like collecting information related to the given problem or retrieval previous experience that may be conducive to the successful solution. They can engage only in some general preparation beyond specific cognitive tasks, especially general control mechanism and enhanced readiness for monitoring completing responses, such as directing attention inwards, keeping in a calm state, and actively suppressing irrelevant thoughts.

The stage of the set-triggered/impasse-related restructuring, as an incubation-like process of insight, is roughly comparable to the incubation stage of the Wallas' model. The incubation stage of insight sequence refers to the period related to restructuring (Sandkühler & Bhattacharya, 2008; Weisberg, 2013), in which participants make attempts to solve the given problem and encounter one or more mental impasses elicited by inappropriate knowledge base (Wiley, 1998) or incomplete heuristics (Knoblich, Ohlsson, Haider, & Rhenius, 1999; Knoblich, Ohlsson, & Raney, 2001). During this stage, to shift the autonomically activated set or break the unwarranted impasse, solvers have to decompose the initial or misleading representations, selectively encode and retrieve relevant but previously unattended information, recombine or regroup elements of newly accessed information, re-organize and restructure the problem in a new way (Luo & Knoblich, 2007; Ohlsson, 2011; Weisberg, 2015) by consciously suppressing or inhibiting dominant but spontaneously activated knowledge nodes from memory which would further start the process of forming remote associations and eventually lead to a subjective "Aha" accompanying sudden solutions. In other words, the insight-related incubation is actually a failure-driven breaking of mental set/impasse process in which solvers experience an initially bias representation, repeated solution attempts, and restructuring (e.g., chunk decomposition, constraint relaxation; Ohlsson, 2011; 1984; Zhao et al., 2013).

The stage of forming novel associations is analogous to Wallas' illumination stage and often considered to represent sudden insight. Previous studies on neurocognitive mechanism underlying insight, particularly those used event-related potentials, showed two dissociated cognitive processes, namely breaking impasse-related sets and forming novel associations (Luo & Niki, 2003; Luo et al., 2011; Zhao et al., 2013), corresponding to temporally separable stages of insight sequence and the process of accessing novel associations preceding an immediate solution. In contrast to the breaking of warrant impasses in the incubation-like stage, the often-reported process of accessing and forming non-obvious association is thus more appropriate to take place in the illumination-like stage of insight. Once the solver had established the novel and useful associations, the sudden solution to insight problems would immediately and spontaneously come forth, without any conscious inference. Perhaps for this reason, the illumination-like stage of insight is figuratively termed the flash of insight. Further, the positive affect accompanying sudden solution, termed aha experience, often occurs in the illumination-like stage of insight.

The stage of insight solution verification or appreciation is equivalent to Wallas' verification stage (Weisberg, 2013). Traditionally, the stage of verification is primarily associated with the process of elaboration and evaluation of the solution that has been suddenly achieved in the illumination-like stage of insight sequence. For insight sequence, the fourth stage is dominantly determined by providing the correct solutions to the participants (Ludmer, Dudai, & Rubin, 2011; Luo & Niki, 2003), in which solvers could make them compare the solutions they drew with the displayed ones, validate and further refine their solutions, and even experience the feeling of verification to some degree. In this regard, the stage of post-solution verification of insight likely involves the elaboration (refinement) and validation of the suddenly achieved or the illuminated solution.

Based on the above analogies, the present study attempted to dissociate the dynamical neural correlates of the four stages of insight. Based on existing findings, we derived the following hypotheses: (i) the stage of mental preparation of successful insight can elicit greater activation in the left ACC that is considered to be responsible for cognitive control (Kounios et al., 2006; Subramaniam, Kounios, Parrish, & Jung-Beeman, 2009); (ii) the stage of impasse-related insightful incubation might induce stronger activation in widespread prefrontal regions whose lesions can improve insight (e.g., Reverberi, Toraldo, D'Agostini, & Skrap, 2005; Cerruti & Schlaug, 2009); (iii) the stage of spontaneous insightful solution may exhibit greater activation in distributed brain regions including the (para) hippocampal regions (e.g., Jung-Beeman et al., 2004; Zhao et al., 2013), the anterior STG (e.g., Jung-Beeman et al., 2004), and the amygdala (e.g., Ludmer et al., 2011; Zhao et al., 2013) since these regions have been widely found to process weak or novel associations; (ix) the stage of post-solution verification of insight may activate some prefrontal regions (e.g., Rodriguez-Moreno & Hirsch, 2009; Luo & Niki, 2003; Fangmeier, Knauff, Ruff, & Sloutsky, 2006). Additionally, we hypothesized that more complex brain networks encompassing interhemispheric interaction reflected as brain activations distributed across both hemispheres would be involved in the incubation-like and illumination-like stages of the insight process, and few interhemispheric brain activations would be observed in the preparation-like and verification-like stages of insight.

2. Methods

2.1. Study search and selection

To access appropriate articles for the meta-analysis of insight, the online electronic databases of PNAS, Oxford, SAGE, PsycINFO, Wiley-Blackwell, Elsevier Science, Springer, Web of Science, and PubMed were searched using the term combination of "topic" + "technique" like "insight fMRI". The "topic" terms include "insight", "heuristic", "illumination", "remote associates", "aha", "convergent thinking" and "anagram", whereas technique terms consist of "MRI", "fMRI", "neural", "neuroimaging", "brain", "PET", "neurophysiological" and "neuroanatomical". To obtain as much insight neuroimaging literature that is complete as possible, we explored several other sources (e.g., google scholar), including the bibliography and citation indices of the pre-selected papers and direct searches on the names of frequently appearing authors in this filed. A total of 36 neuroimaging studies on the neural correlates of insight were selected building on the following inclusion/exclusion criteria: (1) all studies were published in English[1], and the participants were healthy, (2) the target process of insight is about creative insight or insight in problem solving rather than clinical insight (e.g., self-awareness) or the process of insight in psychosis, (3) the neuroimaging method used in the study was fMRI or PET, (4) the coordinates in each of the studies were from the standard Montreal Neurological Institute or Talairach space, and (5) a clear contrast representing brain activation existed for the insight condition compared with the non-insight condition or other baselines. In addition, studies only reported the results on the region of interest (ROI) rather than the whole brain results or only examined the neural connectivity of insight through structural MRI or resting-state fMRI were eliminated. In each study, only insight-related experiments or independent contrasts were included. If several contrasts in the same study were dependent, only results from the well-matched contrast were included. Forty-three contrasts or experiments (Table 1) from these thirty-six studies met these criteria and were included in the current meta-analysis. All MNI coordinates were converted to Talairach space (Brett, Leff, Rorden, & Ashburner, 2001) before the formal analysis. A total of 464 activation foci (for the comparison of insight vs. non-insight in Table 1) representing brain regions with markedly greater activation for insight as opposed to that for non-insight controls were extracted from these articles. Only eleven contrasts from ten studies reported stronger activations in some brain regions (in a total of 90 activation foci, and, of them, 59 foci from 6 contrasts appeared in the 2nd stage) for non-insight conditions compared with insight conditions.

To reveal the neurodynamics of the four stages of insight, we sorted studies into four categories (see Table 1), depending on the timing used and the nature of the insight tasks. Categorization was based on either the explicit aims of the original authors—i.e., on the stage that the authors aimed to analyze (e.g., brain activation of mental preparation, see Kounios et al., 2006) or, if no stage was explicitly mentioned in the original study, on other studies relating the original finding to a particular processing stage (Sandkühler & Bhattacharya, 2008). If none of these sources of information was available, we used multiple (but mostly temporal) criteria to determine the possible stage, e.g., by considering whether the activation accompanies an insight solution; the timing of isolating insight-related brain activation (pre-insight or post-insight); and cognitive analysis on the characteristics of the task triggering insight (e.g., the NRT; see Haider & Rose, 2007). Four other ALE analyses were also applied based on the sub-lists that categorize different contrasts or experiments into the four stages of insight sequence. The numbers of foci included in the meta-analyses for the stages of mental preparation, impasse-related insightful incubation, spontaneous insight solution, and insight solution verification were 28 foci (4 experiments), 178 foci (16), 149 foci (17), and 109 foci (6), respectively. We applied the same analysis and threshold approaches as we did for the meta-analysis[2] determining the general pattern of insight-related brain activity as mentioned above.

2.2. Meta-analysis methods

In this study, the ALE method that has been proven to be a common method integrating neuroimaging results across studies (Laird et al., 2005; Mincic, 2015; Turkeltaub et al., 2002) was applied to identify brain areas where the reported foci of activation converge across different experiments. Previous evidence showed that the markedly activated foci, the coordinates reported, were treated not as a single point but the peaks of the 3D Gaussian probability distribution. This

[1] Includes a Chinese study, namely the first author's doctoral dissertation.

[2] The ALE meta-analyses were conducted for both the general pattern, in which all sample studies were included, and the stage-specific dynamics of insight sequence, which is mainly because the integrated perspective of insight process has been examined in recent studies (e.g., Martinsen et al., 2016; Weisberg, 2013, 2015) and could help illustrate task-general processes of insight. Importantly, the results on the general pattern of insight are helpful to determine the precise role of brain regions that are co-activated in the two meta-analyses, which also provides a general reference framework for future study to explain or compare their insight-related brain activations. However, the primary focus of this study is to identify the stage-specific neural underpinnings of insight.

Table 1
Details of studies included in the quantitative meta-analysis.

study	N	stage	design	materials	contrast
Rose et al. (2002)	10	4th	within-subject	number sequences	post-insight vs. pre-insight
Luo & Niki (2003)	7	4th	within-subject	Japanese brain teasers	insight solution vs. fixation
Luo, Niki, & Phillips (2004a)	13	4th	within-subject	Chinese logographs	aha trials vs. no-aha trials
Luo, Niki, & Phillips (2004b)	11	2nd	within-subject	Japanese brain teasers	riddles with set-shifts (varied) vs. those without set-shifts (fixed)
Jung-Beeman et al. (2004)	13	3rd	within-subject	CRA	insight solutions vs. non-insight solutions
Rose, Haider, Weiller, & Buchel (2004)	18	3rd	between-subject	number sequence	insightful sequence vs. non-insightful sequence
Goel & Vartenian (2005)	13	3rd	within-subject	Matchstick problem	successful solution vs. unsuccessful solution
	13	2nd	within-subject	Matchstick problems	the Match Problem solving vs. baseline task
Luo, Niki, & Knoblich (2006)	13	2nd	within-subject	Chinese characters	tight chunk vs. loose chunk
Kounios et al. (2006), Exp. 2	20	1st	within-subject	CRA	insight preparation vs. non-insight preparation
Subramaniam et al. (2009)	27	3rd	within-subject	CRA	insight solutions vs. non-insight solutions
	27	1st	within-subject	CRA	insight preparation vs. non-insight preparation
Anderson et al. (2009), Exp.1	20	3rd	within-subject	CRA	insight solutions vs. non-insight solutions
Aziz-Zadeh et al. (2009)	18	3rd	within-subject	English anagrams	insight solutions vs. search solutions
Pang, Tang, Niki, and Luo, (2009)	13	2nd	within-subject	Chinese characters	tight chunk vs. loose chunk
Qiu et al. (2010)	16	3rd	within-subject	Chinese logographs	aha trials vs. no-aha trials
Darsaud et al. (2011)	18	4th	within-subject	number sequences	post-insight vs. pre-insight
Ludmer et al. (2011).	14	4th	within-subject	degraded pictures	post-insight vs. pre-insight
Tian et al. (2011)	16	1st	within-subject	Chinese logographs	insight preparation vs. non-insight preparation
Amir, Biederman, Wang, & Xu, (2015)	15	3rd	within-subject	pictures and words	trials with aha understanding vs. those without aha understanding
Hao et al. (2013)	17	2nd	within-subject	scientific inventive problems	heuristics involving set-shifts vs. those not set-shifts
Luo et al. (2013), Exp. 1	19	2nd	within-subject	scientific inventive problems	novel heuristics vs. old heuristics
Exp. 2	17	2nd	within-subject	scientific inventive problems	novel heuristics vs. old heuristics
Kleibeuker et al. (2013)	36	2nd	mixed design	Matchstick problem	successful insight task vs. successful routine task
Tong et al. (2013)	16	2nd	within-subject	scientific inventive problems	the solved vs. the unsolved
Wu, Knoblich, & Luo (2013)	14	2nd	within-subject	Chinese characters	familiar-tight vs. familiar-loose
	14	2nd	within-subject	Chinese characters	unfamiliar-tight vs. unfamiliar-loose
Zhao et al. (2013)	17	1st	within-subject	Chinese Chengyu riddles	insight preparation vs. non-insight preparation
	17	3rd	with-subject	Chinese Chengyu riddles	insight solutions vs. non-insight solutions
Shen (2014)	13	3rd	with-subject	Chinese CRA	insight solutions vs. non-insight solutions
Terai et al. (2014)	18	2nd	within-subject	Japanese characters	insight problems vs. routine problems
	18	2nd	with-subject	Japanese characters	successful restructuring vs. successful non-restructuring
Zhang, Liu, and Zhang, (2014)	18	2nd	within-subject	Functional features words	novel function heuristics vs. routine function heuristics
Zhao, Zhou, Xu, Fan, and Han, (2014)	17	3rd	within-subject	Chinese Chengyu riddles	insight solution vs. non-insight solution
Zhou, Xu, Zhao, Zhao, and Liao, (2014)	10	3rd	within-subject	two-part allegorical sayings	novel associations vs. routine associations
	10	3rd	within-subject	two-part allegorical sayings	sayings with new meanings vs. those with routine meanings
Huang, Fan, & Luo (2015)	15	3rd	within-subject	Chinese characters	novel-appropriate solution vs. familiar-inappropriate solution
Milivojevic et al. (2015)	19	3rd	with-subject	pictorial narratives	before vs. after representation/strategy change
Tang et al. (2015)	22	2nd	parametric	Chinese characters	tight chunk vs. loose chunk vs. baseline
Tong et al. (2015)	16 (32)	2nd	between-subject	scientific inventive problems	insightful illustrations vs. non-insight illustrations
Kizilirmak, Thuerich, Folta-Schoofs, Schott, and Richardson-Klavehn, (2016)	26	4th	with-subject	German CRA (encoding stage)	insight CRA vs. no-insight (unsolvable) controls
Huang, Tang, Sun, & Luo, (2018)	20	3rd	with-subject	Chinese riddles	novel-appropriate solution vs. familiar-inappropriate solution
Tik et al., (in press)	29	3rd	with-subject	German CRA	stronger aha solutions vs. weaker aha solutions

Notes: those problems solved through the breaking of tight chunk involves creative insight process as opposed to problems solved through the breaking of loose chunk as demonstrated in the representation change theory (RCT); the generation of novel appropriate solutions as compared to that of familiar-inappropriate solutions can better reflect the forming of novel association necessary for creative insight and trends to treat the former processes as insight processes.

algorithm could clearly reveal the spatial uncertainty of the significantly reported activation foci from various neuroimaging results, enabling the 3D Gaussian distributions to be summed to create a voxel-wise statistical map (exhibiting the activation likelihood of each voxel from the selected studies) with better goodness-of-fit and validity (Laird et al., 2005). For statistical inference, the ALE results were assessed against a null-distribution of random spatial associations of foci across contrasts ((Eickhoff et al., 2009).

The ALE-based meta-analysis described here was executed using GingerALE 2.3.6 software (Eickhoff et al., 2009; Laird et al., 2005; available at http://brainmap.org/) with the embedded revised ALE algorithm (Turkeltaub et al., 2012). A random-effects analysis was firstly conducted to determine statistical significance through a permutation test of randomly generated foci with 1000 permutations (full-width at half-maximum of 9 cm) (Eickhoff et al., 2009). To optimize brain patterns of insight or brain activation during the four stages of the insight process, we adopted a more conservative method (GingerALE User Manual, p. 6), namely the Voxel-level Family-Wise Error (FWE) *p*-threshold corrected for multiple comparisons following the recommended P level of 0.05 ($P < 0.05$) with a minimum volume of 250 mm^3 (31 voxels). In addition, the ALE meta-analytical result images were visualized using Mango software (http://ric.uthscsa.edu/mango/) and overlaid onto a standardized anatomical template (colin_tlrc_1 × 1x1.nii; http://www.brainmap.org/ale/) incorporating the Talairach coordinates.

3. Results

Thirty-six fMRI publications concerning insight were included in the present ALE-based meta-analysis. As exhibited in Table 2, the meta-analysis of the studies demonstrated insight events, as opposed to non-insight events, significantly activated broad regions distributed across hemispheres (see Fig. 1), including the left inferior frontal gyrus (IFG; BA 6), the right medial frontal gyrus (MdFG; BA 8), the right hippocampal gyrus, and left amygdala (Amy). In contrast, the left cuneus (BA 18), the right precentral/postcentral gyri (Pre/Post, BA6/43) and the left superior temporal gyrus (STG, BA22) exhibited greater activations for non-insight controls compared with insight.

Table 2
List of brain structures activated in the ALE meta-analysis for integrated pattern of insight.

Brain regions	BA	Talairach coordinates			ALE (×10-3)	volume (mm3)
		x	y	z		
insight > non-insight						
Left inferior frontal gyrus	BA 6	−48	10	30	13.13	8368
Right medial frontal gyrus	BA 8	2	16	44	9.72	2632
Right hippocampal gyrus	/	28	−8	−12	8.68	1024
Left amygdala	/	−24	−8	−12	9.09	952
non-insight > insight						
Left cuneus	BA 18	0	−76	16	4.61	2256
Right precentral gyrus	BA 6	52	−8	8	3.85	1048
Right postcentral gyrus	BA 43	48	−14	18	3.82	/
Left superior temporal gyrus	BA 22	−54	−8	6	4.08	632

Given that growing evidence has shown that the insight process is a dynamic sequence rather than a transient moment, this study attempted to further dissociate potential functional brain regions engaged during the different stages of insight. As Table 3 shows, we categorized the fMRI studies of insight included in the present meta-analysis into four classes that correspond to the four stages of creative process in Wallas' approach. As expected, insight exhibited greater activation in the left anterior cingulate cortex (ACC, BA 32) for insight events in the mental preparation stage (Fig. 2). Greater activation in broad regions across both hemispheres was found for insight in the incubation-like stage. As Table 3 shows, these regions included the bilateral IFG (BA 44 and BA 47), the right MdFG (BA 8), the middle frontal gyrus (MFG; BA 6), and the middle occipital gyrus (MOG; BA 19). The above result indicates that the incubation-like process within dynamic insight is relatively complex and involves many areas widely distributed across hemispheres (Fig. 3). The illumination -like process of insight is primarily characterized by the right hippocampal gyrus and the left amygdala. The last stage, the verification-like stage of insight sequence, was dominantly associated with brain activations in the right IFG. No marked activation clusters were found in the opposite contrasts across the four stages, except activations in the right STG (x, y, z = 56, −6, 8; BA 22, ALE value = 3.09×10^{-3}, volume = 64 mm^3) at the second stage.

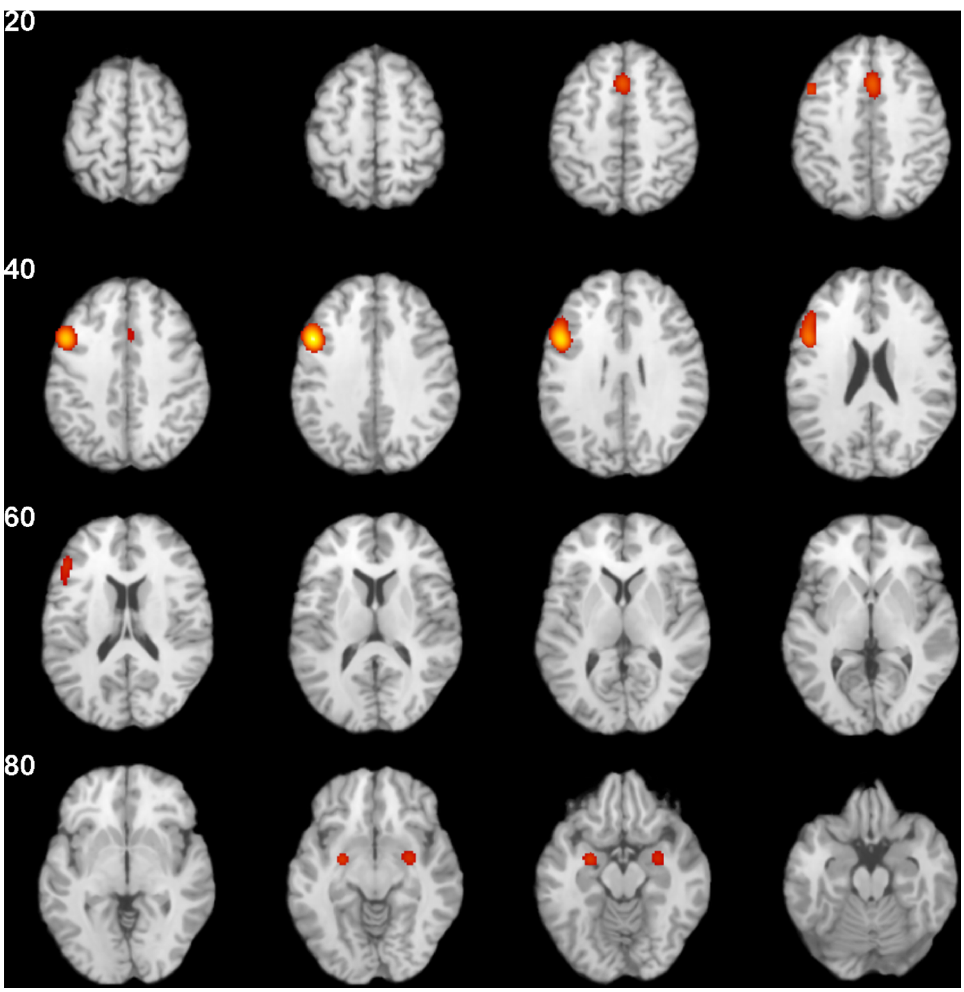

Fig. 1. The whole pattern of ALE-based brain activations triggered by various insight tasks, which manifests the insight-specific brain mechanisms that generalize across various insight tasks.

Table 3
List of brain structures activated in the ALE meta-analysis for staged insight process.

Stage	Brain regions	BA	Talairach coordinates			ALE ($\times 10^{-3}$)	volume (mm^3)
			x	y	z		
1st							
	Left anterior cingulated cortex	BA 32	−6	42	6	2.97	552
2nd							
	Left inferior frontal gyrus	BA 44	−48	12	28	7.55	7472
	Right medial frontal gyrus	BA 8	2	20	44	6.75	4736
	Right inferior frontal gyrus	BA 47	34	26	−12	6.53	2104
	Left middle frontal gyrus	BA 6	−24	2	48	5.14	384
	Left middle occipital gyrus	BA 19	−28	−82	18	5.01	272
3rd							
	Right hippocampus	/	28	−8	−12	6.29	2552
	Left amygdala	/	−26	−6	−14	5.49	1176
4th							
	Right inferior frontal gyrus*	BA 47	50	38	0	3.80	56

Notes: * denotes this result was drawn from a less conservative volume (> 1). All the nearest brain regions were extracted based on the reported anatomical coordinates and Yale brain atlas.

4. Discussion

Insight is a dynamic processing sequence often characterized, (1) by breaking away from the mental impasse resulting from initially activated but misleading representations, (2) by mental restructuring and the establishment of novel, task-related associations leading to a sudden solution, and (3) by positive affect accompanying the emerging solution – termed the aha moment. In this study, an ALE-based meta-analysis was utilized to identify the brain patterns that accompany insight and related dynamic brain activations to different stages of the insight process. Our results provided evidence for an insight-related brain network consisting of the left IFG, the right MdFG, the right hippocampal gyrus, along with marked activations in the left amygdala. Additionally, significant differences in activation and activation dynamics were observed in brain regions that we hypothetically related to Wallas' four stages of insight. Only the activation of the left ACC was observed in the mental preparation stage and only the activation of the right IFG in the verification stage. The other two stages were associated with the activation of more complex interhemispheric networks. Activity in the bilateral IFG (BA 44, 47), right MdFG, left MFG, and the MOG was obtained in the incubation-like stage, whereas only right hippocampal gyrus and left amygdala were activated in the illumination-like stage. Of note, the observed activations were mainly from previous studies using neuroimaging measures that actually provide correlational data. The possible functions of these brain systems in creative insight are discussed below.

4.1. Roles of the prefrontal cortex in creative insight

Our meta-analysis reveals that prefrontal cortex (PFC), including the bilateral IFG, the left MFG, and the right MdFG were particularly active in the incubation stage. In terms of the psychological processes underlying insight sequence, numerous studies have pointed to three common and critical components: breaking mental sets (through restructuring), forming weak or remote association, and triggering subjective experience (mainly positive affect) accompanying sudden solutions (e.g., Shen et al., 2017; Sandkühler & Bhattacharya, 2008; Weisberg, 2013). As mentioned early, incubation or incubation-like stage is closely associated with mental impasse in which the solvers have no idea and cannot obviously advance the progress of the problem they are facing. In other words, the incubation-like stage of insight is actually a working stage of mental set or the stage prior to the breaking of mental impasse (accompanying new and/or obvious advance in problem-solving progress). It thus has reasons to believe that these key components are likely reflected by the incubation-related brain activity. A growing number of neuroimaging and electrophysiology studies of

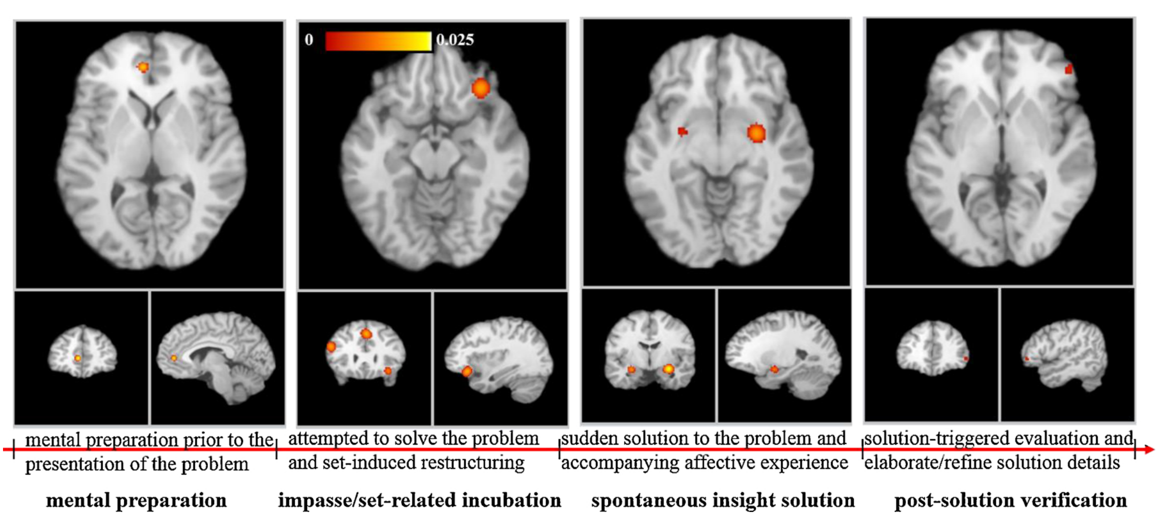

Fig. 2. The ALE-based brain activations associated with four stages of insight sequence, which primarily reflect stage-specific neurodynamic of insight, in particular the brain underpinnings of mental preparation, impasse/set-related incubation, solution-related sudden insight or termed as insightful illumination, and post-solution verification stages of an insight sequence.

insight have indeed reported evidence for a role of PFC in the breaking of mental sets or impasses (e.g., Qiu et al., 2010; Aziz-Zadeh et al., 2009; Zhao et al., 2013; Goel & Vartanian, 2005; Seyed-Allaei, Avanaki, Bahrami, & Shallice, 2017; Cerruti & Schlaug, 2009; Reverberi, Toraldo, D'agostini, & Skrap, 2005), presumably by inhibiting less useful and/or activating more useful mental sets (Anderson et al., 2009; Aziz-Zadeh et al., 2009; Zhao et al., 2013) and restructuring the problem space (e.g., Schuck et al., 2015; Powell & Redish, 2016).

The PFC is a multi-functional, complex system. Similarly, the process of breaking a mental set through restructuring is not a simple process but involves diverse process components (Yuan & Shen, 2016), such as the controlled inhibition of inappropriate thought patterns or prepotent but irrelevant associations. In this regard, various prefrontal regions engaged in the incubation-like stage of insight might functionally dissociate and take on distinct roles. In fact, our results provide evidence that different prefrontal regions were active in distinct stages of insight: the right IFG was activated in the incubation-like stage and the verification stage, whereas the left IFG was active in the incubation-like stage and the general pattern of insight beyond the specific insight task. Functionally, the IFG has been associated to a wide range of cognitively demanding information processing (see Gernsbacher & Kaschak, 2003). In particular, Jung-Beeman (2005) found that IFG is possibly involved in retrieving and selecting remote conceptual or semantic representations (Lundstrom, Ingvar, & Petersson, 2005) and in inhibiting competing stimuli and activated concepts that are stored in long-term memory (Aron, Robbins, & Poldrack, 2004; Shen et al., 2013). Moreover, this region has also reported to be responsible for organizing or integrating loosely related knowledge nodes (Abraham et al., 2012; Goel & Vartanian, 2005; Qiu et al., 2010), and eventually verbal elaboration of ideas (e.g., Wu et al., 2015). Together with the observed activation of the right IFG in the insight-related verification stage that generally assumed to associate with the elaboration of suddenly illuminated solution that were obtained/achieved in the illumination-like stage of insight sequence, this group of findings suggests that the right IFG likely involves the elaboration and appreciation of suddenly achieved solutions while the left IFG may respond to suppressing inappropriate mental sets or dominantly activated associations.

The MdFG, an essential part of the default mode network (DMN; Mayseless, Eran, & Shamay-Tsoory, 2015), was observed in both the general pattern of insight and the insight-related incubation-like stage. Although the specific role of the MdFG in insight remains unclear, contrary to the well-defined roles of ventral frontal regions in inhibition (e.g., Garavan, Ross, & Stein, 1999), an increasing number of recent studies have implicated the prominent activation of this region in restructuring or representation change (Bartholow et al., 2005; Schuck et al., 2015; Yuan & Shen, 2016). For example, a recent neuroimaging study (Schuck et al., 2015) adopted a well-designed spontaneous strategy switch task to investigate the function of the medial prefrontal cortex (MPFC) in representation change and showed that the activation in the MPFC was only different immediately prior to or after the representation change-point. That is, an abrupt change in the MPFC appeared during the transition from an old representation to a new representation. Further, the MPFC was involved in encoding currently task-irrelevant stimulus features that were thought to indicate the planning of an alternative strategy or representation (Schuck et al., 2015). During insight, a process of internally driven strategy change (Yuan & Shen, 2016), solvers were expected to experience the like strategy shift. In this sense, the MdFG might involve the strategy shift or representation change underlying the breaking of mental set. As an alternative, MdFG might play a role in enhancing persistent motivation for problem-solving. During problem-solving, participants might encounter one or multiple impasse-related difficulties resulting from inappropriate or misleading representations and should overcome them if they want to obtain the final (correct) solution or they have successfully solved the given problem. This might deplete cognitive resources or impair persistent motivation for problem-solving, eventually causing them to give up solving the problem (Payne & Duggan, 2011). As argued by Dietrich (2004) and emphasized by Aziz-Zadeh et al. (2009), this brain region may function as metacognition including internalizing values and societal standards that are imperative to insight. The MdFG allows participants to execute and achieve their goals of problem-solving through self-generated or internal drives rather than external rewards or stimuli novelty, altogether with the left insula and the right caudate. Taken together, the MdFG is particularly related to set shift and likely serves self-generated or internally driven representation/strategy change, either cognitive or motivational.

MFG activity was observed in the insight-related incubation-like stage only. Much research has indicated that MFG activation is associated with working memory manipulations (e.g., McCarthy et al., 1994; Rajah, Languay, & Grady, 2011) and executive control processes, such as attention selection and switching (e.g., Richeson et al., 2003). For example, Metuki, Sela, and Lavidor, (2012) reported that anodal stimulation over the left DLPFC did not enhance solution generation but did improve solution recognition for hard problems if only a relatively short interval was given for solving a problem—suggesting an effect on cognitive control rather than semantic processing. Therefore, we speculated that the left MFG might play a compensatory role for control mechanisms of the IFG through mediating right IFG (Goel & Vartanian, 2005; Luo & Knoblich, 2007; Mayseless & Shamay-Tsoory, 2015) in restructuring-related processes (Anderson et al., 2009; Shen et al., 2013) that could help the left IFG to find an appropriate balance between inhibiting irrelevant thoughts and selecting a remote association.

4.2. Roles of the hippocampal gyrus and amygdala in dynamic insight

The hippocampus is a major component of the limbic system and located in the medial temporal lobe. Insight relies on memory, at least to the degree that switches between mental sets and the restructuring of knowledge is involved. Therefore, the activation of hippocampus in insight tasks does not come as a surprise (e.g., Luo & Niki, 2003; Jung-Beeman et al., 2004). Indeed, our ALE meta-analytical results showed the activation of the right hippocampal gyrus in the general pattern and the illumination-like stage of insight assumed to establish remote associations. As mentioned above, the general pattern of insight may consist of a multitude of different and separable processes expressed by activities in discrete regions across cortices and functional connectivity among them. Considering the three underlying processes – breaking mental set, forming novel association, and triggering insight experience, this suggests that the general pattern reflects the cross-task consistency of these three processes (see Luo & Niki, 2003; Weisberg, 2013). However, the illumination-like stage of insight did not involve the process of breaking mental set. Of particular relevance, unlike the conventional roles of the hippocampus in spatial memory (see Shen et al., 2013), navigation (e.g., Luo & Niki, 2003), and relational memory (see Zhao et al., 2013), the hippocampus has been increasingly reported to serve critical roles in establishing weak, remote, and novel task-related semantic or episodic associations (Luo & Niki, 2003; Milivojevic, Vicente-Grabovetsky, & Doeller, 2015; Zhao et al., 2013) by accessing available associations that are distributed or stored in semantic and episodic memory systems (Shen et al., 2017). Furthermore, the production of insight experience often accompanies the emerging solution. In terms of temporal order of such processes, the breaking of mental set usually precedes the forming of novel association crucial to solution emergence that is followed or accompanied by insight experience. Accordingly, these converged evidence supports the role of hippocampal gyrus in establishing novel or non-salient semantic associations between seemingly irrelevant information. Some studies argued that the STG is involved in forming of novel, weak, and metaphoric association underlying insight. In our study, however, no significant activation in the STG was observed in the comparison of insight versus non-insight solutions. On the contrary, greater activity in the left STG was found in the reversed comparison.

With regard to the amygdala, it was observed to activate in both the third stage and in the general pattern of insight and was likely responsible for the internally generated emotional experience accompanying an insight solution (Shen, Yuan, Liu, & Luo, 2016). There are at least two lines of evidence favoring for the role of the amygdala in subjective experience or aha feeling of an insight solution. First, the amygdala is usually established as a key node of the affective network (Pessoa & Adolphs, 2010) and has been implicated in various kinds of emotional functions (Kragel & LaBar, 2016; Shen et al., 2017). In support of this idea, an increasing number of studies have documented the robust activation of this cortical structure in processing all kinds of emotional stimuli (e.g., Zhao et al., 2013; Cardinal, Parkinson, Hall, & Everitt, 2002), including experiencing and regulating emotion or affect. During insight, no emotional stimuli are provided but the absence or presence of a successful solution determines the affective experience (Shen, Yuan, Liu & Zhang et al., 2016). Moreover, the "Aha" experience accompanying an insight solution itself is actually hedonic and rewarding in nature (see Amir, Biederman, Wang, & Xu, 2015; Shen et al., 2017; Huang, Tang, Sun, & Luo, 2018), which is in accordance with the affective role of amygdala. Second, an increasing number of recent reports (Amir et al., 2015; Huang et al., 2018; Ludmer et al., 2011; Shen, Yuan, Liu & Zhang et al., 2016; Zhao et al., 2013) on brain-based insight have indeed shown that the "Aha" feeling accompanying insight solutions is mainly linked with activation in the amygdala. For instance, Zhao and colleagues (2013) utilized a paradigm of answer selection to identify neurodynamic from insight while participants solved Chinese idiom riddles. They found that insight solutions in the late period produce stronger activity in several regions than non-insight solutions, including the hippocampus and amygdala. The activation of the amygdala was assumed to reflect insight affect or experience accompanying insight solutions. Therefore, the amygdala can be assumed to elicit internally generated affective experience accompanying the insight solution.

4.3. Roles of the ACC and MOG in dynamic insight

Our ALE results showed robust activity in the left ACC during the mental preparation stage of insight and, interestingly, the ACC was only involved in mental preparation. Consistent with this finding, Qiu, Li, Jou, Wu, and Zhang, (2008) observed a more positive ERP deflection primarily originating from the left ACC in the mental preparation of successfully as compared to unsuccessfully solved riddles from −1000 to −800 ms before the onset of the target riddles. Kounios et al. (2006) stressed that this preparation stage of insight is a distinct brain state that is conducive to subsequently presented insight problem solving independent of specific problems (Kounios et al., 2006; Wang et al., 2009). The functions most frequently attributed to the ACC – attention focusing, attention shifting, and error detection or resolution – form the basis of conflict monitoring and detection which in turn serves to signal the need for cognitive control in the maintenance or switching of attentional focus or the selection from competing responses (e.g., Kounios et al., 2006; Badre & Wagner, 2004; Miller & Cohen, 2001; Zhan, Liu, & Shen, 2015). During the mental preparation preceding the presentation of a problem, the solver can thus be assumed to mentally prepare for having an "insight" or "aha" solution, presumably by focusing attention inwardly or get ready to switch to a new trains of thought, and probably by actively silencing irrelevant thoughts and rumination. This would fit with the idea of Kounios et al. (2006) and consider the ACC as a general control mechanism to prepare a focused (rather than a defocused) state that, similar to sleep in delayed insight (Wagner, Gais, Haider, Verleger, & Born, 2004), suppresses unrelated thoughts (Kounios et al., 2006).

Similar to the ACC, the left MOG takes part only in the incubation-like stage of insight. As discussed earlier, the process in the second stage is likely to consist of set-related representation restructuring. Participants need to abandon the initially incomplete or misleading representations (Knoblich et al., 2001) and find more appropriate ones through chunk decomposition or constraint relaxation, largely relying on the occipital regions such as the MOG. In a recent study (Shen, Yuan, Liu & Zhang et al., 2016), the activation of the MOG has been reported to provide critical information for representational changes and the reorganization of visual imagery during insightful problem solving (see Luo et al., 2006; Qiu et al., 2010). Accordingly, the left MOG may be related to visualizing or re-encoding the problem space to mentally re-establish more appropriate representations of the given problem.

5. Conclusions and implications

Insight as a type of creative cognition has attracted a great deal of interest for nearly a century and has been regarded to involve a large number of cognitive processes including memory search and retrieval, analogical reasoning, semantic activation, cognitive control, and even spatial navigation. To quantify the brain network of insight, the ALE approach was adopted here to determine the general pattern drawn from the activation foci converging from those insight-related fMRI studies using different tasks. Given the dynamic characteristics of the sequence of insight-related processes (Weisberg, 2013), the current work further conducted a staged ALE-based meta-analysis to identify the dynamic cortical mechanisms engaged in the four stages of the insight process. All neuroimaging studies included in the analysis of the general pattern were sorted into four categories according to the characteristics of the insight tasks and periods each experiment involved, which were taken to indicate the respective stage of the heuristic four-stage insight model taken from Wallas. Our quantitative meta-analysis demonstrated that the comprehensive brain network of insight comprised of a set of distributed regions across the two hemispheres, including the PFC, the left ACC and the right hippocampal gyrus, and the left amygdala.

Moreover, our phasic ALE data exhibited different interhemispheric brain patterns engaged in the various stages of the insight process. With regard to brain laterality, the left brain seems to act as a key part of the insight-related preparation-like stage and the right brain in the verification-like stage, whereas an interhemispherically balanced pattern was observed for the insightful incubation stage and illumination-like stage, respectively. Also, various brain areas in both hemispheres were variably recruited during the four stages of insight. In the mental preparation stage of insight, ACC activation was observed in preparing either a focused state or a default brain state (presumably reflecting mental preparation) for insight. In the second stage, reflecting restructuring and set-shifting, extensive interhemispheric brain regions encompassing the bilateral IFG, the left MFG, the right MdFG, and the left MOG were activated. In the illumination-like stage, the hippocampal regions previously established in forming non-obvious associations (e.g., Luo & Niki, 2003; Zhao et al., 2013) and the amygdala involved in insight experience were activated. In the verification-like stage, the right IFG's activation was found, which is thought to involve controlled elaboration of an insight solution. In this work, sorting the neuroimaging studies on insight into four categories to conduct the ALE meta-analysis turned out to be feasible, and indeed a similar analytical approach has been used in previous studies (e.g., Mincic, 2015), but we emphasize that the sample size of some of the categories is still small. Given very limited availability of studies on the four hypothetical stages, conclusions from the present study need to be drawn cautiously.

In addition to strengthening the importance of the prefrontal cortex, temporal regions (mainly hippocampus), amygdala, and the middle occipital region for dynamic insight, one key implication of our study relates to models of creativity and the role of incubation in the creative process. Sparked by the anecdotal records of incubation and insight, various efforts have been made to demystify incubation effects. Although the incubation effect has been largely replicated, its specific mechanism remains unclear. A new approach based on unconscious process theory argues that the underlying neural basis of incubation may be the DMN (Baird et al., 2012; Ritter & Dijksterhuis, 2014) observed repeatedly in mind wandering (also called micro incubation, see Sawyer, 2011). However, our findings provide a challenge for this claim of an association between incubation and the DMN by showing that the insightful incubation process recruited the prefrontal control network. That is, the incubation-like process seems not only to activate the DMN (e.g., MdFG), but also to activate the prefrontal control network (lateral PFC). This finding might be taken to suggest that incubation is not an (entirely) unconscious activity based on the DMN. Instead, the incubation period, or at least the insight-related incubation-like stage, relies on neural recruitment in both default and executive network regions, with the latter presumably being related to conscious experience. These findings actually parallel research in the creativity literature on divergent thinking and other modes of creative thought, which has shown consistent engagement and interaction of these brain networks (for reviews, see Jung, Mead, Carrasco, & Flores, 2013; Beaty, Benedek, Silvia, & Schacter, 2016). In this sense, insightful incubation and even some incubations in other modes of creative thought such as divergent thinking may depend on some yet to be determined interaction between conscious cognitive control and unconscious processes, supporting our view of dual-process of incubation (Yuan & Shen, 2016).

Conflict of interest statement

The authors declare that they have no potential conflicts of interest to disclose.

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