

Neural correlates of Eureka moment



Giulia Sprugnoli^a, Simone Rossi^a, Alexandra Emmendorfer^b, Alessandro Rossi^a, Sook-Lei Liew^c, Elisa Tatti^a, Giorgio di Lorenzo^{e,f}, Alvaro Pascual-Leone^b, Emiliano Santarnecchi^{a,b,d,*}

^a Brain Investigation & Neuromodulation Laboratory, Department of Medicine, Surgery and Neuroscience, University of Siena, Siena 53100, Italy

^b Berenson-Allen Center for Non-Invasive Brain Stimulation and Division of Cognitive Neurology, Beth Israel Medical Center, Harvard Medical School, Boston, MA 02120, USA

^c Chan Division of Occupational Science and Occupational Therapy, University of Southern California, Los Angeles, CA, USA

^d Center for Complex System Study, Engineering and Mathematics Department, University of Siena, Siena 53100, Italy

^e Laboratory of Psychophysiology, Chair of Psychiatry, Department of Systems Medicine, University of Rome "Tor Vergata", Rome, Italy

^f Psychiatry and Clinical Psychology Unit, Department of Neurosciences, Fondazione Policlinico "Tor Vergata", Rome, Italy

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ABSTRACT

Insight processes that peak in “unpredictable moments of exceptional thinking” are often referred to as Aha! or Eureka moments. During insight, connections between previously unrelated concepts are made and new patterns arise at the perceptual level while new solutions to apparently insoluble problems suddenly emerge to consciousness. Given its unpredictable nature, the definition, and behavioral and neurophysiological measurement of insight problem solving represent a major challenge in contemporary cognitive neuroscience. Numerous attempts have been made, yet results show limited consistency across experimental approaches. Here we provide a comprehensive overview of available neuroscience of insight, including: i) a discussion about the theoretical definition of insight and an overview of the most widely accepted theoretical models, including those debating its relationship with creativity and intelligence; ii) an overview of available tasks used to investigate insight; iii) an ad-hoc quantitative meta-analysis of functional magnetic resonance imaging studies investigating the Eureka moment, using activation likelihood estimation maps; iv) a review of electroencephalographic evidence in the time and frequency domains, as well as v) an overview of the application of non-invasive brain stimulation techniques to causally assess the neurobiological basis of insight as well as enhance insight-related cognition.

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* Corresponding author at: Berenson-Allen Center for Non-Invasive Brain Stimulation and Division of Cognitive Neurology, Beth Israel Medical Center, Harvard Medical School, Boston, MA, USA.

E-mail addresses: sprugnoli3@student.unisi.it (G. Sprugnoli), rossissimo@unisi.it (S. Rossi), emmendorfer.a@gmail.com (A. Emmendorfer), rossiale@unisi.it (A. Rossi), sliew@chan.usc.edu (S.-L. Liew), elisattati@msn.com (E. Tatti), di.lorenzo@med.uniroma2.it (G. di Lorenzo), apleone@bidmc.harvard.edu (A. Pascual-Leone), esantarn@bidmc.harvard.edu (E. Santarnecchi).

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1. Introduction

Although research on insight processes began over a century ago with Köhler's observations on the problem-solving abilities of chimpanzees (Köhler, 1925), a comprehensive definition of "insight processes" remains elusive. During the last twenty years, several theories have been proposed to explain the insight phenomenon. Over the past decade, experimental support for some of these theories has been gathered thanks to recent advances in neuroimaging and neurophysiological techniques. In the present review, we provide a comprehensive summary of the neuroscience of insight. We first provide an overview of the most relevant theoretical definitions and the most commonly used tools for the investigation of insight moments. Second, we present original results from a quantitative meta-analysis of available functional magnetic resonance imaging (fMRI) data, as well as a summary of the evidence collected with electroencephalography (EEG), focusing on brain oscillations and event-related analysis. Third, we critically discuss emerging evidence from perturbation-based and neuromodulatory approaches, such as repetitive transcranial magnetic stimulation (rTMS) and transcranial electrical stimulation (tES), which add a causal dimension to traditional neuroimaging mapping data, allowing for the transient modification of regional brain dynamics underlying insight processes. Finally, we address the possibility of using non-invasive neuromodulation as a tool to enhance insight problem-solving abilities.

2. Defining the topic: definitions, theories, and tasks

2.1. An insight into insight

Many great scientific discoveries have relied on insight moments (e.g., Newton's finding of the law of gravitation, Kekulé's discovery of the structure of benzene, Poincaré's discoveries in mathematics, Einstein's first theorization of the General Relativity theory; Sandkühler & Bhattacharya, 2008). The first known *Aha!* moment typically refers to Archimedes of Syracuse, who, after discovering the

principle of displacement while taking a bath, reportedly ran naked down the street shouting "*Eureka!*". This funny anecdote highlights the unpredicted, unfettered nature of *Aha!* moments, thought of as "a special gift of Muses" by the Greek. While solid theory has been proposed for the biological network of intelligence (Jung & Haier, 2007), valid scientific explanations are largely lacking for insight. This leaves the *Eureka* moment as one of the most intriguing and unexplained processes of the human mind (Sternberg & Davidson, 1995), despite many relevant correlations with fluid intelligence (Paulewicz, Chudersky, & Necka, 2007; Sternberg & Davidson, 1995), switching ability and working memory (WM) capacity (Murray & Byrne, 2005). It was not until the beginning of the 20th century that Gestalt psychologists attempted to create a proper definition of insight (Dietrich & Kanso, 2010), describing it as "a process based on reconstructing the core of a problem, rethinking its basic assumptions and originating a new and creative solution, a process usually occurring in an unexpected and unpredictable manner" (Köhler, 1925).

To better characterize the *Aha!* moment, a valid heuristic approach might be to discard what is *not* considered insight problem-solving. In general, problem-solving strategies can be divided into three types: analytical problem-solving, memory retrieval, and insight (Novick & Sherman, 2003). Analytical problem-solving is characterized by three main features: (i) it is deliberate and predominantly conscious, (ii) it advances step by step from the initial processing of information to the resolution and (iii) its steps are available to WM, so that subjects are able to explain in details how they were able to approach the solution. In contrast to analytical problem-solving, which is marked by a deep understanding of the problem, memory retrieval processes can be described as a simple mental retrieval of previously acquired knowledge, which fits to the problem at hand (Aziz-Zadeh, Kaplan, & Iacoboni, 2009).

Insight problem-solving is thought to be very different from these other two strategies. The *Aha!* moment consists of a sudden, unexpected, and somehow "obvious" solution that cannot be explained by a sequential solution process. Unlike analytic problem-solving, the subjects cannot readily explain the exact path they followed to reach

the solution. Often, a sense of being stuck precedes the insight phenomenon, and the way out of this mental impasse is provided by the creation of novel associations, rendering insight problem-solving a multistep process (Bowden & Jung-Beeman, 2007; Bowden, Jung-Beeman, Fleck, & Kounios, 2005). Interestingly, insight solutions are generally more accurate than analytical ones (Salvi, Bricolo, Kounios, Bowden, & Beeman, 2016). A possible explanation could rely on the all-or-none nature of *Aha!* moment, which does not allow the subject to provide intermediate responses and contributes to the positive burst of emotion when an insight comes to consciousness (Salvi et al., 2016).

Recently, a new definition of the *Eureka* moment (Kounios & Beeman, 2014) described it as “any sudden comprehension, realization, or problem solution that involves a reorganization of the elements of a person’s mental representation of a stimulus, situation or event to yield a nonobvious or nondominant interpretation”. In this view, the process is happening almost entirely at the unconscious level. Interestingly, a mental impasse is not considered a necessary feature of insight in this definition, because this aspect would implicitly exclude insight moments that occur when: (i) subjects are not concentrating on problem solutions (e.g. while taking a shower), (ii) use the analytic problem-solving method but have not yet reached an impasse, or (iii) are suddenly struck with a new idea. Finally, the authors considered the positive burst of emotion (that usually accompanies the *Aha!* moment) as an additional, but not necessary, feature, as it is not always present.

In summary, a few features of the *Aha!* moment seem to systematically overlap across theories and models: (i) insight takes form as a sudden comprehension of the solution to a problem; (ii) the subject has no access to the analytical steps leading to the insight moment; (iii) insight triggers a sense of surprise and a burst of positive emotions spanning from satisfaction to euphoria.

2.2. Defining processes

A proper understanding of insight problem-solving requires going beyond definitions and considering the underlying mental operations.

Multiple theories have been proposed to explain the *Aha!* moment, including the *Progress Monitoring Theory* (MacGregor, Ormerod, & Chronicle, 2001), the *Representational Change Theory* (Knoblich, Ohlsson, Haider, & Rhenius, 1999) and a recent conceptualization by Bowden and Beeman (Bowden et al., 2005).

The *Progress Monitoring Theory* by MacGregor, Ormerod, and Chronicle, is based on the hill-climbing method, and has been adapted to the performance of a classic insight problem, the Nine-dot problem (Fig. 1). The hill-climbing method can be applied to problems that have many solutions. It begins with the assumption of a random solution, which is subsequently manipulated making small changes, each time getting closer to the goal. When such a process does not produce results anymore, the subject comes to an impasse and starts searching for a new approach, following a trial and error heuristic path. This theory implies that solvers constantly monitor their own progress in order to promptly switch to a different problem-solving strategy in case the current one is not successful. This theory suggests that the *Aha!* moment may be achieved with an incremental approach, with constant monitoring of the own cognitive processes as a pivotal feature, making the *Eureka* moment more like a conscious epiphenomenon of a general problem-solving process (*Theory of Business as Usual*; Bowden et al., 2005) rather than a burst of uncommon cognitive processes (*Theory of the Special Process*; Bowden et al., 2005; see also the paragraph “Multifactorial nature of *Aha!*: intelligence, memory, attention, mood, cognitive control and sleep”).

In contrast to the *Progress Monitoring Theory*, Knoblich and colleagues introduced the *Representational Change Theory* (Knoblich et al., 1999) to emphasize the importance of the reorganization of a problem’s representation. In general, the authors suggest that the main issue of problem-solving relies on the spontaneous human tendency to set unnecessary constraints through a very restricted and reductive mental representation of the problem at hand, which is modeled on past and consolidated knowledge. To overcome the impasse and reach the solution, subjects must: (i) remove these unnecessary constraints by deactivating the recalled knowledge linked to the problem, and (ii)

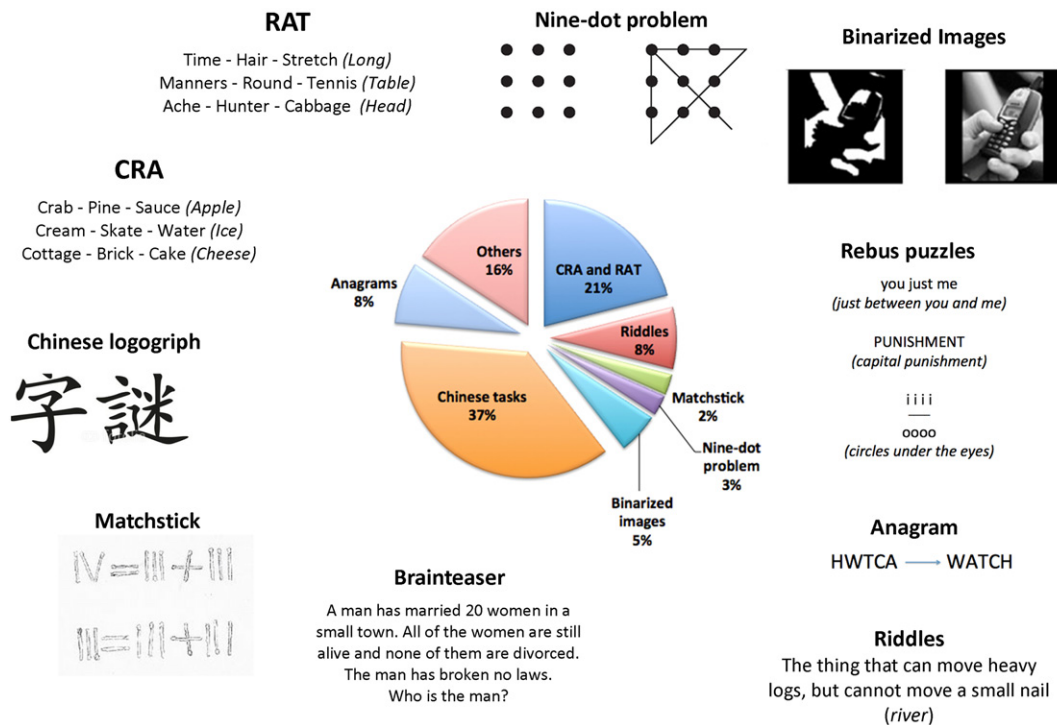


Fig. 1. Insight tasks. Examples of different tasks used to assess insight problem-solving are shown, highlighting the heterogeneity of available assessment tools reported in the literature. Pie chart refers to the percentage of studies implementing each different task (“Chinese tasks” referred to Chinese logographs, characters, character-generation task, Chinese riddle and puzzles; “others” referred to: ambiguous sentences, technical problems, prototypes, number reduction task, brainteasers; see the paragraph “Insight tasks” for additional details and also Tables 1, 2, S1, S2, S3, S4).

make a decomposition of the elements of the task by dividing it into perceptual chunks. Constraints and chunks might differ: local and global constraints respectively apply to a single part or to the whole problem representation, while loose and tight chunks can or cannot be divided into further chunks. Knoblich and colleagues ascribe to the mastering of these mechanical and fairly analytical steps the ability to create a new representation of the problem and reach the *Aha!* moment, somehow again minimizing the unconscious nature of the insight phenomenon.

Both the *Progress Monitoring Theory* and the *Representational Change Theory* have received some experimental support, with the former showing a better fit to multi-step problems (e.g. Nine-dot problem, see Fig. 1), and the latter being more suited to single-step problems (e.g. Matchstick arithmetic problems, Fig. 1).

Bowden and Beeman have proposed another theory to explain the *Eureka* moment. They suggest that the steps leading to an insight moment include (i) a strong activation of useless consolidated information, coupled with a weak (unconscious) activation of new information crucial to reach the solutions; (ii) a secondary integration and reorganization of the elements in a non-dominant way respect to the initial representation of the problem, and finally (iii) the restructured representation reaching consciousness (Bowden et al., 2005). The “unconscious trajectory” was the principal limitation in investigating the neural basis of insight process in humans. However, the intrinsic difficulty in measuring – or quantifying – a construct cannot constitute a limitation to our understanding of human cognition and has not been a constraint for other controversial topics, such as creativity and memory retrieval (Schooler & Melcher, 1997). More appropriate tools are needed in order to reveal the underlying anatomy and physiology of insight problem-solving, with fMRI, EEG and non-invasive brain stimulation (NiBS), and combinations of these methods, constituting valuable solutions. Neurophysiological correlates of insight supporting this framework through spatially and temporally distributed inter-hemispheric activations are now emerging as its first unconscious step (shared also with creativity process, see also “Creativity and insight” paragraph; Simonton, 2001; Schooler & Melcher, 1997). An initial weak semantic activation, characterized as the first stage of problem-solving, occurs in the right hemisphere as a general semantic encoding process, while the fine semantic encoding takes place in the left hemisphere (Bowden et al., 2005). The weak coarse semantic activation is assumed to be crucial in insight problem-solving because it implies the access of alternative meanings and distant semantic associations between the items at hand. Considering it is a faint and non-dominant activation, it is initially blocked and suppressed by potentially misleading left-sided activations, leading to an impasse. When subjects overcome the consolidated and dominant coding, an *Aha!* moment is likely to occur. To verify the hypothesis of an essential role played by the right hemisphere, Bowden and colleagues conducted a series of experiments using a visual-hemifield presentation of Compound Remote Associations (CRA, Fig. 1) problems with a priming paradigm (Bowden & Jung-Beeman, 1998). The results confirmed their prediction: subjects provided faster responses when stimuli relevant for the solution were presented to the left visual field/right hemisphere rather than to the right visual field/left hemisphere (see also Beeman & Bowden, 2000; Bowden & Jung-Beeman, 2003). The authors suggest hemispheric asymmetry (with the prominent role of right hemisphere) as the structural and functional basis for insight problem-solving. Ultimately, in line with studies reporting the role of the right anterior superior temporal gyrus in the creation of distant semantic relations (Mashal, Faust, & Hendlar, 2005; Mason & Just, 2004), Bowden and colleagues hypothesized the unconscious reorganization of the problem as a result of the activation of this region, consequently shifting the attention towards this brain area as a core node of the insight network in humans (the same region is also highlighted by our fMRI analysis, see fMRI discussion section). However, it is worth noting that these findings are specific for insight solutions achieved with CRA task, so their applications to insight

in general may not be appropriate before extensive experimental EEG and fMRI validations.

Despite the various conceptualizations discussed above, a clear theoretical representation of insight is still not available. Except for core elements, such as the creation of mental associations and the restructuring of the problem in a novel and useful way, more robust neurophysiological models of the *Eureka* moment are necessary to settle on an evidence-based definition.

2.3. Insight or insights?

A topic of lively discussion is whether the *Eureka* process is specific to the problem-solving domain, and to what extent it is separated from the analytical method. Although the majority of scientists consider the insight process as related only to higher order problem-solving, Bowden and colleagues suggest that it could be a more general phenomenon encompassing *perception* (e.g. the sudden recognition of an object in a blurred or ambiguous picture) and *language comprehension* (e.g. the sudden comprehension of a joke or metaphor; Bowden & Jung-Beeman, 2007). According to this view, the *Aha!* moment reflects a generalizable process of acquired knowledge across domains, including perception, language, decision making, problem-solving, etc. Thus, all moments of insight require finding a particular piece of information that has not been declared from the background, and integrating it with prior knowledge at the unconscious level, to reach a conscious solution (Bowden et al., 2005). Moreover, they postulate a discrete overlay between the insight problem-solving processes and non-insight processes, with the former implying more unique features than the others.

Taking into account the various fields where insight-like processes seem to be involved, Bowden and colleagues postulate that all types of *Eureka* moments would need a basic neural network and mental operations, which are partially shared with analytical problem-solving (Schooler & Melcher, 1997). If so, it might be possible to identify a common insight process across all domains – as partially revealed for mathematical and verbal tasks (Bermejo, Castejon, & Sternberg, 1996) – and specific insight processes for each subfield of cognition where *Eureka* moments might occur (Bowden & Jung-Beeman, 2007).

2.4. Insight tasks

Given the multitude of non-univocal theories and definitions of insight, many tasks have been developed to address it. Gestalt psychologists were the first to introduce insight tasks almost a century ago, such as the “Nine-dot problem”, the “Dunker candle task” and the “Eight Coin problem” (for a review see Chu & MacGregor, 2011 and Fig. 1). Despite being widely used in the assessment of insight problem-solving, these classical insight problems have a number of limitations: (i) they are usually so difficult that only a small percentage of participants can solve them in an experimentally compatible amount of time, (ii) their solution usually requires a very complicated generative-operative process, (iii) they cannot be re-tested due to their single-trial/item nature, (iv) they are mostly visuo-spatial problems (independent from the verbal knowledge) and (v) very heterogeneous. Moreover, these tasks are characterized by the fact that they cannot be solved through other problem-solving strategies (i.e., the analytical method) and thus depend fully on insight problem-solving, limiting experimental controls by shifting strategies. Therefore, these classical insight tasks are not ideal for appropriately controlled experiments (Bowden et al., 2005).

To overcome the limitations of classical insight tasks, a second generation of insight problems was developed. Largely based on verbal comprehension, they are easier to solve when used with the appropriate linguistic population, they include many more items for each trial type and they are generally faster to solve. Examples are tasks based on riddles or anagrams, as well as ad-hoc designed tasks such as the matchstick arithmetic problems, Chinese logogriphs, rebus

puzzles, the Remote Associates Task (RAT) and the CRA. For a graphical depiction of each task, see Fig. 1.

The Rebus puzzles (MacGregor & Cunningham, 2008) are composed by visual and verbal information that has to be integrated to find a familiar phrase. In this type of task, the subject must relax the constraints implemented by grammatical rules and reading (i.e., deactivate the recalled knowledge and assumptions linked to language) to bring out the real meaning of the compound stimulus (as required in the *Representational Change Theory*).

The Matchstick arithmetic problems (developed by Knoblich in 1999) are false equations written in Roman numerals using matchsticks, therefore they are not dependent on language and verbal comprehension. Subjects can move only one matchstick to transform the false statement into a correct mathematical relation (Knoblich et al., 1999).

The anagrams (Novick & Sherman, 2003) and riddles (Luo & Niki, 2003a) are pure verbal problems. Anagrams require the rearrangement of letters to create a new word, whereas riddles, in the context of insight research, are phrases with double or veiled meaning, in which one has to guess the answer.

Brainteasers are verbal puzzles with practical content, which require unconventional thinking with given constraints in mind (Sheth, Sandkühler, & Bhattacharya, 2009).

The Chinese logogriphs are a particular type of riddle in which the answer is a Chinese character that indicates a phrase, a Chinese proverb or a sentence in a poem that must be solved by the addition, subtraction or substitution of strokes, after having understood the riddle's implicit meaning (Wang et al., 2009).

Binarized images are two-tone (usually black and white; Giovannelli et al., 2010) pictures representing low-resolution version of an original one. They appear meaningless at first sight, while becoming recognizable after a single exposure to its original version (i.e., priming). This purely visual task has been specifically used to assess the perceptual learning component of *Eureka* moment.

Mednick's RAT (Mednick, 1962) was created in the 1960s to measure creative convergent thinking and is often used to assess creativity in general (e.g. Gibson, Folley, & Park, 2009). It is also employed to estimate insight problem-solving capacity (Cerruti & Schlaug, 2009; Razumnikova, 2007), since it was demonstrated that the performance on RAT correlates with score at classical insight problem-solving (i.e. anagrams correlation coefficient $r = .55$, Schooler & Melcher, 1997). The RAT inspired the creation of the CRA by Bowden and colleagues, one of the most widely used tests to assess insight performance (Bowden et al., 2005). Both RAT and CRA stimuli consist of three words and the subject has to find a fourth related word. However, while in the CRA the solution must form a compound word with the others (i.e. "crab, pine, sauce", solution: "apple = crabapple, pineapple, applesauce"), this constraint is not present in the RAT (i.e. "falling, actor, dust", solution: "star = falling star, movie star and stardust").

The advantages of RAT and CRA are pivotal for insight research: (i) they can be solved in just a few seconds by many people, (ii) can be presented in a small visual space, (iii) the solution is a unique word, facilitating scoring, (iv) there are many degrees of difficulty, (v) several items, and, an important feature, (vi) they can be solved with both insight or analytical problem-solving processes (the strategy being used can be subjectively reported), thus allowing for a proper comparison between these distinct mental mechanisms, in order to reveal the unconscious restructuring characterizing the initial stages of insight elaboration. This possibility marked a break from the old conception of insight tasks, for which the type of problem was the key determinant of the occurrence of an insight or an analytical mental operation (Bowden & Jung-Beeman, 1998; Bowden & Jung-Beeman, 2003; Bowden & Jung-Beeman, 2007). According to this innovation, CRA score correlates with two and three-dimensional classical insight tasks, (respectively $r = .549$ and $r = .430$; Mourgues, Preiss, & Grigorenko, 2014). However, correlations between classical and new insight tasks are not very strong,

underscoring the innovative measurement of insight introduced by the CRA task.

2.5. Creativity and insight

Most classical insight tasks are also used to study creativity. It is therefore important to address the relationship between creativity and insight. Whether insight moments should be considered a component of human creativity remains controversial, with experimental and theoretical work supporting conflicting views (Schooler & Melcher, 1997). Indeed, creativity is one of the most complex human abilities, the *primum movens* of progress and innovation in all fields. Creativity is broadly understood as the ability to change existing thinking patterns, producing something that is useful, novel and generative (Sternberg & Davidson, 1995). This universally accepted conception of creativity could also include the latest definition of insight: "...a reorganization of the elements of a person's mental representation of a stimulus, situation or event to yield a nonobvious or nondominant interpretation" (Kounios & Beeman, 2014). Moreover, creativity and insight seem to share many essential characteristics (Martindale, 1999) as defocused attention, unconscious processing (Schooler & Melcher, 1997; Simonton, 2001) and less prefrontal activation (for details about insight correlations see the next paragraph).

Thus, the *Aha!* moment seems to represent a specific sub-process in which creative cognition could reach consciousness (Aldous, 2007; Dietrich & Kanso, 2010). Supporting this theory, evidence of positive correlation between performance at insight and creative tests (e.g. CRA and Drawing Production: $r = .274$, $p < .001$; CRA and Alternative Uses: $r = .275$, $p < .001$; Rebus Puzzle and Drawing Production: $r = .307$, $p < .001$; Rebus Puzzle and Alternative Uses: $r = .211$, $p < .05$; Mourgues et al., 2014) as well as on other tests assessing different cognitive abilities not related to analytical reasoning (e.g., perception) is available (Bowden et al., 2005). In addition, insight is not involved in all phases of creative thinking (e.g. the critical evaluation of an idea), and is not a necessary feature of creative thinking, which could also arise from an analytical process based on a defined multi-step approach (Mumford & Whetzel, 1996). Furthermore, not all insight moments lead to a creative process if we refer to the broader definition of insight, including perception and language comprehension. This could explain the very low correlations between insight and creativity tasks, supporting a more segregated view of these processes. Finally, as previously mentioned, tasks used to assess creativity and insight are not completely and clearly separable, thus such weak positive correlation could simply be the consequence of measurement error. Most creativity tasks, such as the Alternate Uses Task, require divergent thinking, the ability to generate multiple solutions for an open-ended problem (Guilford, 1967). On the other hand, many insight tasks rely only on convergent thinking, the ability to find a single correct solution for a problem, or on a combination of the two (Abraham & Windmann, 2007). However, CRA and RAT problem-solving could be divided into a first process involving divergent thinking, which is needed to explore the possible connections between the available stimuli, followed by a second step in which the subject converges to a single solution (convergent thinking). Therefore, tests of creative thinking often involve an initial step requiring insight moments. In order to fully disentangle the nature and organization of insight and creativity, a more in-depth comprehension of their neurophysiological underpinnings should constitute an absolute priority (see also "The insight network" in the discussion paragraph).

2.6. Multifactorial nature of *Aha!*: intelligence, memory, attention, mood, cognitive control and sleep

As one of the most complicated and volatile cognitive phenomena, insight has captured the attention of different fields of cognitive neuroscience and has been linked to diverse features of human behavior. For

instance, the role of intelligence, attention levels, cognitive control, mood, and sleep quality have been investigated, introducing numerous complex, but intriguing, scenarios.

2.6.1. *Intelligence and memory*

A correlation between insight and intelligence was demonstrated in children (Bermejo et al., 1996), with high-intelligence performers showing a stronger disposition to using insight problem-solving than lower-intelligence performers. In adults, insight abilities were found to strongly correlate with general fluid intelligence measures (Sternberg & Davidson, 1995). Subsequent studies showed intelligence scores explaining almost 75% of variance in insight scores (Paulewicz et al., 2007), even though doubts about the construct validity of the tasks used to assess the two abilities has been raised due to excessive overlap in task mechanics. In addition, a lesion study (Barbey, Colom, & Grafman, 2013) revealed that psychometric intelligence strongly predicts cognitive flexibility, a key component of insight problem-solving (Subramaniam, 2008). Different aspects of WM were found to correlate with insight problem-solving, including spatial WM (Chein, Weisberg, Streeter, & Kwok, 2010), verbal short-term memory (Fleck, 2008), WM storage and processing (Murray & Byrne, 2005), verbal spans and spatial storage capacity (Gilhooly & Fioratou, 2009). Such a relationship is thought to be relevant in order to evaluate insight reasoning within the two dominant theories, i.e. the *Special Process* or the *Business as Usual* view (Chudersky, 2014; see the “Defining processes” paragraph). Accordingly to the former, WM should not correlate with insight (Van Stockum & DeCaro, 2013; for a review see Wiley & Jarosz, 2012), whereas the second view predicts a link between WM and insight tasks as shown for other high order cognitive functions such as creativity and abstract reasoning (Chein et al., 2010; Murray & Byrne, 2005). Following recent work by Chudersky (2014), factorial analysis on a large dataset of insight, WM, and analytical reasoning tasks suggest that WM accounts for one third of variance in insight problem-solving abilities. Considering both WM and analytical reasoning, two thirds of insight variance can be explained. In addition, while both components of WM (storage capacity and executive control) seem to be involved in insight, reasoning and insight appear to be two separable variables (i.e. they shared only 26% of variance). Overall, both theories might fit the data, with a significant WM contribution to insight problem-solving, but still a significant amount of unexplained variance even when reasoning is considered.

2.6.2. *Attention*

High attentional levels are commonly considered a typical feature of highly creative subjects (Carson, Peterson, & Higgins, 2003; Mendelsohn & Griswold, 1966; Rowe, Hirsh, & Anderson, 2007). Interestingly, while high-insight subjects (participants using lots of insight problem-solving strategies) seem to show high outward visual attention level in the resting state (Kounios et al., 2008, see Discussion section and Fig. 5), a switch to more inward attention is observed during the mental preparation time (Kounios et al., 2006), which lasts until just before the intuition of a solution (Jung-Beeman et al., 2004). This finding was recently confirmed using eye-tracking (Salvi, Bricolo, Franconeri, Kounios, & Beeman, 2015). Finally, a modulation of insight ability in relation to specific attention patterns has been proposed (Wegbreit, Suzuki, Grabowecy, Kounios, & Beeman, 2012), with subjects reaching higher scores in CRA problems after completing a broad attention-priming task.

2.6.3. *Mood*

Mood has been found to influence insight processes as well: in line with previous studies (Amabile, Barsade, Mueller, & Staw, 2005; Estrada, Joung, & Isen, 1994; Isen, Daubman, & Nowicki, 1987; Rowe et al., 2007), participants with higher positive mood solved more CRA

problems relying on insight strategies (Subramaniam, Kounios, Parrish, & Jung-Beeman, 2009). In addition, mindfulness meditation, previously shown to have effects on mood modulation and introspection levels (Santarnecchi et al., 2014), seems to correlate with performance in solving rebus puzzles (Ostafin & Kassman, 2012). Associations between mood and insight abilities can also be reflected in event-related potentials (ERPs), such as the N400 component, classically thought to reflect the semantic processing and integration of a word in the provided context (McPherson & Holcomb, 1999). The amplitude of N400 is inversely related to the relationship of a provided word in its context (Kounios, 1996): interestingly, positive mood represents a good modulator of its amplitude (i.e. it induces a smaller N400; Federmeier, Kirson, Moreno, & Kutas, 2001; for further details about N400 see the paragraph about ERPs). Therefore, positive mood may facilitate the accessibility of weak activation, making the provided stimuli (words) more related to their semantic context. Another explanation is that positive mood modulates attention and cognitive control, facilitating perception and processing of external stimuli (Kounios & Beeman, 2014).

2.6.4. *Sleep and cognitive control*

Finally, roles for sleep and cognitive control have been proposed as well. Linked to many scientific discoveries (e.g., the periodic table of Mendeleev), sleep is likely to accelerate mental restructuring of given information, a crucial component of insight problem-solving (Wagner, Gais, Haider, Verleger, & Born, 2004). As for cognitive control, Wieth and colleagues have recently shown that participants perform better in tasks of insight problems during their non-optimal mental times of day assessed by the Morningness Eveningness Questionnaire (Wieth & Zacks, 2011). Intriguingly, this result suggests that less cognitive control (i.e. less prefrontal inhibitory dynamics in general) actually represents the optimal cognitive context to release constraints on weak semantic information and ease *Eureka* moments.

2.7. *Overview of neurophysiological evidence about insight processes*

In order to provide a comprehensive picture of the neural underpinnings of insight, we first performed an original quantitative meta-analysis of available fMRI data. We also examined existing EEG evidence involving both spontaneous brain oscillations and ERPs. Finally, a discussion of the evidence from studies involving brain neuromodulatory approaches such as repetitive transcranial magnetic stimulation (rTMS) and transcranial electrical stimulation (tES) is offered.

3. *Methods*

3.1. *Literature search*

We performed a literature search in PubMed and Google Scholar databases, without temporal restrictions, to retrieve potentially relevant articles. To specify the object of the present review, terms such as “functional magnetic resonance imaging”, “electroencephalography”, “magnetoencephalography”, “transcranial magnetic stimulation”, “transcranial direct current stimulation”, “transcranial alternating current stimulation”, “transcranial random noise stimulation” and related abbreviations (fMRI, EEG, MEG, TMS, tDCS, tACS, tRNS) were individually combined with insight-related keywords such as “Insight”, “Insight problem solving”, “Insight divergent thinking”, “Divergent thinking”, “Eureka”, “Aha”, “Aha reaction”, “Aha moment”. The searches for methods and research topic were combined with AND operator. References of retrieved studies were examined for relevant publications as well. We intentionally excluded (i) studies including patients with organic illness, (ii) exploring magic ideation, (iii) focusing solely on behavioral data, (iv) review papers, (v) studies not mentioning insight in their abstract unless they used an insight task such as CRA, RAT or

Table 1

ERPs and fMRI studies. A complete list of all publications included in the fMRI and ERPs sections of the paper are displayed. Sample size, the specific task being used and a summary of the main findings are reported. Note: g. = gyrus; HFF condition = heuristic prototypes presented with highlighted functional features labeled above the prototype knowledge; OHFF condition = heuristic prototypes presented without highlighted functional features; SUSL = the base logograph and target logograph share some word; STSL = the base and target logographs do not have any words in common; BSL = the base and target logographs are all simple character-generation tasks; DLPFC = dorso-lateral prefrontal cortex; ACC = anterior cingulate cortex; PCC = posterior cingulate cortex; PFC = prefrontal cortex; RAT = Remote Associates Test; CRA = Compound Remote Associates problems (see Tables S1 and S2 for further details about experimental protocols).

Authors	Sample size (mean age, years)	Method	Task	Main results
fMRI studies				
1 Aziz-Zadeh et al., 2009	12 (26)	fMRI	Anagrams	Bilateral insula, Broca's area, right ventral prefrontal cortex, anterior cingulate cortex
2 Dandan et al., 2013	16 (22.38)	fMRI	Technical problems with prototypes	Left dorsolateral prefrontal gyrus, left angular gyrus (more significantly activated when presented with related prototypes than with unrelated prototypes)
3 Hao et al., 2013	17 (22.1)	fMRI	Learning prototypes-solving problems	Middle temporal gyrus, middle occipital gyrus (more activated under the HFF condition compared with the OHFF condition)
4 Jung-Beeman et al., 2004	13 (18–29)	fMRI	CRA	Increased activity in right hemisphere anterior superior temporal gyrus (RH aSTG), left medial frontal gyrus, left posterior cingulate, bilateral amygdala or parahippocampal gyrus
5 Luo and Niki, 2003a	7 (20–22)	fMRI	Riddles	Bilateral superior frontal gyrus, bilateral middle frontal gyrus, left anterior cingulate cortex, right precentral gyrus, bilateral inferior frontal gyrus, right cingulate gyrus, bilateral superior temporal gyrus, right hippocampus, right subgyral, left caudate, left inferior temporal gyrus, left inferior parietal lobule, left superior parietal lobule, right precuneus, bilateral occipital lobe (activations shown for the presentation of the correct answer)
6 Luo, Niki and Phillips, 2004a	13 (26.7)	fMRI	Ambiguous sentences	ACC, left lateral PFC, bilateral cingulate gyrus, left insula, inferior frontal gyrus, left middle frontal gyrus, left precuneus, left superior, frontal gyrus, left sub-gyral, left inferior temporal gyrus
7 Luo, Niki, and Phillips, 2004b	21 (21–35)	fMRI	Chinese puzzles	(i) Vs the resting baseline, solving of "cerebral gymnastics" puzzles (condition A): anterior cingulate gyrus, medial frontal gyrus, bilateral inferior frontal gyrus, right precentral gyrus, left postcentral gyrus, right superior, inferior temporal gyrus, left middle temporal gyrus, left inferior parietal lobule, left thalamus, left red nucleus, right medial globus pallidus, left angular gyrus, left precuneus; (ii) vs the resting baseline, solving of "homophone" puzzles (condition B): bilateral inferior frontal gyrus, bilateral insula, left anterior cingulate gyrus, left inferior parietal lobule, left supramarginal gyrus, left angular gyrus, left and right red nucleus, left precuneus
8 Luo et al., 2013	30 (23.5)	fMRI	Heuristics prototypes and relative problems	(i) NSI (new scientific innovations) – OSI (old scientific innovation): lingual gyrus; OSI – NSI: right middle temporal gyrus, left medial frontal gyrus, left posterior cingulate gyrus, right thalamus, left superior temporal gyrus; (ii) NSI – OSI: left precuneus, lingual gyrus; OSI – NSI: right medial frontal gyrus, right medial frontal gyrus, left inferior frontal gyrus, left middle temporal gyrus, left superior-parietal lobule, right supramarginal gyrus, right inferior parietal lobule
9 Qiu et al., 2010	16 (22.6)	fMRI	Chinese logographs	Precuneus, left inferior/middle frontal gyrus, inferior occipital gyrus, cerebellum
10 Tian et al., 2011	16 (22.6)	fMRI	Chinese logographs	Left middle/medial frontal gyrus, left middle/superior temporal gyrus, right cerebellum, bilateral claustrum, left postcentral gyrus
11 Vartanian and Goel, 2005	15, (26.5)	fMRI	Anagrams	(i) Unconstrained vs. baseline trials: right ventral lateral PFC, occipital–parietal sulcus, right insula, left occipital gyrus, frontopolar cortex, bilateral superior parietal lobe, post central gyrus, cerebellum; (ii) unconstrained versus semantically constrained trials: right ventral lateral PFC, right superior parietal lobe, occipital–parietal sulcus frontopolar cortex, left superior frontal gyrus, right post central gyrus, cerebellum
12 Wu, Knoblich, and Luo, 2013	14 (19–25)	fMRI	Chinese characters	(i) Familiar (F) vs unfamiliar (U) chunks during tight chunk decomposition: ACC, bilateral inferior frontal gyrus; (ii) F-tight minus U-tight: activation in prefrontal areas; (iii) F-loose minus U-loose: right cingulate cortex, right middle frontal gyrus, right superior frontal gyrus, left superior frontal gyrus, left middle frontal gyrus, left inferior frontal gyrus, left fusiform gyrus
13 Zhao et al., 2013	17 (23.6)	fMRI	Chinese riddles	(i) Insight (I) vs non-insight (NI) in the early period of solution: left superior temporal pole, inferior temporal gyrus, ACC, middle frontal gyrus, right inferior frontal gyrus, parahippocampal gyrus, bilateral gyrus, middle temporal gyrus; (ii) I vs NI in late period: left olfactory, middle frontal gyrus, ACC, medial frontal gyrus, inferior parietal gyrus, right putamen, amygdala, bilateral middle temporal gyrus, hippocampus, angular gyrus; (iii) Timecourse activity: left and right middle temporal gyrus, left ACC, middle frontal gyrus (started at the beginning of the answer presentation and continued until the riddle's solution); left hippocampus and right amygdala (started just before the riddle's solution)
ERPs studies				
1 Lang et al., 2006	26 (24)	ERPs	Number reduction task	Large parietally focused SPW (slow positive wave), frontocentral P3a was larger, anterior N1 amplitudes were larger, P300 complex decreased (solvers vs nonsolvers)
2 Luo et al., 2011	13 (22.4)	ERPs	Chinese logographs	(i) More negative N400 in centro-parietal scalp in STSL respect to SUSL and BSL; (ii) more positive P900–1700 ms in SUSL and STSL respect to BSL; (iii) more negative N1100–1300 over posterior scalp regions in STSL respect to SUSL
3 Mai et al., 2004	14 (22.2)	ERPs	Chinese riddles	More negative N250–500 ms, maximal amplitude was at Cz
4 Qiu et al., 2006	12 (21.4)	ERPs	Chinese logographs	(i) Aha answer (AA)/Uncomprehended answer (UA) vs No-aha answer (NA): more negative ERP deflection (N250 and 400 ms); (ii) AA minus NA and UA minus NA: peak amplitude and latency between 250 and 400 ms at Fz, Cz and Pz sites, maximal amplitude was at Pz, latency was 320 ms (negative component N320 in central posterior region, mainly at right temporal parietal); (iii) difference wave AA – NA: dipole one located near the ACC, dipole 2 located near the thalamus
5 Qiu et al., 2008	18 (22.3)	ERPs	Chinese logographs	More positive P200–600, generator in left superior temporal gyrus and in parieto-temporo-occipital cortex; more negative N1500–2500 in left frontal regions; generator of N1500–2000: ACC, generator

(continued on next page)

Table 1 (continued)

Authors	Sample size (mean age, years)	Method	Task	Main results
6 Shen, Liu, Yuan, Zhang, and Luo, 2013	13 (23–28)	ERPs	Chinese riddle problems	of N2000–2500: PCC PWI (problems with impasses) elicited a greater anterior P2 than POI (problems without impasses), frontocentral P2 emerged earlier in peak latency and was larger in amplitude for PWI, difference wave in the time course of 620–800 ms has seven neural generators, most important was left superior frontal gyrus and near the left cuneus
7 Wang et al., 2009	12 (21.4)	ERPs	Chinese logogriphs	Insight problems vs routine problems: more negative N300–800, more negative N1200–1500 over fronto-central scalp regions, more positive P300–800 and more positive P1200–1500 over parieto-occipital scalp regions; dipoles location: ACC and parahippocampal gyrus for 300 and 800 ms, in parahippocampal gyrus and the superior frontal gyrus for 1200 and 1500 ms
8 Wu et al., 2013	14 (19–25)	ERPs	Chinese characters	the amplitude of the P3a was significantly larger when familiar-tight chunks had to be decomposed than in all other conditions in centro parietal region (P350–650 ms)
9 Xing, Zhang, and Zhang, 2012	12 (23.4)	ERPs	Chinese logogriphs	Insight condition vs non-insight conditions: more negative N300–500 for most of the scalp regions, more positive P600–1100 in frontal, fronto-central and central scalp regions
10 Zhang et al., 2011	12 (22.3)	ERPs	Chinese characters	Insight solutions vs search solution: more positive P400–600, more positive LPC between 640 and 780 ms; in 400–600 ms interval: source on the fusiform gyrus; in 640–780 ms interval: source on right superior temporal gyrus
11 Zhao et al., 2011	13 (21.9)	ERPs	Chinese character-generation task	BMS (breaking mental set condition) respect to REP (repetition condition): more positive P500–700 in centro parietal scalp region, more positive P900–1300 over centro-parietal scalp regions
12 Zhao et al., 2014a	17, (23.3)	ERPs	Chinese riddles	(i) Semantic (SR) and homophonic punny riddles (HR) elicited a lower amplitude vs control condition at center and at centro-parietal regions and a N350–500 over the central scalp; (ii) SR induced a positive deflection over temporal cortex at 400 to 0 ms before riddles were solved; (iii) HR induced a positive deflection over the temporal cortex and a negative one in left frontal cortex

riddles, and (vi) studies not reporting fMRI activations coordinates in MNI or Talairach coordinates space (this criterion was used only for neuroimaging studies). The final selection comprised thirteen studies related to fMRI, one study related to rTMS, twenty studies investigating insight using EEG, four studies related to tDCS (Figs. S1 and S2). Tables 1, 2, S1, S2, S3, and S4 provide an overview of the papers included in the review for each investigated methodology.

3.2. fMRI studies

For each fMRI study, the following information was retrieved: (i) number of subjects, (ii) mean age, (iii) experimental design, (iv) cognitive task details, and (v) main results (Tables 1 and S1). Data about the specific activation foci was also collected and included in a quantitative activation likelihood estimation (ALE) analysis for the identification of the most commonly reported brain regions involved in insight processes. For details about the computation of the ALE meta-analysis maps, see below. Results of the ALE map computation are reported in Fig. 2.

3.2.1. Computation of the ALE meta-analysis maps

The quantitative evaluation of spatial fMRI patterns published about insight was carried out using the ALE technique implemented in the GingerALE software v2.3.2 (www.brainmap.org; Turkeltaub et al., 2012; Eickhoff et al., 2009a; Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012). This method yields a statistical map that indicates the set of brain voxels that are more active than would be expected by chance. Different from within-study statistical parametric mapping analysis, where every voxel in the image space is tested against a null hypothesis of no activation, the ALE method assumes that for each study of interest there is a given spatial distribution of activity and an associated set of maximal coordinates. Therefore, the algorithm tests to what extent the spatial locations of the activation foci correlate across independently conducted fMRI studies investigating the same construct.

Coordinates collected from studies that were reported in Talairach space were converted into MNI space using the “tal2mni” algorithm implemented in GingerALE. First, activation foci from each study were modeled as Gaussian distributions and merged into a single 3D volume. The ALE algorithm modeled the spatial uncertainty (Eickhoff et al., 2009a; Eickhoff et al., 2012) of each activation focus, using an estimation

of the inter-subject and inter-study variability usually observed in neuroimaging experiments, rather than applying an a priori full-width half maximum (FWHM) kernel. Therefore, the number of participants in a given study influenced the spatial extent of the Gaussian function used. GingerALE first modeled the probability of activation over all studies at each spatial point in the brain, returning localized “activation likelihood estimates” or ALE values. As a second step, ALE values were compared to a null distribution created from simulated datasets with randomly placed foci in order to identify significantly activated clusters (1000 permutations). Following Eickhoff and colleagues’ arguments supporting a better balance between sensitivity and specificity for Cluster-based corrections over False-Discovery-Rate (FDR) and Family Wise Error (FWE) ones (Eickhoff et al., 2012), we applied a cluster correction for multiple comparisons with an uncorrected $p < 0.001$ threshold for cluster-formation and a $p < 0.05$ for cluster-level inference. Only clusters with a size exceeding the cluster size recommended by ALE were reported (range in our sample = 250–1000 mm³). Anatomical labels of final cluster locations were provided by the Talairach Daemon (<http://www.talairach.org/daemon.html>) and available as part of the GingerALE output. Entering the insight meta-analysis were thirteen studies with a total of 236 Talairach/MNI coordinates (Table 1). ALE maps were computed for each of the 13 studies, and areas of significant activity along with their Talairach coordinates are reported in Table 3. Given the relatively low number of studies, the results are shown for the average activation map built by averaging activation patterns for different insight tasks (Fig. 2). Each ALE map was visualized using MriCronGL 64 (<http://www.mccauslandcenter.sc.edu/CRNL/tools/>).

3.3. EEG studies

For each EEG study, we retrieved: (i) number of subjects, (ii) mean age, (iii) experimental design, (iv) cognitive task used and (v) main results regarding brain oscillations (changes in topography and power/coherence) and ERPs (changes in power; Tables 1, 2, S2 and S3). Moreover, studies showing correlations between spontaneous brain functioning and insight abilities were analyzed as well. Given the impossibility to run a quantitative analysis of published EEG results about spectral power or coherence, EEG evidence has been collected, discussed and summarized by the authors as shown in Figs. 3, 4 and 5.

Table 2

NiBS and brain oscillations studies. A complete list of all publications included in the NiBS and brain oscillations sections of the paper are displayed. Sample size, the specific task being used and a summary of the main findings are reported (see Tables S3 and S4 for further protocols' details). Note: Δ = delta activity; α = alpha activity; θ = theta activity; β = beta activity; γ = gamma activity; ERS = event-related synchronization for higher task-related power compared to the baseline (see Figs. 4 and 5 for the specific oscillatory frequencies); DLPFC = dorso-lateral prefrontal cortex; ATL = anterior superior temporal lobe; tDCS = transcranial Direct Current Stimulation; rTMS = repetitive Transcranial Magnetic Stimulation; RAT = Remote Associates Test; CRA = Compound Remote Associates problems.

Authors	Sample size (mean age, years)	Method	Task	Main results
Brain oscillations studies				
1 Danko et al., 2003	30 students	EEG	RAT (variation)	Higher EEG spectral power of the Δ and θ bands in the right anterotemporal area; higher power of Δ band in the left anterotemporal area; coherence in Δ , θ , $\alpha 1$, $\alpha 2$, and $\beta 1$ frequency bands lower in right prefrontal–left anterotemporal electrodes; in the Δ , θ , $\alpha 1$, and $\alpha 2$ bands coherence lower in left frontal–right anterotemporal areas; for Δ , θ , and $\alpha 1$ bands lower in left prefrontal–right anterotemporal lobes
2 Jung-Beeman et al., 2004	19 (18–29)	EEG	CRA	Sudden burst of γ band in anterior right temporal electrodes, α band activity over right posterior parietal cortex (i) Sustained power decrease in α and β bands after stimulus onset in all 3 conditions (NN: no-recognition + no recognition; NR: no-recognition + recognition; RR: recognition + recognition); (ii) larger β power decreases in NR minus NN for centro temporal cluster (source in temporal, parietal, subcortical regions) and in the NR – RR for parietal cluster, (sources in parietal regions and in subcortical regions); (iii) γ band: significant cluster in frontal regions in NR vs RR; (iv) NR vs NN and NR vs RR overlapped in medial parietal cortex, mainly precuneus
3 Minami et al., 2014	13 (24.6)	EEG	Binarized images	Widespread enhancement of power and coherence in the $\beta 2$, the $\theta 1$ power increase in frontal cortex; increased desynchronization of the $\alpha 1$, $\alpha 2$ mainly over posterior cortex; $\alpha 1$ coherence decrease in prefrontal sites; originality scores of the verbal associate: increase of $\alpha 1$ coherence focused in fronto-parietal regions of both hemispheres in the $\beta 2$ and in left parieto-temporal loci
4 Razumnikova, 2007	39 (17–20)	EEG	RAT	Strong γ band responses at parieto-occipital regions and later θ frequency band cluster; strong upper α ERS in right temporal regions; decreased α power in right prefrontal cortex
5 Sandkühler and Bhattacharya, 2008	21 (26.4)	EEG	CRA	Reduction in β power over the parieto-occipital and centro-temporal regions on all four conditions: correct vs. incorrect solutions, solutions without vs. with external hint, successful vs. unsuccessful utilization of the external hint, and self-reported high vs. low insight. “Aha!” versus “non-Aha!”: reduction in power in β frequency band in central-parietal regions, increased power in lower α frequency band (difference was significant over the right frontal region in γ frequency band)
6 Sheth et al., 2009	18 (21.2)	EEG	Brainteasers	(i) Insight preparation: greater neural activity (less α) over mid-frontal, left temporal, right temporal, right inferior frontal, and bilateral somatosensory cortex; (ii) noninsight preparation: less α power than insight preparation in occipital cortex
7 Kounios et al., 2006	19	Mental preparation-EEG	CRA	Low Insight (LI) group had more high α than the High Insight (HI) group over occipital cortex. HI showed: (i) HI subjects showed less $\beta 1$ EEG power over occipital midline (EC); (ii) EO: less occipital $\beta 1$ power with a broader distribution; (iii) greater low α power at left inferior–frontal and anterior–temporal sites, less power in right dorsal–frontal region; (iv) greater $\beta 2$ power at right inferior–frontal and anterior–temporal sites, less $\beta 2$ power in left occipital and parietal sites; (v) EC: greater $\beta 3$ power at right frontal–temporal sites and less power at left parietal sites, EO: greater $\beta 3$ power at right parietal and temporal–occipital electrodes; (vi) EC: greater γ power at right inferior–frontal and left temporal electrodes and less power for HI subjects in right inferior–parietal sites; EO: more γ band power at right-parietal electrodes and a weaker left-parietal area
8 Kounios et al., 2008	26 (22)	Resting-state-EEG	Anagrams	
NiBS studies				
1 Cerruti and Schlaug, 2009	(i):18 (25.5) (ii): 12 (25.4)	tDCS	RAT	(i) Increase in performance after anodal tDCS on left DLPFC (F3) vs sham and cathodal stimulation; (ii) F3 anodal stimulation produced a significant effect on RAT; right DLPFC stimulation did not
2 Chi and Snyder, 2011	60 (22)	tDCS	Matchstick arithmetic problem	(i) 60% of participants solved matchstick with anodal tDCS (right ATL); (ii) 20% of participants did so with sham stimulation; (iii) opposite polarities did not facilitate performance
3 Chi and Snyder, 2012	22 (19–63)	tDCS	Nine-dot problem	(i) 0/11 participants with sham stimulation solved the task; (ii) 5/11 participants solved it with anodal tDCS on right ATL; (iii) opposite polarities of stimulation did not affect performance
4 Metuki et al., 2012	21 (23.1)	tDCS	CRA	Anodal tDCS (left DLPFC) enhanced solution recognition for difficult trials, larger effect for participants with lower approach motivation
5 Giovannelli et al., 2010	33 (24.2)	rTMS	Binarized images	(i) 10 Hz rTMS delivered at the same time of undegraded images' presentation on right and left intraparietal sulcus reduced the percentage of binarized images correctly identified after learning phase (30'); (ii) no effect with rTMS delivered 2 s after undegraded images' presentation

3.4. Non-invasive brain stimulation studies

For each tES study, we retrieved: (i) number of subjects, (ii) mean age, (iii) experimental design, (iv) tES montage (target and reference electrodes' positions, online/offline stimulation), (v) type of cognitive task being modulated, and (vi) main results (Tables 2 and S4). For rTMS literature, we extracted: (i) number of subjects, (ii) mean age, (iii) experimental design, (iv) TMS setup (Sham method, stimulation site), (v) task specifics, and (vi) main results. Results of the literature

search and a summary of main findings regarding NiBS are reported in Fig. 6.

4. Results

4.1. Insight-related fMRI activations

The results highlight a complex network composed of the anterior cingulate cortex (ACC), prefrontal and parietal lobes, claustrum,

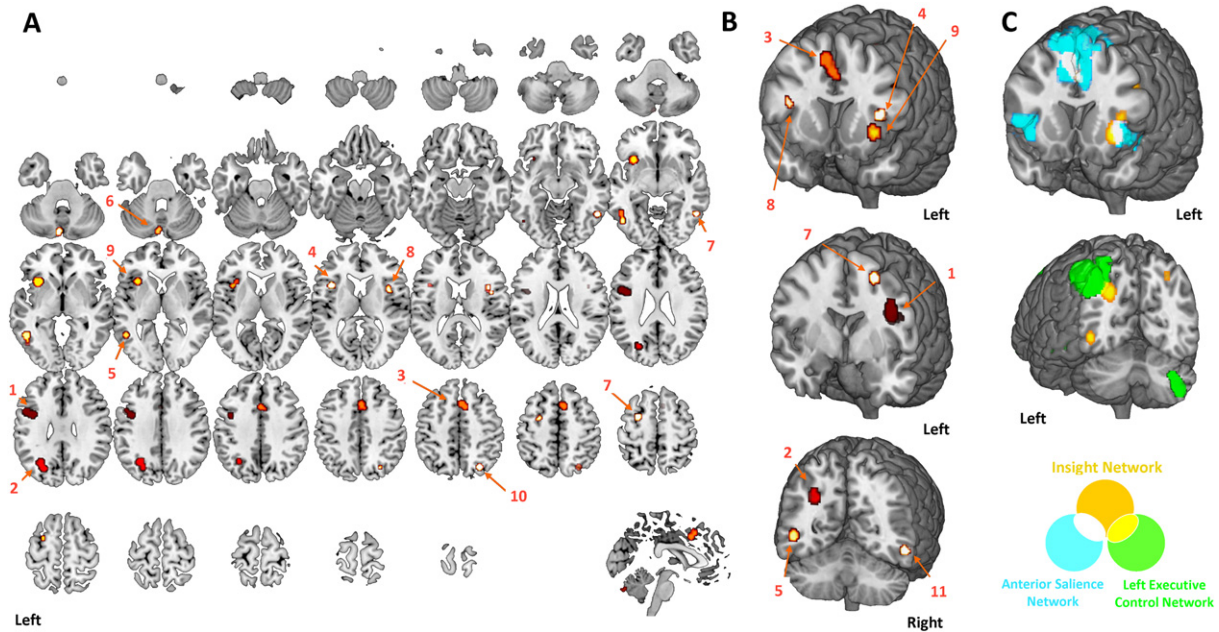


Fig. 2. Insight-related fMRI activations. The results of cluster-based statistics performed on the studies retrieved using the keywords specified in the supplementary methods section of the paper are displayed. The map refers to studies assessing insight problem-solving without any discrimination for trial or task types. Shown in both axial (A) and coronal 3D (B) views, it is therefore a non-specific, global representation of insight-related cognitive processing in the brain. The quantitative meta-analysis highlighted a network of brain regions consisting in: 1 = left premotor/supplementary motor area, 2 = left middle temporal gyrus and precuneus, 3 = right superior frontal gyrus and left cingulate gyrus, 4 = left claustrum, 5 = left middle temporal and occipital gyri, 6 = uvula (cerebellum), 7 = left precentral gyrus/frontal eye fields, 8 = right insula, 9 = left insula, 10 = right precuneus, 11 = right middle temporal gyrus, (uncorrected $p < 0.001$ threshold for cluster-formation, corrected $p < 0.05$ for cluster-level inference, threshold for cluster size = 250 mm^3). Given the functional roles commonly reported for these regions, mostly involved in executive functions and abstract reasoning processes, a qualitative analysis of the overlap with resting-state fMRI networks has been completed (C), resulting in major similarities between the “insight network” and the anterior salience and the left executive functions networks. A complete set of coordinates for each cluster is available in Table 3. Both weighted binary and cluster-based versions of the meta-analysis map are available for download as nifti “.nii” volumetric files at <http://www.tmslab.org/santalab.php>.

temporo-occipital regions, middle temporal gyrus and insula (Fig. 2A & B, Table 3). Surprisingly, the majority of activations are localized in left hemisphere. More in detail they are: precentral gyrus, middle temporal gyrus, precuneus, cingulate gyrus, claustrum, middle occipital gyrus, uvula (inferior vermis - cerebellum) and insula. As right activations, the map shows: superior frontal gyrus, insula, precuneus and middle temporal gyrus. Many insight regions are part also of other networks, as left executive functions network and creativity (see Fig. 2 and Discussion section). The ALE meta-analysis map is available for download as a nifti “.nii” volumetric file at <http://www.tmslab.org/ESantarn>. Files include a weighted map of the entire network, cluster-based

parcellation of the insight network in 11 functional nodes that can be used as separate ROIs for volumetric and functional connectivity analysis, and an excel spreadsheet reporting coordinates for each cluster as well as size and anatomical labels.

4.2. Insight-related ERPs

ERPs findings show a bilateral network, ranging from frontal lobe to the occipital pole (see Fig. 3). Most studies report widespread increased amplitudes of early positive and negative peaks resembling the P300 and N400 component (latency ranges 200–800 and 250–800

Table 3

Results of ALE Meta-analysis. The results of cluster-based statistics performed on studies retrieved using the keywords specified in the supplementary methods section of the paper. Volume; coordinates and local maxima for each cluster; as well as labels based on the Brodmann atlas and anatomical localization at cortical and subcortical level (lobe/gyrus/region) are provided (uncorrected $p < 0.001$ threshold for cluster-formation; corrected $p < 0.05$ for cluster-level inference; threshold for cluster size = 250 mm^3).

Cluster number	Volume (mm^3)	Weighted center			Extrema value and localization			Brodmann area	Hemisphere	Lobe	Gyrus/region
		x	y	z	x	y	z				
1	2112	-44.58	3.96	29.38	0.0202	-42	2	28	Left	Frontal	Premotor/supplementary motor area
					0.0190	-50	6	28			
2	1728	-28.52	-65.42	31.45	0.0193	-30	-62	32	Left	Temporal	Middle temporal gyrus
					0.0175	-26	-70	30			
3	1608	3.59	14.64	45.72	0.0195	6	14	50	Right	Frontal	Superior frontal gyrus
					0.0145	0	12	40			
4	1384	-33.41	17.68	-2.27	0.0281	-34	18	-2	Left	Sublobar	Claustrum
					0.0155	-48	-66	-6			
5	976	-49.05	-58.3	-3.19	0.0189	-50	-56	-2	Left	Temporal	Middle temporal gyrus
					0.0155	-48	-66	-6			
6	440	-5.33	-79.75	-32.55	0.0165	-6	-80	-32	Left	Cerebellum	Uvula
					0.0155	-26	0	56			
7	440	-27.08	-0.93	55.99	0.0124	38	8	14	Right	Subcortical	Insula
					0.0111	44	2	16			
8	368	39.29	7.35	13.77	0.0146	-38	12	10	Left	Subcortical	Insula
					0.0147	26	-70	48			
9	328	-39.29	12.46	10.63	0.0141	52	-56	-10	Right	Temporal	Middle temporal gyrus
					0.0141	52	-56	-10			

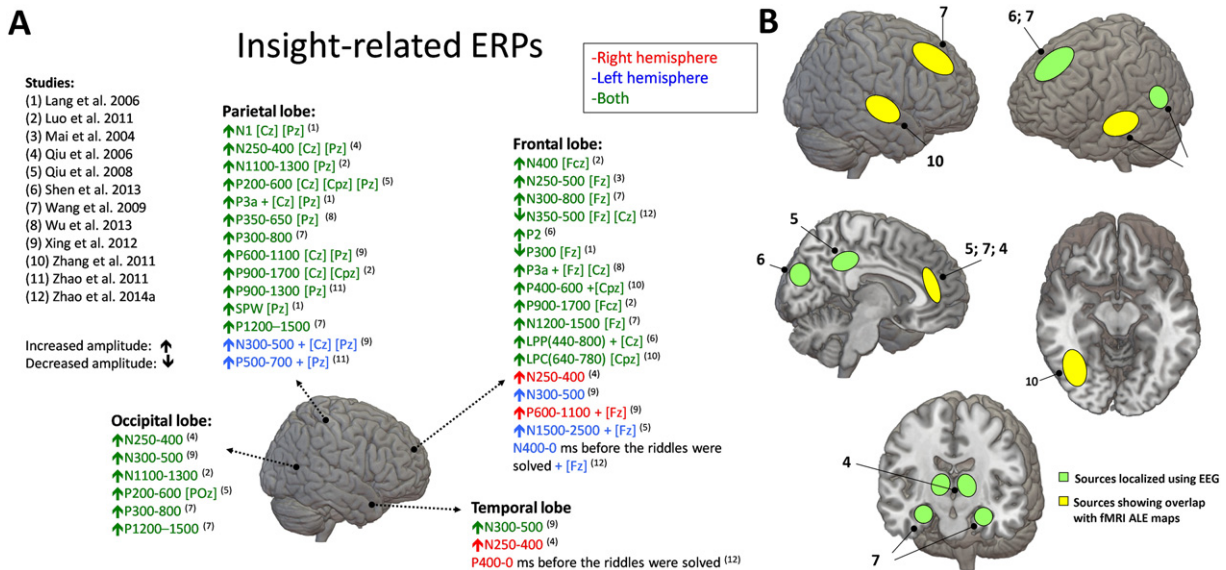


Fig. 3. Insight-related ERPs. (A) Results of the review of ERPs detected during insight problem-solving (mostly using Chinese tasks, for details see Table 1 and S2), using color-coding for activity localized on the right or left hemisphere for each lobe, or both. The activity in each time window is expressed as follow: an “increase” in a specific ERP refers to a bigger response going in the direction of the ERP, which means an increased N400 (↑ N400) represents a more negative N400, while a decreased P300 (↓ P300) means a less positive P300. (B) Anatomical mapping of electric sources identified in various studies are reported (i.e. using LORETA or similar approaches), with yellow markers also highlighting sources roughly overlapping with regions identified in the ALE fMRI map shown in. Note: LORETA = Low Resolution Tomography Analysis.

respectively). Later positive and negative components are displayed, as N1200–1500, in frontal, parietal and occipital lobes and P1200–1500 in parietal and occipital regions.

4.3. Brain oscillations during insight

During insight problem-solving, a consistent decrease of α power in the right hemisphere and of coherence (bilaterally) is observed in the frontal lobe (Fig. 4; Sandkühler & Bhattacharya, 2008; Danko,

Starchenko, & Bechtereva, 2003; Razumnikova, 2007). These experiments used very similar tasks to assess insight (i.e. RAT and CRA) so the concordance of their results is not surprising; nevertheless, the experimental protocols were not identical. Danko created a new version of RAT in which subjects had to find a link between 12 words from different semantic fields; in Sandkühler et al., participants were given 45 s to solve CRA problems and an additional clue was provided if they were not able to solve the trials. Finally, Razumnikova’s protocol followed the canonical use of RAT problems, with participants solving each item with

Brain Oscillations during Insight

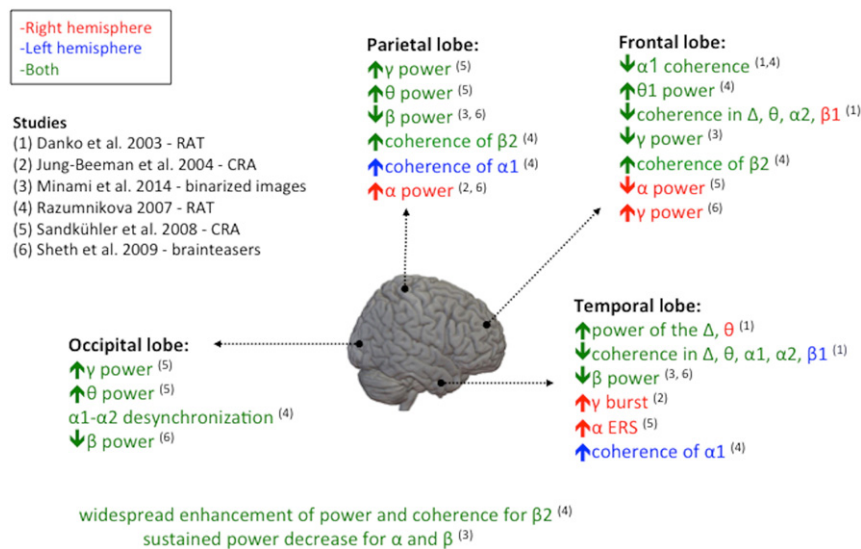


Fig. 4. Brain Oscillation during Insight. Results of the review of brain oscillatory activity recorded during insight problem-solving. Color-code indicates hemispheric distribution. Details about the specific publications evaluated are also reported. Note: Δ = delta activity between 1.5 and 3.5 Hz; $\alpha 1$ = alpha activity between 7.5 and 9.5 Hz in (1) and between 8 and 10 Hz in (4); $\alpha 2$ = alpha activity between 10 and 12.5 Hz in (1) and between 10 and 13 Hz in (4); $\theta 1$ = theta activity between 4 and 6 Hz in (4); $\beta 1$ = beta activity between 13 and 18 Hz in (1) and between 13 and 20 Hz in (4); $\beta 2$ = beta activity between 18.5 and 30 Hz in (1) and between 20 and 30 Hz in (4); γ = gamma activity above 35 Hz up to 70 Hz; ERS: event-related synchronization for task-related power compared to the baseline (5).

Brain Oscillations during Mental Preparation and Resting-State Activity

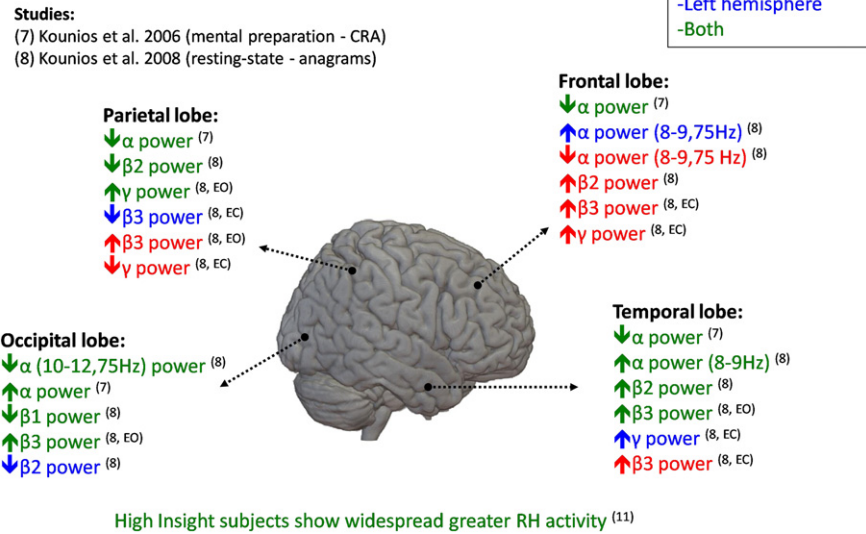


Fig. 5. Brain Oscillations during Mental Preparation and Resting-State Activity. Brain oscillatory activity detected right before an insight solution or during spontaneous resting-state is displayed. Color-code indicates hemispheric distribution for each lobe. Details of the specific publications being evaluated are also reported. Note: EO = eyes open, EC = eyes-closed; α = alpha; θ = theta; β_1 = beta activity between 13.00 and 17.75 Hz; β_2 = beta activity between 18.00 and 24.75 Hz; β_3 = beta activity between 25.00 and 29.75 Hz; γ = gamma.

no time limit (for further details see Tables 2 and S3). We must note that α activity seems to be important also for creativity, however in the opposite way: transcranial alternating current stimulation (tACS) in the α band (i.e. 10 Hz) delivered over bilateral prefrontal lobes during the Torrance Creativity Test improves creativity score, suggesting a beneficial role for α oscillations (Lustenberger, Boyle, Foulser, Mellin, & Frohlich, 2015). While suggests a differential contribution of α activity for insight and creativity, it should be noted that the tasks used are very different.

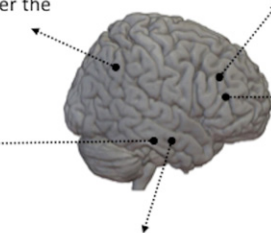
The α insight pattern is usually accompanied by an opposing pattern in the β range (i.e. bilateral increase of coherence, Razumnikova, 2007) as well as by a bilateral increase in θ power (Razumnikova, 2007). Conversely, results about γ activity in the frontal lobe are characterized by an increase of γ activity in the frontal lobe (Sheth et al., 2009) but a bilateral decrease is also reported in a different study (Minami, Noritake, & Nakauchi, 2014). However, we had to highlight that the protocol and the stimuli used in these two studies are very different: for example, Minami et al. analyzed the “perceptual insight”

tDCS:
-anodal
-cathodal

NiBS and Insight

10 Hz rTMS right lateral/left lateral Parietal Cortex (vs sham, baseline and over the vertex): reduced mean percentage of **binarized images** correctly identified 30 min after the learning phase (Giovannelli et al. 2010)

Left ATL - Right ATL: 60% of participants solved **matchstick problems**, only 20% of them did it with sham stimulation (Chi and Snyder 2011)



1) **Left ATL - Right ATL:** 5/11 pt solved the **Nine-dot problem** (vs 0/11 with sham)
 2) **Left ATL - Right ATL:** did not affect performance (Chi and Snyder 2012)

Left DLPFC - reference in right orbitofrontal cortex: enhanced solution recognition for difficult **CRA problems** (vs sham) (Metuki et al. 2012)

1) **left DLPFC vs left DLPFC vs sham:** increase in **RAT score** after **left DLPFC**;
 2) **left DLPFC vs right DLPFC vs sham** in both of them: **left DLPFC** stimulation produced a significant effect on **RAT score** (reference electrode over the contralateral supraorbital region) (Cerruti et al. 2009)

Fig. 6. Non-Invasive Brain Stimulation and Insight. Results of the qualitative analysis of tDCS and rTMS (rTMS-10 Hz: excitatory effect) evidence when stimulation was applied during insight problem solving. Color-code indicates polarity of tDCS arranged by site of application. “Sham” stimulation refers to “placebo” stimulation.

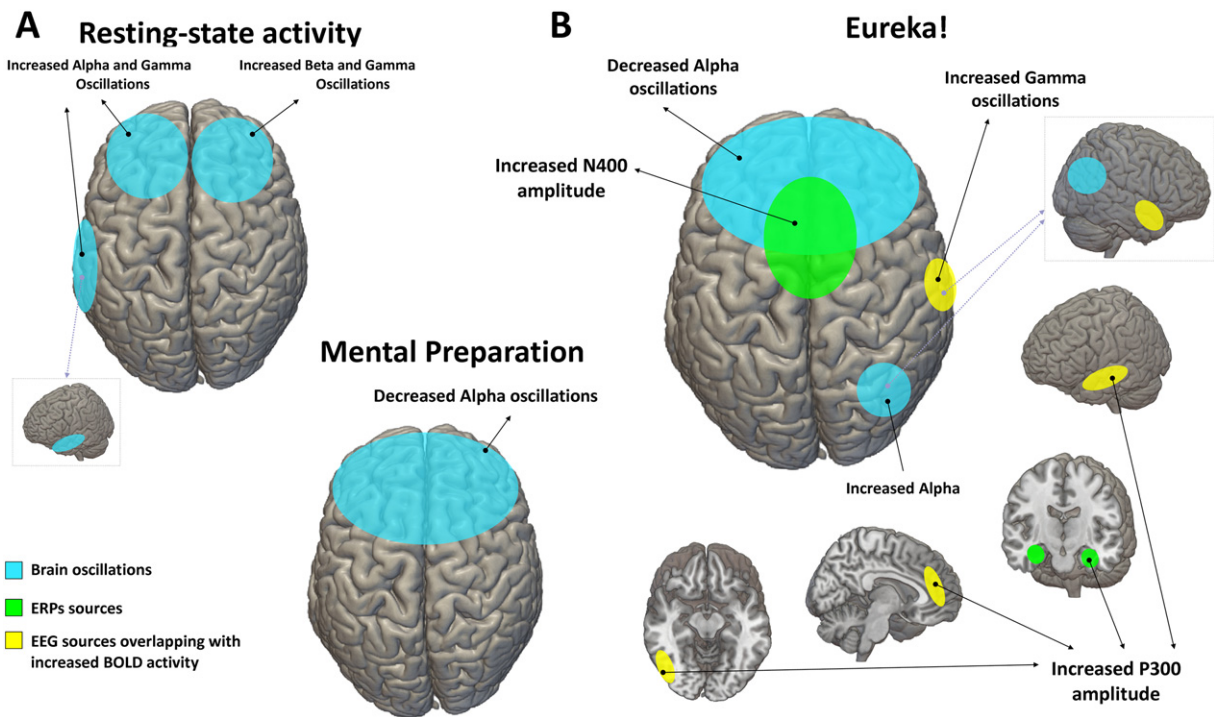


Fig. 7. Correlates of the Insightful Mind. The most widely reported correlates of *Aha!* Moments are summarized, with different sets of results for experimental findings related to (A) the resting-state brain activity and the mental preparation phase preceding insight-related answers, as well as (B) evoked activity during actual *Eureka* moments. Results are color-coded accordingly to electrophysiological correlates related to brain oscillations, event related potentials and the overlap between EEG and fMRI patterns highlighted at the ALE meta-analysis.

using the binarized images, on contrary Sheth et al. administered brain-teasers to participants (for further protocol's details see Table S3). Overall, these activation patterns suggest a bilateral pattern with a right-lateralization only somewhat clearly present for α power.

Regarding the parietal lobe, an increase in power for almost all the frequency bands (i.e. α , θ and γ ; Jung-Beeman et al., 2004; Sheth et al., 2009; Sandkühler & Bhattacharya, 2008), and in coherence for $\alpha 1$ (7, 5–9, 5 Hz) and $\beta 2$ (18–24.75 Hz) bands, is reported (Razumnikova, 2007). As observed for the frontal lobe, a bilateral pattern seems to define insight processes, with an exception for a right-lateralized increase in α power as the only evidence supporting the idea of right-hemispheric dominance (the increase in α coherence is indeed restricted to the left hemisphere; Razumnikova, 2007; Fig. 4).

The temporal lobe shows less consistent results, with studies demonstrating different oscillatory activity including a burst of γ activity (Jung-Beeman et al., 2004) and an increase of θ power in the right hemisphere (Danko et al., 2003), as well as a bilateral decrease in Δ 1.5–3.5 Hz, θ , α and β coherence (Danko et al., 2003). Overall, these activations seem to be more lateralized, with a dominance of the right hemisphere, especially in the γ band (Fig. 4).

Finally, occipital lobe activations are completely bilateral but studies are not consistent across the results provided. One study reports an increase in θ and γ power (Sandkühler & Bhattacharya, 2008), while others report α desynchronization and a decrease in β power (Sheth et al., 2009; Razumnikova, 2007; Fig. 4). Nonetheless, different protocols and tasks could be considered responsible of these varying results. In fact, only two studies (Jung-Beeman et al., 2004; Razumnikova, 2007) created a simple protocol in which subjects had to solve insight problems without hints, through using RAT and CRA, with and without time limits, respectively (Table S3).

4.4. Brain oscillations during mental preparation and resting-state activity

We found only two studies on mental preparation and resting-state activity, both analyzing the performance in two verbal tasks: CRA and

anagrams (Kounios et al., 2006; Kounios et al., 2008; Fig. 5). The study on mental preparation (Kounios et al., 2006) focused on the stream of brain activity occurring while the subjects elaborated about available information prior to an actual insight event (*pre-Aha!*). They reported a decrease of α power in frontal, parietal and temporal areas. These regions, traditionally associated with cognitive control and semantic processing, suggest that such oscillatory patterns could be a sign of increased activity in regions related to semantic activation (Mashal et al., 2005; Mason & Just, 2004). Additionally, the occipital cortex presents an increase of α power, which could indicate a removal of focused attention on external stimuli and an increase in more introspective mental processes that aid the “insightful subject” in finding the most distant association between the stimuli at hand.

Intriguingly, oscillatory activities observed during mental preparation are in contrast with the resting-state results shown by Kounios et al. (2008). Here, better insight skills seem to correlate with an increase of α power in left frontal and bilateral temporal lobes, as well as with its decrease in the bilateral occipital cortex (Fig. 5, Tables 2, and S3). As for the rest of the frequency spectrum, a lateralized pattern appears in the frontal lobe, with the enhancement of γ and β power revealed only in the right hemisphere. With all the limitations of an observation based on two samples, it seems intuitive that the oscillatory pattern found during mental preparation is very different (almost the opposite) from the resting-state activity of insightful subjects.

4.5. NiBS and insight

Only five papers examined the application of TMS or tDCS, with variability in the type of insight task and stimulation sites (Fig. 6, Tables 2 and S4). The first study used tDCS over the prefrontal cortex to enhance insight problem-solving (Cerruti & Schlaug, 2009). In this experiment, the authors demonstrated that anodal stimulation over the left dorsolateral prefrontal cortex (DLPFC) increased RAT scores in contrast to cathodal or sham tDCS over the same site, which showed no effects on performance (anodal is supposed to induce an excitatory effect while

cathodal leads to an inhibitory one, sham refers to placebo stimulation). In a second experiment, the authors tested the effect of anodal tDCS on the right DLPFC, confirming the improvement in test scores after stimulation of left prefrontal cortex (in both experiments the return electrode was placed over the contralateral supraorbital region; Cerruti & Schlaug, 2009). In another study by Metuki and colleagues (Metuki, Sela, & Lavidor, 2012), anodal tDCS over the left prefrontal cortex enhanced CRA performance compared to sham stimulation (with cathode over the right orbitofrontal cortex). However, this study did not follow the standard CRA procedure. In fact, participants were asked whether a presented word was the correct solution for the trial at hand. This might constitute a significant deviation from the canonical assessment of insight through CRA problems, therefore these results must be considered carefully.

As for those papers showing effects during tES over the temporal lobe, the same montage was applied with anodal and cathodal stimulation respectively targeting the right and left anterior temporal lobe (Fig. 6; Chi & Snyder, 2012; Chi & Snyder, 2011). Even though insight was indexed by means of two different tasks (i.e. nine-dot and matchstick problems), both studies reported an increase in performance during anodal stimulation over the right hemisphere compared to sham stimulation or to the reverse electrical pattern (anode on the left temporal lobe, cathode on the right temporal lobe). Importantly, the nine-dot problem is a single trial task with consequently important limitations in the terms of results reliability: while none of participants solved the nine-dot problem during sham stimulation, 40% of them correctly solved the task within the 3 min of tDCS or immediately after (Chi & Snyder, 2012). While these results are promising, single trial tasks should be avoided during the assessment of complex cognitive functions such as insight, in favor of more reliable and reproducible tools, e.g. the RAT or CRA.

Along the same line, the authors presented another study involving matchstick problems where only the 20% of participants solved the hardest trials (i.e. type 2) during sham tDCS, while the percentage of success reached 60% during tDCS stimulation (Chi & Snyder, 2011). The same pattern was reported for easier trials (type 3), where the percentage increased from 45% during sham tDCS to 85% during anodal tDCS over the right temporal lobe.

Finally, we retrieved one study about rTMS and insight, evaluating the perceptual recognition of degraded images as a measure of insight-perceptual ability (Fig. 6, Tables 2 and S4). Repetitive TMS at 10 Hz (known to induce an excitatory effect, Tang et al., 2015) was applied over the vertex as well as over the right and left lateral parietal cortices in three separate sessions. Results showed that right and left intraparietal sulcus stimulation delivered during stimulus presentation reduced the percentage of binarized images (i.e. two-tone picture, black and white) correctly recognized 30 min after the learning phase. Even though it was a single observation, this data does not support the idea of a dominant role for left or right parietal cortex in *Eureka*-related processes. In line with the EEG findings, the nature of the stimuli supports both parietal lobes as a crucial hub of the perceptual-insight processing, especially during the consolidation phase, given that rTMS showed no effect on recognition of degraded images when applied 2 s after stimulus presentation.

5. Discussion

A systematic review of the available fMRI, EEG and NiBS literature of insight has been provided, in an effort to integrate what is currently available about the neurophysiological basis of the *Eureka* moment. A complex yet fascinating picture arises, with several models and theories gaining support from experimental evidence, while other facets of insight still remain obscure. Given the relevance of the insight process in everyday life as well as in technological achievements and human progress in general, it is of absolute importance to deepen our knowledge of this pivotal feature of human cognition. This is a pre-requisite to inform

potential interventions aimed at enhancing such a capability by means of NiBS. A discussion of the main findings highlighted during the review process will follow (see Fig. 7 for a summary), pointing out those considered as the most relevant features of insight in humans.

5.1. The insight network

Examining the regions active during insight processes reveals a degree of overlap with other brain regions underlying divergent (e.g. creativity) and convergent thinking abilities (e.g. fluid intelligence, executive functions, Fig. 2). Firstly, activity in the middle frontal gyrus (MFG), inferior frontal gyrus (IFG) and ACC has been repeatedly associated with memory, attention, inhibition, switching, language (Benn et al., 2014; Colom, Jung, & Haier, 2007; Roth, Serences, & Courtney, 2006; Yin et al., 2012), general cognitive control (Miller & Cohen, 2001) and creativity (Boccia, Piccardi, Palermo, Nori, & Palmiero, 2015). Furthermore, the dorso-lateral prefrontal cortex (DLPFC) has been linked to problem-solving tasks exploiting analogous relationships (Borojerd et al., 2001; Wharton et al., 2000) and relational complexity (Kroger et al., 2002). The same regions were found activated also during creativity tasks (Boccia et al., 2015), suggesting a common substrate for executive functions in either creative or insight problem-solving processes (i.e. top-down control of attention and cognition; Beaty, Benedek, Kaufman, & Silvia, 2015), rather than representing a specific network for these two processes.

The same applies to temporo-occipital regions and to the middle temporal gyrus, often reported in studies investigating embodied perspective taking (Wang, Callaghan, Gooding-Williams, McAllister, & Kessler, 2016), language and memory (Bogels, Barr, Garrod, & Kessler, 2015), mental imagery (Kosslyn & Thompson, 2003), as well as creativity (Boccia et al., 2015), all functions in which long-term memory might play a relevant role in restructuring available information (Fink et al., 2012). As for the overlap with creativity, the right fusiform gyrus was found selectively activated during musical improvisation tasks (Boccia et al., 2015), in line with the evidence of its role in non-verbal test of associative semantic knowledge (Mion et al., 2010). Additionally, the left supplementary motor area/frontal eye fields seem to represent a common area for insight and creativity networks. This is not surprising, considering its anatomical connection of the DLPFC and visual cortices, in the frame of its possible role in the visually guided behavior (Wright & Lawrence, 2008). In addition, there is evidence for its implication in the control of spatial attention (Moore & Fallah, 2004), top-down control of visual areas, as well as of many aspects of visual cognition (Vernet, Quentin, Chanes, Mitsumasa, & Valero-Cabre, 2014), all essential operations required for the internal search of a creative solution or insight moment.

As reported in Fig. 2, many areas are shared with the salience network, such as the middle temporal gyrus, the claustrum, and the precentral gyrus. The salience network is important for reallocating attentional resources in relation to external inputs and internal brain events (Bressler & Menon, 2010) and it seems involved in dynamic switching between the default mode network and the executive control network (Sridharan, Levitin, & Menon, 2008). Considering the involvement of all these networks in creativity and insight moments, salience regions could be fundamental to permit a dynamic switching between opposite networks during these cognitive processes (Beaty et al., 2015).

Brain imaging and electrophysiological studies have suggested the insula as a key node for interoception, as well as bodily and emotional awareness (Craig, 2009), due to its extensive visceral-sensory inputs from the periphery and reciprocal connections with limbic, somatosensory, prefrontal and temporal cortices (Augustine, 1996; Mesulam & Mufson, 1982). The insula has been specifically linked to the monitoring of visceral functions of the body, and its possible role in interoception offers a possible basis for its involvement in all subjective feelings (Nieuwenhuys, 2012), with recent evidence also showing structural changes after interventions aimed at increasing self-awareness

(Santarnecchi et al., 2014). It is possible that insight (and creativity, see Boccia et al., 2015) processing implies a balancing of externally and internally driven brain states, making the insula a key node for the modulation (i.e. suppression) of bodily sensation in favor of a more thought-centered monitoring. On the other hand, insula was linked to many stages of language comprehension/production (Ackermann & Riecker, 2004; Blank, Scott, Murphy, Warburton, & Wise, 2002; Eickhoff, Heim, Zilles, & Amunts, 2009b; Oh, Duerden, & Pang, 2014), as articulatory planning and phonological recognition (Ardila, Bernal, & Rosselli, 2014). In particular, anagrams were found to elicit a bilateral (Aziz-Zadeh et al., 2009) and right lateralized (Vartanian & Goel, 2005) insula activation. Curiously, analytical solutions elicited only a left activation (Aziz-Zadeh et al., 2009), supporting the bilateral involvement of brain's network necessary for insight problem-solving (as theorized by Bowden and Beeman), in which left and right insula cooperate for the linguistic component of solving anagrams. In Vartanian and Goel (2005), the unconstrained trials elicit activation of right insula compared to baseline trials in which the solution is presented to the participants. In addition, Adank (2012) finds insula activations during distorted speech comprehension, which could aid explaining Luo, Niki, and Phillips (2004a) insula activation in response to ambiguous sentences.

The claustrum might constitute an underrated node of the insight network. This subcortical gray matter region, located lateral to the putamen and medial to the insular cortex, is part of the basal ganglia circuitry (Schmitt, Eipert, Kettlitz, Lessmann, & Wree, 2016). The claustrum's activity has been related to attention (deBettencourt, Cohen, Lee, Norman, & Turk-Browne, 2015; Fall, Querne, Le Moing, & Berquin, 2015; Goll, Atlan, & Citri, 2015) and more specifically to interhemispheric communication between attention-related regions (Smith & Alloway, 2014). Little is known about the claustrum's specific functions, with some clinical evidence suggesting a possible role in maintaining consciousness. A recent study documented a case of "on-off" switching of level of consciousness resulting from stimulation of the claustrum in an epileptic patient (Koubeissi, Bartolomei, Beltagy, & Picard, 2014). In the context of insight-related processing, the claustrum could act as a monitoring center for mind-wandering, allowing the subject's mind to drift off during the first reorganization of the available information, letting the correct answer arise from its subconscious representation.

Finally, other regions playing a major role in insight processing are located in the left prefrontal lobe (i.e., IFG and MFG), precuneus and inferior occipital regions (Qiu et al., 2010). Interestingly, a distinction between "preparation" for insight problem-solving and actual insight processing has been proposed (Tian et al., 2011), suggesting a tighter link between the first processing step and IFG-MFG, left temporal lobe and bilateral claustrum activity. This pool of regions has been suggested as a separate network whose activity precedes the activation of structures in the right temporal lobe responsible for the actual *Aha!* experience (Tian et al., 2011; Zhao, Zhou, Xu, Fan, & Han, 2014b). Such hemispheric segregation – or interplay if one looks at the overall process – is the most popular theory on the neural basis of creativity and divergent thinking in general (Beaty et al., 2015; Beeman & Bowden, 2000; Jung-Beeman et al., 2004). Additionally, recent studies suggest a tight link between individual cognitive profile and hemispheric differences in the spontaneous electrical (Gotts et al., 2013) and BOLD-related connectivity patterns (Santarnecchi, Tatti, Rossi, Serino, & Rossi, 2015), suggesting the importance of future investigations aimed at uncovering the relationship between insight and interhemispheric dynamics (see the next paragraph).

As we have highlighted, insight network shared many areas with salience, executive control, fluid intelligence and creativity networks. However, the relative rarity of fMRI studies (thirteen in literature) and the variety of task and protocols used, (Table S1, Fig. 1), limits the validity of these results. More standardized experimental protocols are needed, with a larger sample of fMRI investigations for each type of insight task, in order to reveal the real insight neural substrates and the role of the overlaps with others networks.

5.2. The timing of an insightful solution: event-related potentials during *Eureka!*

As shown in Fig. 3, results are apparently cloudy, showing several short and long-latency components with positive and negative polarities. However, the qualitative analysis suggests a major role for ERP activity involving midline regions in the frontal and parietal lobes, with no standing left or right hemispheric dominance (Fig. 3, Tables 1 and S2). Remarkably, however, ERP data is mostly based on brain activity during the Chinese logogriphs task (Table 1), which could limit the generalization of these results to other insight processes. Here we first discuss the negative components, which are thought to represent (i) cognitive impasse, (ii) the feeling of warmth and creations of new associations, followed by positive components, which are thought to underlie: (i) breaking of mental set and (ii) forming novel associations.

5.2.1. Negative potentials around 400 ms

The most consistent result is a positive correlation between insight problem-solving and an N400-like peak recorded at frontal sites (Fig. 3), with only one study reporting a negative correlation (Zhao, Li, Shang, Zhou, & Han, 2014a). Well-known in the context of semantic information processing, the N400 typically has its maximum amplitude in the centroparietal lobe during the processing of written words and is interpreted as an ERP index of semantic processing and integration of a word in the current context (McPherson & Holcomb, 1999). An increase in the amplitude of N400-like components in insight could therefore reflect a greater effort of the brain in the integration of the stimuli within a given context (Lau, Phillips, & Poeppel, 2008). Other interpretations of this negative potential have been suggested. Mai, Luo, Wu, and Luo (2004) proposed that this negativity (N380 with central focus) might be a marker of breaking the mental set. This interpretation stems from a dipole analysis (Mai et al., 2004), which localized the generator of the N380 wave in the ACC, an area that has been related to N200 and error-related negativity (ERN) components. Although Qiu et al. (2006) found a similar result (Aha-answers elicited a larger N320 component than non-Aha-answers; Qiu et al., 2006), the introduction of another variable (i.e. the comprehension of the correct answer) led to another (more specific) conclusion. The fact that non-comprehended answers also elicited a larger N320 suggests that this component could be a marker of the cognitive conflict that occurs when new ways of thinking are employed to overcome the cognitive impasse.

5.2.2. Later negative components

Moving toward later time windows, deflections with different latencies have also been correlated with insight problem-solving in several studies (Fig. 3). In a pair of studies by Qiu and colleagues using the Chinese logogriphs (Qiu et al., 2008; Wang et al., 2009), late negative deflections in the 1500–2000 ms and 2000–2500 ms latency ranges were related to insight problem-solving. In their first study, these components showed distinct activations over left frontal scalp regions with generators located, respectively, in the ACC and in the posterior cingulate cortex (PCC). The PCC involvement (an area that has been related to the cognitive processing of emotions; Aoki, Cortese, & Tansella, 2015) is interesting because it could be a marker of the feeling of warmth that follows an *Aha!* moment. In contrast, the dipole analysis performed in the second study (Wang et al., 2009) found the source of this component in the parahippocampal gyrus and the superior frontal gyrus, two areas that respectively involved in forming novel and effective associations and in the resolution of conflicts (Luo & Niki, 2003a). An explanation to these non-consistent findings could be due to different protocols used in the experiments: a learning-testing model in the first study with true- and false-matching logogriphs and a simple solving paradigm in the second one.

Using a different task, Luo et al. (2011) compared structural similarity logogriphs (STSL) with surface similarity logogriphs (SUSL) and

found a negative peak in the time range of 1100–1300 ms in posterior scalp regions for STSL (Luo et al., 2011). This component may also reflect a delayed N400-like component taking into account their similar topographical distribution, highlighting the need to control for late solvers.

5.2.3. Positive components around 300 ms

Positive components have been typically interpreted as a mark of the creation of novel associations, in the frame of the “context closure” model (Picton, 1992). The P300 component, one of the most studied ERP waveforms, has been associated with online WM updating and recollection of information stored in long-term memory. Its latency varies between 300 and 600 ms from stimulus onset based on the duration of stimulus classification, and its amplitude seems to reflect attentional load (Wilson, Harkrider, & King, 2012). P300-like components have been the focus of attention of several ERP studies on insight problem-solving (Fig. 3). Qiu et al. (2008) showed that successfully completed logogriphs were correlated with a larger positive deflection (P200–600) than unsuccessfully completed logogriphs, with generators localized to the left superior temporal gyrus and parieto-temporo-occipital cortex (Qiu et al., 2008). These areas, commonly associated with the creation of associations (Luo et al., 2003b), could be interpreted as the initial attempt to inhibit the superficial meaning of the logogriphs and to find deeper elements useful for their solution.

Nevertheless, given the relatively short latency of these components, they have been also related to the process of breaking mental set. Wang et al. (2009) compared insight with routine problems and found that insight problem-solving was associated with a more positive ERP deflection (P300–800) over parieto-occipital scalp regions than routine problems, with generators localized in the ACC and parahippocampal gyrus. Another change in the adopted reference state led to an additional finding: insight solutions showed a greater positive deflection (P400–600) when compared to search solutions (analytical problem-solving). Intriguingly, this activity was shown to generate from the fusiform gyrus, an area implied in perceptual processing (Zhang, Tian, Wu, Liao, & Qiu, 2011).

Finally, the paradigm (Chinese character-generation task) adopted by Zhao et al. (2011) showed a larger positive deflection (P500–700) in the “breaking mental set” condition (i.e. participants had to use a different method to create a new Chinese character; Zhao et al., 2011) than in “repetition condition” (i.e. participants generate a new Chinese character using the preceding method), providing further evidence for later P300 components as a marker of breaking the mental set.

5.2.4. Later positive components

Further evidence suggests that the early positive deflections outlined above are followed by additional later positive deflections (Fig. 3). These have been generally interpreted as markers of the creation of novel associations and with rehearsal/retention operations in WM. More positive ERP deflections related to insight solutions were found by Wang et al. (2009) 1200–1500 ms after the onset of the stimuli, and in the 640–780 ms time window in a later study by the same group (Zhang et al., 2011). Dipole analysis of the 1200–1500 ms peak comparing insight and routine problems (Wang et al., 2009) showed a generator in the parahippocampal and in the superior frontal gyri, while the generator for the 640–780 ms peak (comparing insight solutions and search solutions) was localized in the right superior temporal gyrus. Both results stress the role of parahippocampal gyrus in the generation of connections between elements and support the idea of the superior frontal gyrus being related to conflict resolution. Similarly, Luo et al. (2011) found another positive slow going wave between 900 and 1700 ms in SUSL and STSL trials, namely when the subjects try to find a new character after understanding or breaking the surface meaning of the logogriph. Therefore, it seems reasonable that later positive components could play a role in the processes of forming new associations across pieces of information.

5.3. Hemispheric asymmetry and insightful processing

A large part of neuroimaging and neurophysiological studies converge to the notion that hemispheric asymmetry as the fundamental structural and a potential functional basis for insight problem-solving (Dietrich & Kanso, 2010), with a prominent role of the right hemisphere (Bowden et al., 2005; Kounios & Beeman, 2014). In particular, a critical role has been attributed to the right anterior superior temporal gyrus because of its involvement in finding distant semantic relationships between words and, in general, in coarse semantic coding (Bowden & Jung-Beeman, 2007). However, our analysis of the literature does not support this view, with a less striking lateralization of brain oscillatory activity (Fig. 4) and/or fMRI activations during both mental preparation and insightful events (Fig. 5; i.e. from our ALE maps only middle temporal gyrus and precuneus show a unilateral activation pattern, Fig. 2). Rather, in the “pure insight” studies (Fig. 4), most of the activations are widespread and bilateral, with bilaterality supported also by perturbation-based investigation using rTMS (Giovannelli et al., 2010), as well as by most of NiBS studies (see below and Fig. 6). This is particularly relevant, since NiBS is the only approach that can provide causal, rather than correlational, information. Only few oscillatory patterns (i.e. γ activity burst in temporal and frontal lobes, α band activity in the parietal lobe, as well as θ in the temporal lobe) are specific to the right hemisphere (Fig. 4; Jung-Beeman et al., 2004; Danko et al., 2003; Sheth et al., 2009). In terms of left hemispheric activation, we only found evidence of a link between insight and increased coherence in β and α frequency bands in the left parietal and temporal lobes during insight problem-solving (Danko et al., 2003; Razumnikova, 2007). The same bilateral pattern seems to be present also during the mental preparation (Kounios et al., 2006), with results showing a widespread, bilateral decrease in α power (Fig. 5).

As for resting-state EEG activity, an interesting pattern arises when the activity of subjects unaware about the type of task they had to solve is taken into account (Fig. 5). Indeed, lateralized activations correlated with higher insight ability: spectral power in the β and γ frequency bands are increased in the right frontal lobe, whereas an increase in α and γ power are reported in, respectively, the left frontal and left temporal lobe regions (Kounios et al., 2008). This is interesting considering how a link between brain functional asymmetry at rest and cognition in humans has been recently experimentally supported (Santarnecchi et al., 2015b), as well as many of the lateralized resting-state oscillatory patterns at hand display a flipped pattern respect to what has been described during actual insight problem-solving (e.g. γ burst in the right temporal lobe).

In conclusion, even though the EEG and fMRI literature is not homogenous and only a handful of studies are available, the results seem to not support a complete dominance of the right hemisphere during *Eureka* moments. It seems more likely that right activations are more pronounced specifically during resting-state activity of high insight subject, whereas insight problem-solving is more related to a widespread synergistic activation of bilateral areas, with specific brain oscillations playing a major role in the right hemisphere (i.e. γ burst in temporal and frontal lobe).

5.4. Electric signatures of an insightful mind

Despite the use of similar tasks, an agreement about the role of different brain oscillations during insight does not appear to be present to date (Fig. 4). However, a major role for α (and possibly γ) activity seems to emerge, with the most consistent findings suggesting a reduction of α power and coherence in the frontal lobe, coupled with an increase in α power in the right parietal lobe during insight processing (Fig. 4). As for ERPs, overall the increase of the N400 amplitude seems to be one of the most replicated findings across all the literature, as well as the positive deflection P300 (Fig. 3). There is a subtle concordance in the ERPs correlates of insight in the various studies, but their

localization abilities as well as the mechanistic information they convey are far to be exhaustive. Certainly, activity recorded along the midline seems to be the most widely reported. However, fMRI data show a different pattern, with regions from different brain lobes taking part in the *Eureka* moment (Fig. 2). Overall, it seems that regions involved in attention/salience play a pivotal role during insight processes, with a possibly underestimated role for the claustrum. The only region that broadly aligns with the existing literature – even though related to a series of studies performed by the same group – is the right temporal pole, where increase in both BOLD activation and EEG activity – represented by focal γ bursts – have been reported specifically during insight processing but not during non-insightfully generated answers (Fig. 7; Jung-Beeman et al., 2004).

5.5. Insight and NiBS

Only a handful of studies assessed the effects of tES or TMS on the *Eureka* moment, with tES investigations limited to tDCS (Fig. 6, Tables 2 and S4). Evidence converges on the role of the temporal lobes, where an increase in cortical excitability in the right hemisphere induced by anodal tDCS (coupled with a decrease in the contralateral one) seems able to improve insight-related performance. As for prefrontal stimulation, only stimulation of the left hemisphere lead to performance enhancement in both studies available to date (Cerruti & Schlaug, 2009; Metuki et al., 2012), suggesting a dominant role of this region, a finding which is in line with our ALE map results. The only rTMS study available so far (Giovannelli et al., 2010) reports similar enhancing effects for stimulation of right and left parietal cortex. However, this result could be due to the specific task used during rTMS (i.e. binarized images task), which allows for the assessment of a very specific subcomponent of insight processing (perceptual ability) and probably not insight problem-solving per se.

It is important to note that, despite the apparent effectiveness of prefrontal lobe stimulation during insight processes, the variability in electrode montages, especially related to the positioning of the so called “return” electrode, suggests valid concerns about the specific role attributed to the “target” region. With tDCS being a bipolar stimulation where both electrodes deliver an equal intensity but opposite polarity electrical stimulation, it is misleading to attribute null effects to the electrode placed as “return” (i.e. cathode during so-called anodal tDCS, and vice versa; Santarnecchi et al., 2015a). Therefore, tES evidence collected so far might suffer from a generalized lack of focality: anodal stimulation over the left prefrontal lobe while applying the cathode over the right prefrontal cortex might induce significant effects due to (i) increased cortical excitability of the former, (ii) decreased excitability of the latter (with potential cascade effects over interhemispheric inhibitory processes on top of local decrease in activation), and (iii) the combination of both effects. Careful selection of both active and return electrodes positions is a crucial requirement for future studies on insight, with solutions as multifocal/multielectrode stimulation to be considered (Ruffini, Fox, Ripolles, Miranda, & Pascual-Leone, 2014).

Clearly, additional neuromodulatory experiments are needed in order to enlighten the causal role of specific brain region and their oscillatory patterns during the *Eureka* moment. As shown by its exponential application for cognitive enhancement and rehabilitation in the last ten years (Filmer, Dux, & Mattingley, 2014; Nitsche & Paulus, 2011; Rossi & Rossini, 2004; Santarnecchi et al., 2015a), tES should be thought of as a double purpose tool: while the “modulation” of local and distant brain activity has been considered the reason for the reintroduction of tES in modern neuroscience (e.g., Liew, Santarnecchi, Buch, & Cohen, 2014), its potential as a tool for the investigation of the causal role of specific brain regions in a given network/function should not necessarily come as a secondary feature. As observed for TMS in the context of the “virtual lesion” approach (Pascual-Leone, Walsh, & Rothwell, 2000), tES might help establishing specific contribution of a given network, especially in terms of brain oscillatory correlates of *Aha!* when frequency- and

state-dependent effects of alternating current stimulation (tACS) are exploited (Feurra et al., 2011a, 2011b; Santarnecchi et al., 2013). As for real brain lesions, a study by Reverberi and colleagues (Reverberi, Toraldo, D’Agostini, & Skrap, 2005) confirmed the causal role of lateral frontal cortex in insight problem-solving ability: patients with lateral frontal damage were more successful in solving difficult matchstick arithmetic problems with respect to healthy subjects, while medial frontal-lesion patients shown less pronounced difference in performance. Unfortunately, this constitutes to date the only clinical evaluation of brain lesions’ impact on insight ability.

5.6. Caveats and future directions

All the experiments considered in this review only include right-handed subjects. This could be an important bias for the identification of lateralized and diffuse patterns of activity. The variability in the tasks used and the low number of available studies make it difficult to get a clear picture of the neurobiological underpinnings of the *Eureka* moment. While the review at hand probably represents the most complete quantitative meta-analysis on insight available to date, a parcellation of our results in task-specific ALE maps as well as process-specific EEG evoked-activity would be ideal. More carefully designed investigations are needed and collaborative, multicenter efforts should be pursued.

As for NiBS, investigations testing the feasibility of frequency-specific modulation of insight problem-solving are needed, for instance using tACS to test the impact of transcranially induced oscillatory potentials on the EEG signatures of insight summarized in Figs. 4 and 5. The modulation of γ and α oscillations while subjects are solving insight tasks might provide a causal evidence of their relevance. In a near future, closed-loop protocols, where electrical or magnetic stimulation is delivered according to specific patterns of ongoing EEG activity, could probably shed additional light on the physiological mechanism underpinning insight problem-solving and α/γ activity roles in its dynamics.

6. Conclusion

Despite the many neuroimaging and electrophysiological investigations conducted to assess the neural basis of insight during the last twenty years, the findings are more controversial than expected. Evidence about specific insight-related oscillatory patterns are emerging, such as the role of α band in frontal and parietal lobe (Fig. 7). The analysis of resting-state activity and mental preparation, although still in its infancy, reveals interesting findings such as segregation of right hemisphere activity in the frontal lobe, as well as a widespread decrement of α power (Fig. 5). Additionally, the conception of right hemispheric dominance during insight problem-solving does not appear to be confirmed by our meta-analysis of fMRI activations (Fig. 2), although it partially fits with electrophysiological data (Fig. 4). Testing insight abilities in subjects with full right hemispheric dominance might be helpful in this sense. Furthermore, despite showing promisingly coherent results, neuromodulatory studies have been focused mainly on tDCS over two brain regions. More consistent findings seem to be related to stimulation of the right temporal lobe – in accordance with converging EEG and neuroimaging evidence – and the prefrontal cortex, despite the lateralization not being concordant across the studies (Fig. 7). Finally, considering the large variety of insight tasks being used despite their lack of ecological or statistical properties, the validation of new insight tasks able to fully capture the individual variability in covert cognitive processes behind a successful *Aha!* moment should constitute a priority for the scientific community.

Understanding the neurophysiology underpinning the *Eureka* moment, a fundamental manifesto of the human mind, is a central neuroscientific challenge that should not be postponed further.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.intell.2017.03.004>.

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