Intelligence 63 (2017) 9–28

Contents lists available at ScienceDirect

Intelligence

journal homepage: www.elsevier.com/locate/intell

Dissecting the parieto-frontal correlates of fluid intelligence: A comprehensive ALE meta-analysis study

Emiliano Santarnecchi[a,*], Alexandra Emmendorfer[a], Alvaro Pascual-Leone[a,b], on behalf of Honeywell SHARP Team authors[a,b,c,d,e]

[a] Berenson-Allen Center for Noninvasive Brain Stimulation, Beth Israel Deaconess Medical Center, Harvard Medical School, Boston, MA, USA
[b] Institut Universitari de Neurorehabilitacio Guttmann, Badalona, Barcelona, Spain
[c] Honeywell Labs, Honeywell Aerospace, Redmond, WA, USA
[d] Electrical and Computer Engineering Department, Northeastern University, Boston, MA, USA
[e] Department of Experimental Psychology, University of Oxford, Oxford, UK

ARTICLE INFO

Keywords:
Fluid intelligence
Abstract reasoning
fMRI
ALE
Functional connectivity

ABSTRACT

Recent advances in cognitive neuroscience have shown how experience-independent cognitive abilities termed fluid intelligence (G*f*) can predict academic achievement, longevity and resilience to neurodegeneration. Therefore, the understanding of the neurobiological underpinnings of G*f* becomes a crucial step for the implementation of cognitive rehabilitation as well as enhancement interventions. Here we present the result of a quantitative meta-analysis of available fMRI and PET literature about G*f* in humans, including (i) distinct maps for verbal and visuospatial stimuli, (ii) an analysis of brain regions contributing to processing of more complex stimuli as well as (iii) a model-driven distinction of processing stages occurring during G*f*-related problem solving. Results highlight the loading of G*f* components over functionally defined resting-state fMRI networks, with different degrees of overlap in both hemispheres and subcortical structures. A major role for nodes of the dorsal attention network during both verbal and visuospatial abstract reasoning tasks represents the most consistent correlate of G*f*, with additional contributions by regions of the anterior salience and left fronto-parietal control network. Increase in trial difficulty elicits a more pronounced engagement of the language and left fronto-parietal control networks, while inferring the rules subtending a given G*f* task relies on a different anatomo-functional substrate than producing novel solutions. Current findings might allow a clearer association between G*f*-related activity and brain connectivity, also providing quantitative ALE maps to be used in network-based brain stimulation and cognitive training interventions.

1. Introduction

Real-life problem-solving tasks require more than a mere access to previously accumulated experience-based information. When challenged with novel situations, the accurate retrieval from long-term acquired knowledge could be useless if new relations between objects are not captured, immediately capitalized, and correct online solutions based on logic promptly extrapolated. Such crucial, experience-independent, components of human cognition –clustered into the term fluid intelligence (G*f*) (Cattell, 1963)–are fundamental in encoding new information efficiently, which can be exploited successfully as a crystallized form of intelligence (G*c*). As a matter of fact, G*f* has been shown to positively correlate with a vast number of cognitive activities, and to be an important predictor of both educational and professional success (Deary, 2008). G*f*, as other cognitive resources, usually declines with physiological aging and, even more, when pathological processes overlap; hence, its decline contributes to the dramatic functional impairment of many chronic-degenerative neurological conditions (Whalley, Deary, Appleton, & Starr, 2004). However, such vulnerability contrasts with the resilience of G*f* towards influences of education, socialization, drug-related interventions (stimulants) and behavioral training (Baltes, Staudinger, & Lindenberger, 1999)(Gray, Chabris, & Braver, 2003), making it a key element for the implementation of effective cognitive neurorehabilitation programs.

The first step for the enhancement of such a core aspect of human cognition is to understand its neuroanatomical and functional substrates. Several pieces of evidence are available, including investigations focusing on correlates of G*f* using voxel-based morphometry (Colom, Chuderski, & Santarnecchi, 2016b; Colom et al., 2013b, 2016a), surface-based morphometry (Escorial et al., 2015), lesion

* Corresponding author
E-mail address: esantarn@bidmc.harvard.edu (E. Santarnecchi).

http://dx.doi.org/10.1016/j.intell.2017.04.008
Received 16 January 2017; Received in revised form 31 March 2017; Accepted 24 April 2017
Available online 08 May 2017

mapping (Barbey, Colom, Paul, & Grafman, 2014; Barbey et al., 2012), magnetic resonance imaging (MRI) spectroscopy (Nikolaidis et al., 2016; Paul et al., 2016) and functional MRI (fMRI) (Cole, Yarkoni, Repovs, Anticevic, & Braver, 2012; Ebisch et al., 2012; Geake & Hansen, 2005, 2010; Preusse, van der Meer, Deshpande, Krueger, & Wartenburger, 2011). More specifically, neuroimaging and behavioral evidence indicate a limited number of brain areas supporting abstract reasoning abilities: tasks assessing G*f* are usually associated with different levels of frontal and parietal activations (Jung & Haier, 2007)(R. Colom et al., 2013a)(Vakhtin, Ryman, Flores, & Jung, 2014), with parieto-frontal shifts of activity with increasing task difficulty (Houde, 2010); left prefrontal lobe activity has been documented when information is manipulated following perceptual processing involving the parietal lobes (Krawczyk, 2012); additionally, an overlap between visuospatial and verbal analogical reasoning activations in the prefrontal cortices has been proposed, suggesting the existence of a single processing module for distinct modality-specific reasoning tasks (Krawczyk, Michelle, & Donovan, 2011); finally, specific subtypes of logic tasks involving conditional arguments (primarily based on Modus Tollens: e.g. If P then Q; not-Q) seem to map in the prefrontal cortices (mainly left middle frontal gyrus, MFG), while those based on relational syllogisms (e.g. P is to the left of Q; Q is to the left of R; R?) have been linked to the temporo-parietal-occipital junction (Prado, Van Der Henst, & Noveck, 2010). These studies, mostly based on fMRI and positron emission tomography (PET), support the idea of distinct substrates for stimulus types and processing stages. However, their single observation nature limit their value and suggest the need for a comprehensive quantitative meta-analysis of activation patterns during cognitive processing ascribed to G*f*. Most importantly, a detailed characterization of the anatomical substrate of different types of reasoning (e.g. verbal vs visuospatial) across studies is needed, as well as an investigation of brain regions responsible for the different processing stages and those crucially recruited where more challenging trials are faced. Interestingly, the same effort has been put on the definition of similar maps for general intelligence–in the form of intelligence quotient (IQ)—with the conceptualization of the parieto-frontal integration theory (P-FIT) representing a pivotal milestone for the definition of new hypotheses (Jung & Haier, 2007). A similar quantitative understanding of G*f* would help reach a consensus around the localization of such an important feature of human cognition, also offering new insight about potential targets for non-invasive brain stimulation (NIBS) and cognitive training interventions aimed at enhancing cognition (Bestmann, de Berker, & Bonaiuto, 2015). Therefore, we present a quantitative meta-analysis of the G*f* literature available to date, realized analyzing experimental work involving task-fMRI data within the activation likelihood estimate (ALE) statistical framework (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Eickhoff et al., 2009). Quantitative functional mapping for (i) the overall G*f* network, (ii) its verbal and visuospatial components (iii), the different stages of cognitive processing taking place during typical G*f* testing (e.g. rule inference and rule application) and (iv) regions activated during higher difficulty trials, are presented.

Looking at brain spontaneous patterns of metabolic activity might be informative about–and even predict—individual evoked activity during sensorimotor and cognitive tasks (Fox et al., 2005)(Allen et al., 2014; Finn et al., 2015; Shirer, Ryali, Rykhlevskaia, Menon, & Greicius, 2012). Such intrinsic activity is thought to reflect not only the past experiences of the brain as a complex system, but it also forms the functional foundation from which the brain will generate future goal-oriented behavior (Tavor et al., 2016). Differently from canonical task-fMRI paradigm where the signal is derived by contrasting subject's activity during an active and a passive state, this approach relies on the endogenous brain oscillations recorded during spontaneous brain activity, giving rise to a complex pattern of temporally and spatially independent resting-state networks (RSNs)(Biswal et al., 2010). Such intrinsic organization of spontaneous brain activity is captured within the framework of brain connectivity analysis, an approach based on resting-state fMRI analysis (Achard & Bullmore, 2007). Individual connectivity profile has been proven reliable over multiple sessions (Braun et al., 2012)(Choe et al., 2015), and to hold enough information not only to allow the identification of pathological conditions (e.g. multiple sclerosis (Bonavita et al., 2016), schizophrenia (Bassett et al., 2008) and Alzheimer (Agosta et al., 2012)) but also to identify correlates of several cognitive (Santarnecchi, Galli, Polizzotto, & Rossi, 2014)(Santarnecchi, Rossi, & Rossi, 2015b; Santarnecchi, Tatti, Rossi, Serino & Rossi 2015c; Yuan et al., 2012) and psychological traits (Adelstein et al., 2011) in healthy subjects. However, a clear overview of the role played by regions activated during G*f* tasks with respect to existing RSN is not available to date, with potential insight coming from the P-FIT model suggesting a major role for regions of an anatomically defined "fronto-parietal network". To provide such information, we quantitatively compared each G*f* map with those representing different RSNs tapping into domains such as attention, executive control, language, sensorimotor, visual and auditory processing. Results provide an original overview of the link between G*f*-related brain activity and brain functional connectivity in humans.

2. Methods

2.1. Literature search

Potentially relevant articles were retrieved by performing a search in PubMed and Google Scholar database without temporal restrictions. The following terms were individually combined with "functional magnetic resonance imaging", "Position Emission Tomography" and their acronyms: "Fluid intelligence", "G*f*", "abstract reasoning", "logical reasoning", "rule inference", "rule application", "divergent thinking" "convergent thinking", "deductive reasoning", "analogical reasoning", "relational processing", "inductive reasoning", "syllogistic reasoning", "inductive reasoning", "conditional reasoning". References of retrieved researches were examined for relevant publications too. We intentionally excluded (i) studies including patients with organic illness, (ii) studies discussing magic ideation, (iii) review papers, (iv) studies not mentioning any of the keywords in their abstract unless they cite specific G*f* related tasks, (v) studies not reporting fMRI/PET activations coordinates in MNI or Talairach space, (vi) studies using a-priori defined regions of interest, (vii) studies not reporting activation foci in table format or reporting statistical values without corresponding coordinates.

The final selection comprised 47 studies related to fMRI and PET (see Supplementary Table S1). For each study, the following information was retrieved: (i) number of participants, (ii) mean age, (iii) experimental design, (iv) cognitive task parameters, (v) main results. Data for each specific activation foci have been also collected and included in a quantitative Activation Likelihood Estimation (ALE) analysis for the identification of brain regions most commonly reported as involved in G*f* processing. Different maps were created, carefully inspecting each manuscript and extracting activation foci from tables referring to the contrast of interest. As a result, a (1) global "G*f*" map was obtained by including all the coordinates referring to G*f*-related processing, regardless the stage of processing and stimulus type; a (2) "verbal" and a (3) "visuospatial" G*f* maps (vG*f* and vsG*f* hereafter) were computed by including studies using verbal stimuli such as analogies, or visuospatial ones such as Raven matrices (Raven, Raven, & Court, 1998); more specifically, vG*f* refers to studies using written text as part of the experimental stimuli (words, letters, numbers, or any other type of stimuli requiring a stimuli-dependent semantic process), in the context of tasks based on, for instance, analogies (Luo et al., 2003), induction (Green, Fugelsang, Kraemer, Shamosh, & Dunbar, 2006) and syllogistic reasoning (Goel, Buchel, Frith, & Dolan, 2000); differently, studies using original or modified version of well-known G*f* measures such as the Raven's Advanced Progressive Matrix test (Raven et al.,