High fluid intelligence and analogical reasoning

Behavioural and cerebral correlates
and their temporal characteristics

D I S S E R T A T I O N

zur Erlangung des akademischen Grades

doctor rerum naturalium (Dr. rer. nat.)
im Fach Psychologie

eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät II
Humboldt-Universität zu Berlin

von

Frau Diplom-Psychologin Franziska Preusse

Präsident der Humboldt-Universität zu Berlin:
Prof. Dr. Jan-Hendrik Olbertz

Dekan der Mathematisch-Naturwissenschaftlichen Fakultät II:
Prof. Dr. Elmar Kulke

Gutachter:
1. Prof. Dr. Elke van der Meer
2. Prof. Dr. Isabell Wartenburger
3. Dr. Roland Grabner

eingereicht am: 28. Juli 2011
Tag der mündlichen Prüfung: 17. November 2011

Diese Promotion ging hervor aus dem Projekt “Short-Term vs. Long-Term Learning in Mathematical Cognition: Cerebral Correlates, Domain Impacts, and Sources of Individual Differences”, welches im Rahmen des Programms Neuroscience ~ Instruction ~ Learning durch das Bundesministerium für Bildung und Forschung finanziell gefördert wurde (Förderkennzeichen 01GJ0802).
Während meiner Promotionszeit war ich Mitglied der Graduiertenschule Berlin School of Mind and Brain, welche durch die Exzellenzinitiative des Bundes und der Länder und die Deutsche Forschungsgemeinschaft finanziell gefördert wird.

Contents

List of abbreviations

ACC	Anterior cingulate cortex
ave-fluIQ	Average fluid intelligence group
BOLD	Blood oxygenation level dependent
EEG	Electroencephalography
ERD	Event-related desynchronisation
fMRI	Functional magnetic resonance imaging
GLM	Generalised linear model
hi-fluIQ	High fluid intelligence group
NIRS	Near-infrared spectroscopy
PET	Positron emission tomography
PFC	Prefrontal cortex
RAPM	Raven's Advanced Progressive Matrices test

Abstract

High fluid intelligence enables high performance in cognitive tasks. Hitherto, previous research on the cerebral correlates of fluid intelligence was restricted to studying participants of average fluid intelligence solving intelligence test items of varying difficulty, thus not allowing assumptions on interindividual differences in fluid intelligence. Other neuroimaging studies compared participants with varying levels of fluid intelligence but often utilised tasks that do not exclusively demand fluid intelligence.

The geometric analogical reasoning task demands fluid intelligence very purely and thus is an eligible approach for research on interindividual differences in fluid intelligence. As previous findings in this field had been scant, we examined the cerebral correlates of geometric analogical reasoning in a first study and showed the involvement of parietal and frontal brain regions. This is in line with the assumptions of the parieto-frontal integration theory (P-FIT) of intelligence and with what the literature reports for verbal analogical reasoning tasks and for other visuo-spatial tasks. Furthermore, we found that short-term training led to improved behavioural performance. Training related decreases of brain activation are indicative of more automated processing of the task over time.

Building upon these findings, we report results from a second study with high fluid intelligence (hi-fluIQ) and average fluid intelligence (ave-fluIQ) high-school students solving the geometric analogical reasoning task. Again in line with the P-FIT model, we demonstrated that the parieto-frontal network is involved in geometric analogical reasoning in both groups. However, the extent of task-related brain activation was modulated by fluid intelligence; while hi-fluIQ showed stronger involvement of parietal brain regions, ave-fluIQ showed stronger involvement of frontal brain regions. Our results thus partly run counter to the postulates of the neural efficiency hypothesis, which assumes a negative brain activation-intelligence relationship as a marker of cognitive efficiency. We conclude that the brain activation-intelligence relationship is not generally unitary. This is in line with some other findings in the literature and suggests a revision of the neural efficiency hypothesis. It can be conjectured that the adaptive and flexible modulation of brain activation is characteristic of high fluid intelligence rather than neural efficiency in general.

Knowledge on the stability or changeability of the cerebral correlates of high fluid intelligence during late adolescence (the peak age of fluid intelligence) had been sparse. To elucidate this field, we examined the follow-up stability of the behavioural and cerebral correlates of geometric analogical reasoning in hi-fluIQ in a third study. We demonstrated that the relevant brain network is in place already at age 17 and that improvements in behavioural performance at age 18 due to task familiarity are indicative of more efficient use of the cerebral resources available.

Keywords:

high fluid intelligence, geometric analogical reasoning, adolescence, parieto-frontal network, neural efficiency, follow-up, functional Magnetic Resonance Imaging (fMRI)

Zusammenfassung

Hohe fluide Intelligenz ermöglicht hohe kognitive Leistungen. Bisherige Studien zu zerebralen Korrelaten fluider Intelligenz haben Probanden mit durchschnittlicher fluider Intelligenz beim Lösen von Intelligenztestaufgaben mit unterschiedlichen Schwierigkeitsstufen untersucht. Dieser Ansatz ermöglicht keine Aussagen zu interindividuellen Unterschieden in fluider Intelligenz. Andere bildgebende Studien haben zwar Probanden mit unterschiedlichen fluiden Intelligenzlevels untersucht, haben aber häufig Aufgaben verwendet, die fluide Intelligenz nicht in Reinform erfordern.

Die geometrische Analogieaufgabe beansprucht fluide Intelligenz in Reinform und ist daher ein geeignetes Paradigma für die Untersuchung fluider Intelligenz. Da es in diesem Feld bisher kaum Forschungsergebnisse gab, auf denen man aufbauen konnte, haben wir in einer ersten Studie die zerebralen Korrelate des geometrischen analogen Schließens untersucht und nachgewiesen, dass parietale und frontale Hirnregionen involviert sind. Dies steht im Einklang mit der parieto-frontalen Integrationstheorie (P-FIT) der Intelligenz und mit Literaturberichten zu verbalen Analogieaufgaben und anderen visuell-räumlichen Aufgaben. Des Weiteren konnten wir zeigen, dass Kurzzeittraining zu verbesserter behavioraler Performanz führt. Training führt im Verlauf des Experiments ebenfalls zu einer Verringerung der aufgabenspezifischen Hirnaktivierung und deutet auf eine höhere Automatisierung bei der Aufgabenverarbeitung hin.

Aufbauend auf diesen Befunden berichten wir Ergebnisse einer zweiten Studie, in der Gymnasiasten mit hoher fluider Intelligenz (hi-fluIQ) und durchschnittlicher fluider Intelligenz (ave-fluIQ) geometrische Analogieaufgaben lösten. In Übereinstimmung mit den Annahmen des P-FIT-Modells konnten wir zeigen, dass diese Aufgaben in beiden Gruppen das parieto-frontale Netz-

werk beanspruchen. Das Ausmaß der Hirnaktivierung wurde jedoch durch fluide Intelligenz moduliert: Hi-fluIQ zeigten stärkere Beteiligung parietaler Hirnregionen, während ave-fluIQ stärkere Beteiligung frontaler Hirnregionen zeigten. Unsere Ergebnisse widersprechen damit teilweise den Postulaten der neuralen Effizienztheorie, die annimmt, dass ein negativer Zusammenhang zwischen Hirnaktivierung und Intelligenz ein Kennzeichen kognitiver Effizienz ist. Aus unseren Ergebnissen schlussfolgern wir, dass der Zusammenhang zwischen Hirnaktivierung und Intelligenz nicht generell einseitig gerichtet ist. Dies steht im Einklang mit Befunden in der Literatur und ist ein Hinweis, dass die neurale Effizienztheorie überarbeitet werden sollte. Es ist davon auszugehen, dass nicht allgemein neurale Effizienz, sondern die adaptive und flexible Modulation von Hirnaktivierung charakteristisch für fluide Intelligenz ist.

Befunde zur Stabilität und Veränderlichkeit zerebraler Korrelate hoher fluider Intelligenz in der späten Jugend (dem Höhepunkt fluider Intelligenz) waren bisher rar. Um dieses Forschungsfeld zu beleuchten, haben wir die follow-up-Stabilität behavioraler und zerebraler Korrelate des geometrischen analogen Schließens in der hi-fluIQ Gruppe in einer dritten Studie untersucht. Wir konnten zeigen, dass das relevante zerebrale Netzwerk schon im Alter von 17 Jahren etabliert ist und Verbesserungen der behavioralen Performanz im Alter von 18 Jahren bedingt werden durch eine höhere Aufgabenvertrautheit und für eine effizientere Nutzung der verfügbaren zerebralen Ressourcen sprechen.

Schlagwörter:

hohe fluide Intelligenz, geometrische Analogien, Jugend, parieto-frontales Netzwerk, neurale Effizienz, follow-up, funktionelle Magnetresonanztomographie (fMRT)

1 Introduction

This dissertation is based on three peer-reviewed publications concerning the behavioural and cerebral correlates of analogical reasoning and high fluid intelligence in adolescents, and their temporal characteristics. These three articles will be referred to as *Study 1* (Wartenburger, Heekeren, Preusse, Kramer & van der Meer, 2009), *Study 2* (Preusse, van der Meer, Deshpande, Krueger & Wartenburger, 2011), and *Study 3* (Preusse et al., 2010). In this synopsis, I will begin by presenting a brief introduction to the concept of fluid intelligence, to the parieto-frontal integration theory of intelligence, and to the neural efficiency hypothesis. This will be followed by an outline of the research questions of my dissertation. I will conclude by presenting and integrating the main results from the three studies.

1.1 Fluid intelligence

Fluid intelligence defined by Raymond Cattell is the ability to perceive, discriminate, and manipulate relationships of various concepts and various complexities, to think flexibly, and to draw inferences that are independent of prior knowledge (Cattell, 1963; Horn & Cattell, 1966; Cattell, 1987). Consequently, fluid intelligence is a prerequisite for solving novel problems, using adaptive problem-solving strategies in reasoning, and coping with unfamiliar situations, thereby allowing a person to acquire new knowledge and obtain new insights. Fluid intelligence is thus a general foundation of cognitive performance.[1]

[1] The relevant literature in this field does not always clearly demarcate between different concepts of intelligence. A similar – but not identical – concept to fluid intelligence is general intelligence as described by Charles Spearman (Colom, Abad, García & Juan-Espinosa, 2002; Süß, 2003; Blair, 2006; Colom, Jung & Haier, 2006; Asendorpf, 2007). When carrying out research, both concepts of intelligence are often operationalised by assessing participants' intelligence using the Raven's Advanced Progressive Matrices test (RAPM; Raven, Court & Raven, 1980; Carpenter, Just & Shell, 1990; Schweizer, Goldhammer, Rauch & Moosbrugger, 2007). In addition to reviewing findings on fluid intelligence, I will thus partly draw upon literature that labels the subject of their research 'general intelligence' or simply 'intelligence'. However, I will include these reports only if, in my estimation, their focus is close enough to Cattell's

A person's level of fluid intelligence can be assessed using the Raven's Advanced Progressive Matrices test (RAPM; Raven et al., 1980). Taking this standardised intelligence test requires flexible thinking, pattern matching, and relational reasoning (Raven et al., 1980; Bethell-Fox, Lohmann & Snow, 1984; Carpenter et al., 1990; Schweizer et al., 2007).

As can be deduced from the definition of fluid intelligence, people with high fluid intelligence outperform people with average or low fluid intelligence in cognitive tasks (Horn & Cattell, 1966). Several reports in the literature support this fact: Kane and Engle commented that "In memory tasks [. . .], such as verbal fluency and proactive interference tasks, subjects of high intelligence [. . .] outperform those of low intelligence" (cf., Kane & Engle, 2002, page 648). This is corroborated by other reports demonstrating associations between psychometric fluid intelligence and shorter reaction times, or respectively increased task performance, in a number of memory tasks (Vernon, 1983; Grabner, Fink, Stipacek, Neuper & Neubauer, 2004). Furthermore, Grabner, Neubauer und Stern (2006) showed that participants with high intelligence consistently achieved shorter reaction times in differentially demanding speed, memory, and reasoning tasks. Using elementary cognitive tasks, Neubauer, Riemann, Mayer und Angleitner (1997) showed that individuals scoring high on the RAPM have shorter reaction times. In addition, Jausovec (2000) found that highly intelligent individuals score higher on a linear optimisation problem. These relationships can be understood to be a characteristic of the central nervous system that processes information quickly and correctly (Vernon, 1983; Neubauer, 1990; Conway, Cowan, Bunting, Therriault & Minkoff, 2002). Hence, people with high fluid intelligence process information more efficiently. Neuroimaging studies presenting a link between superior behavioural performance in more intelligent individuals and lower brain activation call this phenomenon neural efficiency (Haier, Siegel, Nuechterlein & Hazlett, 1988; Neubauer & Fink, 2009).

In addition to studying the behavioural correlates of intelligence, researchers are increasingly interested in identifying the cerebral correlates of intelligence and in understanding the cerebral characteristics of interindividual differences in fluid intelligence; yet, findings on the cerebral characteristics of extraordinarily high fluid intelligence are sparse. Recent developments in modern neuroimaging technology now allow us to carry out such studies and thus obtain a more comprehensive view of intelligence.

---

concept of fluid intelligence and if they are appropriate to help us understand the nature of fluid intelligence and interindividual differences in fluid intelligence.

Two central concepts currently discussed in this respect are the *parieto-frontal integration theory (P-FIT) of intelligence* and the *neural efficiency hypothesis*. In the following, I will illustrate both concepts because of their central importance to neuroscientific intelligence research and to the research presented here.

1.1.1 Cerebral correlates of fluid intelligence

Neuroimaging studies have identified the involvement of parietal and frontal brain regions in tasks demanding fluid intelligence. For instance, Prabhakaran, Smith, Desmond, Glover und Gabrieli (1997) investigated the cerebral correlates of solving intelligence test items using functional Magnetic Resonance Imaging (fMRI). The bilateral inferior and superior parietal cortex, and bilateral middle and inferior frontal gyrus were reportedly involved in solving the RAPM test items. Thus, Prabhakaran et al. (1997) concluded that a network of parietal and frontal brain regions mediates visuo-spatial relational reasoning and flexible problem solving.

Additionally, Duncan et al. (2000) obtained comparable results in a positron emission tomography (PET) study. Their participants completed items of a non-verbal visuo-spatial task and a non-verbal visuo-perceptive task taken from Cattell's Culture Fair Test (Cattell, 1987). In each item of the visuo-spatial task, four panels that contained several shapes, symbols, or drawings were presented to the participants. The elements inside the panels differed, but all except one panel were related by having identical properties (e.g., symmetry). The participants had to detect the one panel out of each quartet that differed from the other three in a certain subtle property. This task is considered a complex problem solving task and demands intelligence more strongly than the visuo-perceptive task. In the visuo-perceptive task, items still consisted of four panels of shapes, symbols, or drawings but contained only one element each. Three of the panels were physically identical, while the fourth differed in a visually very obvious property (e.g., shape or size). Again, the participants had to detect the mismatching panel. This task was a purely perceptive decision task demanding intelligence less strongly than the visuo-spatial task and thus serving as the control condition. When comparing task-evoked brain activation between these two task-conditions, the medial frontal, bilateral lateral frontal, bilateral parietal, and bilateral occipital brain regions showed stronger involvement during items that more strongly demanded intelligence compared to items that less strongly demanded intelligence. Based on the finding that frontal brain regions related to information integration and cognitive control are recruited in the complex problem solving task, Duncan et al. (2000) concluded that these brain regions particularly contribute to intelligent behaviour.

In this way researchers started to elucidate the cerebral correlates of fluid intelligence using modern neuroimaging technology. From this research, Newman und Just (2005) argue that intelligent behaviour is not associated with the function or processing of a single and specialised brain region; rather, it is associated with the interplay of several brain regions within a large-scale cerebral network.

1.1.2 The parieto-frontal integration theory of intelligence

The aforementioned findings (Prabhakaran et al., 1997; Duncan et al., 2000; Newman & Just, 2005) are in line with what Jung und Haier (2007) report in their comprehensive review of studies on the neurobiology of intelligence. They thoroughly reviewed 37 neuroimaging studies and compiled evidence demonstrating that interindividual differences in intelligence and reasoning task performance are related to interindividual variation in structure and function of the parieto-frontal brain network. Based upon these findings, they framed the P-FIT, which postulates that a network of interacting brain regions (that is, the dorsolateral prefrontal cortex (PFC), anterior cingulate cortex (ACC), inferior and superior parietal lobe, and temporal and occipital lobe regions) is involved in intelligent information processing. Cognitively salient sensory information is acquired from the environment and processed in early sensory brain regions (e.g., in the occipital lobe for visual information and in the temporal lobe for auditory information). From there, the basic sensory information is forwarded to parietal brain regions (namely, the superior and inferior parietal lobe, angular gyrus, and supramarginal gyrus) where structural symbolism, abstraction, and elaboration emerge. Moreover, the parietal and frontal brain regions interact to compare different possible task solutions for a given problem and to ultimately select the appropriate behaviour or task response out of several alternatives. Finally, the ACC is involved in the inhibition of alternative responses (Jung & Haier, 2007).

Besides, the P-FIT model is supported by a number of studies on structural correlates of intelligence. There are various findings of increased grey matter volume within the parieto-frontal network in individuals with higher intelligence test scores (e.g., Colom et al., 2009; Luders, Narr, Thompson & Toga, 2009). Furthermore, there are recent studies examining the genetic (e.g., Bouchard & McGue, 1981; Fisher et al., 1999; Chiang et al., 2009) or biochemical (e.g., Rae et al., 1996;

Jung et al., 1999) correlates of intelligence, which will not be dwelled upon here for reasons of brevity. All of these studies contribute to our understanding of the nature of fluid intelligence.

However, there has been no comprehensive research on the functional characteristics of the parieto-frontal network in individuals with extraordinarily high intelligence. The majority of available studies compared tasks that recruit intelligence to differing degrees and often used samples with unmeasured intelligence levels (e.g., Wright, Matlen, Baym, Ferrer & Bunge, 2008; Ferrer, O'Hare & Bunge, 2009); that is, variation in fluid intelligence was established by means of variation between tasks or items rather than variation between individuals. Other studies made use of tasks that were not exclusive to fluid intelligence (e.g., Neubauer, Freudenthaler & Pfurtscheller, 1995; Gray, Chabris & Braver, 2003; Grabner et al., 2004) or compared sample groups that were assigned to the high or low performance groups a posteriori rather than being selected systematically a priori according to their scores in standardised intelligence tests (e.g., Haier et al., 1988; Neubauer et al., 1995; Geake & Hansen, 2010). Thus, these findings only allow limited inference to the nature of interindividual differences in intelligence and there is a paucity of noteworthy knowledge on cerebral correlates of extraordinarily high fluid intelligence. Research on the cerebral correlates of interindividual differences in fluid intelligence is of utmost necessity.

There are two conceivable possibilities to explain how the cerebral network of intelligent reasoning is characterised in high intelligence individuals. Interindividual differences in fluid intelligence could possibly appear as: 1) the recruitment of differential brain network components (that is, the network associated with intelligent reasoning comprises different brain regions in high intelligence individuals than in average intelligence individuals), or 2) the differential extent of brain activation in a similar network (that is, the network associated with intelligent reasoning comprises the same brain regions in high and average intelligence individuals, but the extent of task-related brain activation is modulated by intelligence).

Thus, interindividual differences in fluid intelligence may manifest cerebrally as differences in spatial characteristics or as differences in activation strength. In the following section, this brain activation-intelligence relationship will be outlined.

1.1.3 The neural efficiency hypothesis

Not only is the link between the parieto-frontal network and the cerebral characteristics of fluid intelligence currently discussed, but the relationship between fluid intelligence and the extent of task-induced brain activation is also subject of current research and debate. The term 'neural efficiency' is frequently used when discussing this issue. Neural efficiency means that individuals with higher intelligence display less task-related brain activation than individuals with comparatively lower intelligence (Haier et al., 1988). By examining cortical metabolic rates (as measured by PET) of solving RAPM items, Haier et al. (1988) initially demonstrated a negative correlation between brain activation and intelligence test performance. To date, a considerable number of studies have substantiated neural efficiency in participants with higher intelligence (e.g., Haier, Siegel, Tang, Abel & Buchsbaum, 1992; Larson, Haier, LaCasse & Hazen, 1995; Neubauer et al., 1995; Jausovec, 1998; Rypma, Berger & D'Esposito, 2002; Geake & Hansen, 2005; Neubauer & Fink, 2003; Grabner et al., 2004; Neubauer & Fink, 2009).

Moderator variables of neural efficiency

Using a number processing task, Neubauer und Fink (2003) found a negative brain activation-intelligence relationship only for the male but not for the female participants. As the aforementioned initial report by Haier et al. (1988) included solely male participants, the findings by Neubauer und Fink are not contradictory. In fact, other studies have identified and discussed sex as a moderator variable. For example, Grabner et al. (2004) reported significant negative correlations between fluid intelligence and cortical activation in three tasks demanding the short-term memory, working memory or executive processes for male but not for female participants. Additionally, Neubauer, Fink und Schrausser (2002) and Neubauer, Grabner, Fink und Neuper (2005) found that female participants showed neural efficiency in verbal tasks, while male participants showed neural efficiency in figural and spatial task. This indicates how the variables of sex and task type play a moderating influence on neural efficiency. Task difficulty and brain region were also identified as potential moderator variables of neural efficiency (Neubauer & Fink, 2009). Again, the literature reports regarding these factors are partly inconsistent.

In a PET study, Larson et al. (1995) demonstrated decreased task-related cortical glucose use (i.e., neural efficiency) in high intelligence participants only for easy backwards digit-span items but not for difficult backwards digit-span items. Yet, Neubauer, Sange und Pfurtscheller (1999) reported that neural efficiency emerged only in high complexity trials of Posner's letter matching paradigm; it should be noted, however, that this task is a little less cognitively demanding than the abovementioned backwards digit-span task. Integrating these reports and results from other studies in their review, Neubauer und Fink (2009) conclude that neural efficiency may be characteristic to tasks of subjectively low to medium difficulty. According to this review, people with high intelligence are able to invest more cortical effort into more difficult tasks than people with lower intelligence, which then reverses the brain activation-intelligence relationship in those tasks.

Moreover, neural efficiency may be specific to frontal brain regions rather than the whole brain (Neubauer & Fink, 2009). When determining the best next moves for given chess game positions, participants with high figural intelligence showed higher neural efficiency in the PFC than participants with lower figural intelligence (Grabner et al., 2006). As Neubauer, Grabner, Freudenthaler, Beckmann und Guthke (2004) report, cortical activation of frontal (but not other) brain regions was negatively correlated with intelligence while solving a figural reasoning task.

Findings challenging the neural efficiency hypothesis

Although there is a large number of studies substantiating neural efficiency, there is also a certain number of studies showing the opposite of neural efficiency: That is, participants with higher intelligence and/or better cognitive performance show stronger task-related brain activation compared to average intelligence participants or participants with poorer performance. For example, Geake und Hansen (2005) reported that when solving a fluid letter string analogy task, the activation of the PFC was positively correlated to intelligence in an adult sample. Likewise, using a three-back working memory task, Gray et al. (2003) showed stronger involvement of the PFC, parietal cortex, and ACC in more intelligent individuals. Interestingly, Duncan (2003) reported stronger recruitment of the ACC, lateral PFC, and inferior parietal cortex in high intelligence participants when executing a figural problem solving task. According to Duncan, the inversion of neural efficiency can be interpreted as being related to a stronger cerebral response to cognitive conflict and conflict resolution. Furthermore, a positive relationship between cognitive ability and brain activation was demonstrated by Grabner et al. (2007). When solving multiplication problems, the left angular gyrus of individuals with high mathematical competence displayed stronger activation than in individuals with lower mathematical competence. In this study, mathematical competence was assessed with the numerical subscale of the Berliner Intelligenzstruktur-Test (Jäger, Süß & Beauducel, 1997).

It can be noted that by and large, there is a number of findings on neural efficiency; yet, further research is needed to explain previous inconsistent results and to characterise neural efficiency more comprehensively. Most of the existing studies investigating and confirming neural efficiency used electroencephalography (EEG) to measure brain activation (e.g., Grabner et al., 2004; Neubauer et al., 2004, 2005; Grabner et al., 2006). More specifically, these studies reported the event-related desynchronisation (ERD) of the EEG upper alpha band, which is indicative of increased event-related cortical activation (Pfurtscheller & Lopes da Silva, 2005). Lower ERD signifies lower cortical activation, that is, higher neural efficiency. Interestingly, the few studies employing fMRI to investigate the cerebral characteristics of intelligence often report findings challenging the neural efficiency hypothesis (e.g., Duncan, 2003; Gray et al., 2003; Geake & Hansen, 2005; Grabner et al., 2007). While the ERD of the upper alpha band is related to semantic information processing (Klimesch, 1999; Doppelmayr, Klimesch, Stadler, Pöllhuber & Heine, 2002), blood oxygenation level dependent (BOLD) signal changes as measured by fMRI are unspecifically related to task-related changes in neural activity (Jezzard, Matthews & Smith, 2003; Logothetis, 2008; Huettel, Song & McCarthy, 2009). Thus, one cannot rule out that the cerebral characteristics of intelligence may be reflected differentially when using different methods. The characteristics of the brain activation-intelligence relationship and of neural efficiency may be more nuanced and more differentiated than currently assumed. Therefore, these concepts clearly necessitate further investigation through a variety of methods, using various experimental tasks, and with samples covering a wider range of individual levels of fluid intelligence. We aimed at contributing further insights by comparing individuals with extraordinarily high fluid intelligence to a group of individuals with average fluid intelligence when solving a task that demands fluid intelligence very purely (Study 2). Furthermore, for the first time, we aimed at characterising the stability of the brain activation-intelligence relationship in a one-year follow-up study (Study 3).

1.1.4 Intelligence and learning

Fluid intelligence constitutes a foundation for successful learning and thus enables individuals to access new knowledge (Cattell, 1963; Horn, 1968). People with high fluid intelligence are known to show greater learning and training success than people with average fluid intelligence (J. F. Beckmann, 2001). This is assumed to be a function of more efficient cognitive strategies in people with high fluid intelligence. In a study by Neubauer et al. (2004) characterising the relationship between intelligence and learning, a sample of participants with distributed intelligence levels received training on the Adaptive Sequential Figure Learning Test (ADAFI; Guthke, Beckmann, Stein, Vahle & Rittner, 1995) and were provided with feedback on the accuracy of their responses. If the initial response to an item was incorrect, the participants received prompts that helped with retrying the item. After the training phase, performance on a figural reasoning test was compared to the pre-training performance on a parallel version of this test. As a result, post-training performance improvements were higher for participants with higher intelligence. Thus, the authors concluded that individuals with higher intelligence showed more efficient learning. The authors also found a negative brain activation-intelligence relationship in frontal brain regions, which evolved only after the training, and was established by EEG measurements that accompanied the pre- and post-training assessments of figural reasoning ability.

1.2 Analogical reasoning

The transfer of relational information from objects or elements with known relation(s) onto objects or elements with unknown relation(s) is called analogical reasoning. This higher-order cognitive process allows us to discover new insights, explain new concepts by means of familiar ones, and acquire new knowledge domains (Gentner, 1983; Vosniadou & Ortony, 1989; Hofstadter & Mitchell, 1997; Hofstadter, 2001; French, 2002). Analogical reasoning is an important process in human reasoning and it is not only useful in problem solving, but also in creative processes and human communication for instance. Analogical reasoning and fluid intelligence are closely related; individuals with high fluid intelligence have a good command of analogical reasoning (Mulholland, Pellegrino & Glaser, 1980; Carroll, 1993; Hofstadter & Mitchell, 1997; Hofstadter, 2001; Geake & Hansen, 2005; Holyoak & Morrison, 2005). For this reason, an analogical reasoning task serves as an eligible approach to examine fluid intelligence. Analogical reasoning involving geometric patterns and their mirroring relations necessitates only limited prior semantic knowledge, thus demanding fluid intelligence very purely. Therefore, to characterise the cerebral correlates of high fluid intelligence, we implemented a geometric analogical reasoning task in Studies 2 and 3.

1.2.1 Cerebral correlates of geometric analogical reasoning

Using PET, Wharton et al. (2000) found that the left medial frontal, left inferior frontal, and left inferior parietal cortex were involved in geometric analogy detection. In their study, participants were asked to indicate whether or not the four geometric shapes inside two consecutively presented panels were analogical. The geometric shapes either were or were not related by abstract visuo-spatial relations, such as texture, colour, shape, or position. The task-related brain activation of solving such a block of analogy detection items was compared to the task-related brain activation of solving a block of control items where participants judged whether or not the presented panels were perceptually identical. Wharton et al. (2000) assumed that the demonstrated brain activation in the left frontal lobe is related to identifying and mapping analogical relations. However, the manner of consecutively presenting the stimuli added a working memory demand to the analogy detection task, which simultaneous presentation would not have posed. One can assume that the involvement of frontal brain regions may be confounded by the additional working memory demand, which is not inherent to geometric analogical reasoning itself. Thus, there is a clear need for further investigation of the cerebral characteristics of geometric analogical reasoning.

As previous neuroimaging findings on geometric analogical reasoning had generally not been sufficient to draw upon for our research on high fluid intelligence, and as there had been no fMRI findings in this respect, we initially conducted an fMRI study to elucidate the cerebral correlates of geometric analogical reasoning (Study 1). Please refer to section 1.4 for an explanation of the advantages of fMRI over PET and other neuroscience methods, and for our specific reasons for employing fMRI.

1.2.2 Training-related changes in geometric analogical reasoning

Many studies examining training effects in cognitive tasks demonstrated improvements in behavioural performance and decreases in brain activation, which are commonly attributed to reduced processing time or more automatic processing and thus represent increased neural efficiency (Risberg, Maximilian & Prohovnik, 1977; Poldrack, 2000; Kelly & Garavan, 2005). However, there are some literature reports that presented different findings. Olesen, Westerberg und Klingberg (2004), for instance, showed an increase in brain activation after successful training on a working memory task. Furthermore, Ischebeck, Zamarian, Egger, Schocke und Delazer (2007) found that short-term training changes the functional neuroanatomy of multiplication. Upon training, activation decreased in frontal and parietal regions, but increased in temporo-parietal regions, indicating a shift in strategy from complex calculation and visualisation to mere result retrieval.

There had been no previous knowledge on the cerebral characteristics of short-term training on geometric analogical reasoning. Study 1 aimed at filling this gap under the assumptions that behavioural performance increases and task-related brain activation decreases with short-term training.

1.3 The development of cognitive abilities

Even though cognitive development and improvements in cognitive performance are possible all throughout life, most development-related changes in cognitive abilities take place during childhood and young adolescence. The same holds true for analogical reasoning ability. Its development begins during infancy and improves during childhood and adolescence (Sternberg & Rifkin, 1979; Gentner, 1988). Young children have limited reasoning ability and often make mistakes when identifying or mapping element relations. The analogical reasoning ability of children improves after the relational shift, which is a developmental process (completed around puberty) that enables people to consider element relations and relational structure when reasoning. Before the relational shift, children primarily focus on the attributes of elements (Levinson & Carpenter, 1974; Gentner, 1988; Goswami, 1991, 1996; Hosenfeld, van der Maas & van den Boom, 1997; Richland, Morrison & Holyoak, 2006; Sodian, 2008).

Inextricably linked with cognitive development during childhood and adolescence are periods of maturation and development of brain structure and function. The development of the frontal cortex (whose function is related to executive processes, analytical thinking, response inhibition, and abstract reasoning) is not complete until late adolescence or the early twenties (Giedd et al., 1999; Blakemore & Choudhury, 2006; Shaw et al., 2006). According to the findings of Shaw et al. (2006), high intelligence is characterised by a strong increase in cortical thickness in the PFC peaking at around age 11, compared to a less pronounced cortical thickening in a control group of average intelligence. Furthermore, individuals with high intelligence showed a delayed onset (around age 13 to 14) of subsequent cortical thinning in the same brain regions, but a more rapid progression of this regular process.

Using a nonsymbolic magnitude processing task, Ansari und Dhital (2006) reported a shift of brain activation from frontal to parietal brain regions during the transition from childhood to adulthood, which they interpreted as the developmental specialisation of cortical regions. In addition, Wright et al. (2008) compared school children and young adults performing a semantic analogical reasoning task and not only did they find that the children performed more poorly but also that the children showed a time delay in recruiting the lateral PFC (which is known to be crucially involved in relational reasoning) when solving the task. This suggests an incomplete development of analogical reasoning ability and response inhibition in children, which later improves with cognitive development.

However, of the behavioural and neuroscience studies in the field, many have focused on the development of cognitive abilities during childhood rather than adolescence or have compared children and adult samples in cross-sectional designs (e.g., Dehaene, Molko, Cohen & Wilson, 2004; Feigenson, Dehaene & Spelke, 2004; Liu, Shi, Zhao & Yang, 2008; Houdé, Rossi, Lubin & Joliot, 2010; Prieto-Corona et al., 2010). Thus, there is a paucity of knowledge on the cerebral correlates of cognitive abilities (and especially analogical reasoning ability) in adolescence and their changes with development. Thus, it is of particular importance to conduct studies with teenage participants involving multiple measuring time points, or to realise longitudinal studies that span from early childhood up to young adulthood.

Moreover, Cattell postulated that fluid intelligence increases throughout childhood and adolescence, reaches its peak in late adolescence, and declines after the early twenties (Cattell, 1963; Horn & Cattell, 1966; Cattell, 1987). This is corroborated by findings from Rammsayer und Troche (2010) who demonstrated that high fluid intelligence is associated with both high speed of information processing (as displayed by short median reaction times) and high consistency in processing speed (as displayed by low intraindividual variability in reaction times) in a sample of young and middle-age adults (ranging from 18 to 39 years) on a modified Hick task. Speed of processing, but not consistency in processing speed, was shown to decline with age.

As analogical reasoning demands fluid intelligence, one can infer that analogical reasoning ability follows a similar developmental course as fluid intelligence. Furthermore, as little is known about the temporal characteristics of particularly high fluid intelligence, it was of great interest to us to examine changes in the cerebral characteristics of analogical reasoning and high fluid intelligence related to development and task familiarity in late adolescence in a follow-up study (Study 3). Given our lack of knowledge on development-related changes of the cerebral characteristics of cognitive abilities and especially fluid intelligence in adolescence, more in-depth studies were urgently required. Moreover, to date, there have only been a few follow-up fMRI studies or fMRI studies with multiple measuring time points (L. Friedman et al., 2008; Bennett & Miller, 2010). Thus, Study 3 was designed to add new insights to our understanding of the temporal characteristics of the cerebral correlates of geometric analogical reasoning in high fluid intelligence adolescents, to the cerebral correlates of task familiarity, and to the stability of the BOLD signal.

1.4 Fundamentals of fMRI

Owing to massive advances neuroscience methods have made in recent years, new possibilities have opened up for cognitive science and thus for the study of human behaviour and task performance. Within the large spectrum of neuroscience methods, fMRI has occupied an important place. Aside from fMRI, there are various other neuroscience research techniques, such as EEG, PET, computed tomography (CT), and near-infrared spectroscopy (NIRS). Each of these methods has specific characteristics, advantages, and disadvantages. Depending on the underlying research question, overall research goal, and sample characteristics, one must carefully select the most suitable research technique. As the research on the characteristics of high fluid intelligence and geometric analogical reasoning presented here used fMRI, I will give a short overview of fMRI and its advantages over other methods regarding our particular research goals. More detailed information on fMRI can be found, for example, in Jezzard et al. (2003), Logothetis (2008) or Huettel et al. (2009).

Cognitive processing demands cerebral activity. The activity of cerebral neurons in one brain region increases local cerebral metabolism and thus requires oxygen, which is supplied by local blood vessels. More precisely, blood oxygen is bound to hemoglobin. Oxygenated and de-oxygenated hemoglobin differ in their magnetic characteristics. FMRI studies utilise this so-called BOLD effect to compare a stimulated state (e.g., cognitive demand and events of interest) with a non-stimulated state (e.g., rest), different types of stimulation, or differing extents of stimulation. Consequently, fMRI measures neural activity indirectly through changes in blood oxygenation.

Whilst the physiological relationship between neural activity and changes in blood oxygenation level seems to be an impressively simple foundation for fMRI measurement, one must be aware that this relationship is more complex than outlined here and not all of its details are currently understood (Heeger & Ress, 2002). As such, the exact relationship between neural activity, brain metabolism, blood oxygenation, and blood flow is the subject of ongoing research and scientific exchange. Even so, previous studies have shown correlations between brain metabolism and regional cerebral blood flow, making fMRI an eminently suitable method for cognitive neuroscience (Villringer & Dirnagl, 1995; Logothetis, Pauls, Augath, Trinath & Oeltermann, 2001; Raichle & Mintun, 2006).

FMRI is characterised by a fine spatial resolution (usually within the range of a few millimeters) and it can record signals from subcortical brain regions. Unlike EEG, NIRS or PET, it thus allows for a very precise spatial localisation of areas of interest within the whole brain. Nevertheless, the temporal resolution of fMRI falls short of the temporal resolution that EEG and NIRS provide, yet surpasses the temporal resolution PET allows. As the increase of the regional blood flow lags with respect to the neural activity of a given brain region and is also much slower than the electrical activity of neurons, the precise duration of cerebral activity cannot be specified with fMRI (Orrison, Lewine, Sanders & Hartshorne, 1995; Gazzaniga, Ivry & Mangun, 2002).

In order to reliably measure BOLD signal changes in response to a stimulus, it is necessary to take repeated measurements within one experimental session. That is, stimulus repetition or multiple stimuli are needed for each experimental condition. These days, fMRI studies are commonly conducted with an event-related experimental design in which different stimuli or experimental tasks are consecutively presented in a randomised (and usually fixed) order. Afterwards, the BOLD signal changes for all stimuli of the same experimental condition are aggregated for analysis. Usually, the generalised linear model (GLM) and correction for multiple comparisons are applied to detect significantly activated brain regions of interest (C. F. Beckmann, Jenkinson & Smith, 2003). As there is no natural baseline of brain activation that can be used as a reference when analysing fMRI data, two task-related functional brain states can be subtracted from one another in order to determine the functional cerebral correlates of the task of interest. Therefore, it is crucial to carefully select an adequate reference task (Cabeza & Nyberg, 2000; Smith et al., 2004). Alternatively, stepwise parametric contrasts can be calculated. This type of fMRI data analysis focuses on brain regions that show a stepwise increase in activation when varying the associated experimental variables (e.g., increasing levels of task difficulty). Furthermore, to make up for the lack of baseline reference of brain activation, between-group comparisons can be calculated. That is, the task-related functional brain activation of two or more groups of participants differing in one experimental variable can be compared. By comparison, PET data analysis does not provide the possibility to incorporate single event information if the event is shorter than 40 seconds. Thus, PET studies usually use block designs and are therefore unable to factor in performance parameters or compare multiple experimental conditions within one participant; that is, stepwise parametric contrasts cannot be calculated (Gazzaniga et al., 2002).

FMRI is a non-invasive technique. Unlike CT and PET, fMRI does not require the administration of ionising radiation or a radioactive contrast agent. This makes fMRI much more participant-friendly than invasive research methods.

Due to its good spatial resolution, ability to locate subcortical brain regions, non-invasiveness, general tolerability in participants, ability to regard multiple experimental conditions and calculate stepwise parametric contrasts, and its ability to provide insights on important properties of the large-scale cerebral networks that underlie cognition, fMRI proved to be the method of choice for our research on the cerebral characteristics of high fluid intelligence and geometric analogical reasoning. Further explanations of the precise procedures and parameters of statistical data analysis can be found in the respective article.

1.5 Goals of the dissertation and hypotheses

It is well established that solving fluid intelligence test items recruits the parieto-frontal network in populations of average intelligence (Prabhakaran et al., 1997; Jung & Haier, 2007). However, the cerebral correlates of exceptionally high fluid intelligence remained elusive and clearly required more investigation in order to better understand fluid intelligence and its important function as a foundation of thinking and cognitive performance. The neural efficiency hypothesis postulates a negative brain activation-intelligence relationship (e.g., Haier et al., 1988; Neubauer & Fink, 2009). Although there is a number of EEG studies supporting the neural efficiency hypothesis, fMRI findings on the topic are sparse.

As geometric analogical reasoning demands fluid intelligence in a very pure way, it serves as an appropriate task to operationalise fluid intelligence for our purposes (e.g., Carroll, 1993; Holyoak & Morrison, 2005). Yet, little was known about the cerebral correlates of geometric analogical reasoning.

Fluid intelligence develops during childhood and adolescence and is most pronounced in late adolescence (Cattell, 1963; Horn & Cattell, 1966). To date, there still is a lack of knowledge on the cerebral correlates of the development of fluid intelligence, especially during adolescence.

Therefore, in my dissertation project I aimed at elucidating the behavioural and cerebral correlates of geometric analogical reasoning (Study 1), and exceptionally high fluid intelligence (Study 2), and characterising their temporal characteristics (Study 3).

More specifically, based on evidence from the literature outlined above, the following hypotheses were postulated:

1. Geometric analogical reasoning recruits the parieto-frontal brain network, more precisely the inferior and superior parietal lobe, PFC, and ACC.

2. Individuals with high fluid intelligence (hi-fluIQ) achieve better behavioural performance than individuals with average fluid intelligence (ave-fluIQ) in the geometric analogical reasoning task.

3. As postulated by the neural efficiency hypothesis, hi-fluIQ display a negative brain activation-intelligence relationship during the execution of the geometric analogical reasoning task.

4. Hi-fluIQ show cognitive development and task familiarity when repeating the task one year later, resulting in improved behavioural performance and decreased task-related brain activation, especially in frontal brain regions.

2 Experimental approaches: Summary of the three studies

In this chapter, I will briefly present and summarise the objectives, methods, and main findings of each study. A comprehensive discussion of the results of all studies can be found in chapter 3.

2.1 Study 1: Cerebral correlates of analogical processing and their modulation by training

Wartenburger, I., Heekeren, H.R., Preusse, F., Kramer, J., van der Meer, E. (2009). Cerebral correlates of analogical processing and their modulation by training. *NeuroImage* 48(1), 291-302.

2.1.1 Background and aim of the study

As there was limited knowledge on the cerebral correlates of geometric analogical reasoning, in Study 1, we aimed to find out which brain regions are involved in geometric analogical reasoning, and whether and how the involvement of these brain regions is modulated by task difficulty. Moreover, we sought to understand how short-term training on geometric analogical reasoning induces changes at the behavioural and brain level. Study 1 laid the groundwork for our further investigations on the cerebral characteristics of high fluid intelligence.

2.1.2 Methods

In this study, 15 male high-school students solved the geometric analogical reasoning task while behavioural and functional brain imaging data were obtained. In this task, participants were asked to judge whether or not the mirroring relationship between two simultaneously presented pattern pairs were equal (i.e., analogical). The task comprised 168 items with three conditions of different task difficulty levels: 1) easy condition = no mirroring (i.e., the second partner of a pattern pair had the same orientation as the first partner), 2) medium condition = orthogonal mirroring (i.e., the second partner of a pattern pair was a mirror image of the first partner, mirrored on one of the orthogonal axes), or 3) difficult condition = diagonal mirroring (i.e., the second partner of a pattern pair was a mirror image of the first partner, mirrored on one of the diagonal axes). Items with the same mirroring between the two pattern pairs were analogy target items. Items with dissimilar mirroring between the two pattern pairs were non-analogy distractor items. The data analysis only comprised analogy target items. Please refer to the original manuscript for a more detailed description of the task and methods.

2.1.3 Main results and interpretation

We found that both reaction times and error rates increased as task difficulty increased. Furthermore, as hypothesised, training improved behavioural performance. More specifically, training led to a slight improvement in performance quality (i.e., decreased error rates) and a statistically significant decrease of reaction times.

Comparable to the findings in the behavioural data, there were main effects of task difficulty and short-term training in the functional imaging data. The left and right superior and inferior parietal lobe, left and right precuneus, left and right middle frontal gyrus, and left and right inferior temporal regions showed an increasing BOLD signal with increasing task difficulty. Additionally, we established that the left superior and inferior parietal cortex, left and right inferior temporal regions, and cingulate gyrus showed a training-induced decrease in BOLD signal in the difficult task condition. There was no decrease in BOLD signal from the first to last third of the experiment in the easy or medium conditions.

The involvement of the parieto-frontal network in the execution of the geometric analogical reasoning task goes in line with what the literature reports for verbal analogical reasoning tasks and for other visuo-spatial tasks (Wharton et al., 2000; Luo et al., 2003; Geake & Hansen, 2005). More specifically, the increase of parieto-frontal BOLD signal with task difficulty reflects an increase in resource demand when solving more difficult items compared to items of easy and medium difficulty. While parietal brain regions are involved in visuo-spatial operations and relational manipulation, frontal brain regions are involved in relation integration, relational mapping, and response selection (Zacks & Michelon, 2005; Green, Fugelsang, Kraemer, Shamosh & Dunbar, 2006). As the difficult items require more complex relation recognition and relational mapping, they thus require stronger involvement of parietal and frontal brain regions.

The reduction of the BOLD signal accompanying improved behavioural performance over the course of the experiment hints to a short-term training effect leading to higher efficiency in cerebral resource use. While performance on the difficult items was associated with a very distinct reduction in the BOLD signal with training, there are no such distinct changes in the BOLD signal for the easy and medium items. This can be attributed to a floor effect; the processing of the easy and medium items is already efficient from the beginning of the experiment, so the reduction of cerebral activity that corresponds to increased efficiency of cerebral resource use is not possible with short-term training.

To summarise this study, we showed that geometric analogical reasoning recruits a similar parieto-frontal brain network as verbal analogical reasoning does. (Note that brain activation solely related to semantic processing in verbal analogical reasoning tasks is usually subtracted out by the data analysis and therefore not reported as analogy-task-related activation). Furthermore, behavioural performance and cerebral involvement are modulated by short-term training.

2.2 Study 2: Fluid intelligence allows flexible recruitment of the parieto-frontal network in analogical reasoning

Preusse, F., van der Meer, E., Deshpande, G., Krueger, F., Wartenburger, I. (2011). Fluid intelligence allows flexible recruitment of the parieto-frontal network in analogical reasoning. *Frontiers in Human Neuroscience* 5(22), 1-14.

2.2.1 Background and aim of the study

As there had been sparse knowledge of the functional cerebral correlates of high fluid intelligence, the aim of the second study was to characterise behavioural and cerebral correlates of interindividual differences in fluid intelligence. Therefore, we drew a sample of high-school students with a high fluid intelligence level (hi-fluIQ) and implemented a slightly improved version of the geometric analogical reasoning task from Study 1. This task is known to function as a prototype to recruit fluid intelligence. We compared the behavioural performance and functional imaging data of the hi-fluIQ to a sample of students with average fluid intelligence (ave-fluIQ).

We hypothesised that hi-fluIQ achieve better behavioural performance on the task than ave-fluIQ. Based on our findings from the previous study, we also hypothesised that a network of parietal and frontal brain regions is involved in geometric analogical reasoning and that its activity is modulated by task difficulty. Furthermore, as the literature is not fully conclusive on the direction of the relationship between task-induced brain activation and intelligence level, we did not establish a directional hypothesis on whether the relationship between the two is exclusively positive or negative.

2.2.2 Methods

Twenty-two hi-fluIQ (IQ range 119 − 145, mean IQ 130, SD 8) and 18 ave-fluIQ (IQ range 91 − 110, mean IQ 104, SD 7) high-school students participated in this study solving the geometric analogical reasoning task while behavioural and functional brain imaging data were obtained. In this task, participants were asked to judge whether or not the mirroring relationships between two simultaneously presented pattern pairs were equal (i.e., analogical). The improved geometric analogical reasoning task comprised 150 items with five levels of task difficulty. The 'no mirroring' condition was the easiest (i.e., the second partner of a pattern pair had the same orientation as the first partner), followed by the vertical mirroring condition (i.e., the second partner of a pattern pair was a mirror image of the first partner, mirrored on the vertical axis), then the horizontal mirroring condition (i.e., the second partner of a pattern pair was a mirror image of the first partner, mirrored on the horizontal axis), then the mirroring on the diagonal tilted left condition (i.e., the second partner of a pattern pair was a mirror image of the first partner, mirrored on the left-tilted diagonal axis), and then the mirroring on the diagonal tilted right condition (i.e., the second partner of a pattern pair was a mirror image of the first partner, mirrored on the right-tilted diagonal axis), which was the most difficult condition. Items with the same mirroring between the two pattern pairs were analogy target items. Items with dissimilar mirroring between the two pattern pairs were non-analogy distractor items. The data analysis only comprised analogy target items. For a more comprehensive description of the sample, task, data acquisition, and analysis methods, please refer to the original article.

2.2.3 Main results and interpretation

In accordance with our hypotheses and the literature, hi-fluIQ generally achieved a better quality of behavioural performance and had slightly (but not statistically) shorter reaction times. Furthermore, we replicated the findings from Study 1 showing that a parieto-frontal network is involved in geometric analogical reasoning and is modulated by task difficulty. Additionally, we found that interindividual differences in fluid intelligence modulate the involvement of parieto-frontal network components; while parietal brain regions (left and right superior parietal lobe and precuneus, stretching into the left middle and superior occipital gyrus) showed greater BOLD signal changes in hi-fluIQ than in ave-fluIQ, frontal brain regions (anterior cingulate cortex and medial frontal gyrus) showed greater BOLD signal changes in ave-fluIQ than in hi-fluIQ. Thus, stronger task-related parietal brain activation is related to superior performance in hi-fluIQ. Concurrently, hi-fluIQ require less extensive cognitive control and executive monitoring than ave-fluIQ when performing the task. The differential recruitment of parietal and frontal brain regions indicate that there is no globally and exclusively positive *or* negative relationship between fluid intelligence and brain activation. Instead, the brain activation-intelligence relationship depends on the particular brain region recruited and the task demand. Therefore, we concluded that adaptive and flexible modulation of regional cerebral activation is characteristic of high fluid intelligence rather than neural efficiency alone.

2.3 Study 3: Long-term characteristics of analogical processing in high-school students with high fluid intelligence

Preusse, F., van der Meer, E., Ullwer, D., Brucks, M., Krueger, F., Wartenburger, I. (2010). Long-term characteristics of analogical processing in high-school students with high fluid intelligence: an fMRI study. *ZDM The International Journal on Mathematics Education* 42(6), 635-647.

2.3.1 Background and aim of the study

As some researchers assumed that analogical reasoning does not emerge until adolescence, there had been a lack of research on the development of analogical reasoning ability for a long time (Goswami, 1991, 1996; Sodian, 2008). Later, other researchers started closing that gap and showed that school children already have analogical reasoning ability, which improves in the course of late childhood (e.g., Levinson & Carpenter, 1974; Gentner, 1988; Vosniadou & Ortony, 1989; Goswami, 1991; Hosenfeld et al., 1997; Richland et al., 2006). Cross-sectional fMRI studies showed that brain activation related to solving analogical reasoning tasks is stronger and has different temporal characteristics in children compared to adults, especially in frontal brain regions (Wright et al., 2008; Crone et al., 2009). Yet, there had been a lack of functional neuroimaging studies on the development of analogical reasoning in adolescents.

Fluid intelligence, which is a foundation for analogical reasoning, increases during childhood and adolescence, and reaches it maximum in late adolescence (Cattell, 1963; Horn & Cattell, 1966; Cattell, 1987). Since our knowledge was scant when it comes to the cerebral characteristics of the development of fluid intelligence and analogical reasoning ability during adolescence, Study 3 aimed at filling this gap, expecting improvements in behavioural performance and a decrease of task-related brain activation. Study 3 is also one of the few fMRI studies with multiple measuring time points.

2.3.2 Methods

The third study is a follow-up of the hi-fluIQ from Study 2 after twelve months. Participants were invited to the lab and solved the geometric analogical reasoning task once again. The experimental setup and procedure in Study 3 remained as in the preceding study.

2.3.3 Main results and interpretation

In the follow-up study after one year, we found a decrease in reaction times and no change in high reaction accuracy. The improvements in reaction times were strongest for the more difficult task conditions. The left and right superior and left inferior parietal lobe, and the left middle frontal gyrus were involved in geometric analogical reasoning at both measuring time points. This is in line with the postulates of the parieto-frontal integration theory of intelligence (Jung & Haier, 2007). Nevertheless, BOLD signal changes did not differ between time points. As the brain regions recruited by the geometric analogical reasoning task were congruent at the two measuring time points, we concluded that the cerebral network for analogical reasoning is stably established by the age of 17 (when the first measurement took place). Improvements in behavioural performance can be achieved through task familiarity and more efficient use of the resources available. That is, hi-fluIQ achieved an improved quality of behavioural performance using the same cerebral resources.

3 General discussion

3.1 Integration of the findings

The main goals of my dissertation were to improve our understanding of the behavioural and cerebral mechanisms of geometric analogical reasoning, of exceptionally high fluid intelligence, and of their temporal characteristics. The three studies I presented aided in fulfilling these main goals by contributing the following main results as summarised and discussed below.

In Study 1, we established that parietal and frontal brain regions are involved in geometric analogical reasoning. Furthermore, we found that short-term training led to improved behavioural performance in all levels of task difficulty and to decreased brain activation in the most difficult task condition. Training related decreases in parietal, temporal, and prefrontal brain regions can be interpreted as indicators of a more automated processing of the geometric analogical reasoning task over time (Risberg et al., 1977).

In Study 2, we showed that hi-fluIQ involve the same parieto-frontal network when executing the geometric analogical reasoning task as ave-fluIQ. These results are in line with the P-FIT model (Jung & Haier, 2007). However, the extent of task-related brain activation was modulated by fluid intelligence; while hi-fluIQ showed stronger involvement of parietal brain regions, ave-fluIQ showed stronger involvement of frontal brain regions. These results run counter to the postulates of the neural efficiency hypothesis, which assumes lower overall brain activation in hi-fluIQ as a marker of cognitive efficiency. I will discuss our results with respect to the neural efficiency hypothesis in section 3.1.3.

The geometric analogical reasoning task involves extracting visuo-spatial feature characteristics of the patterns, identifying the mirroring relations, mapping the mirroring relations to find correspondences between the patterns, and evaluating the similarity of the mirroring relations (Sternberg, 1977; Mulholland et al., 1980; Hummel & Holyoak, 2005). Our results demonstrating the task-related involvement of the parieto-frontal network are in line with results from a PET study of geometric analogy detection (Wharton et al., 2000). Furthermore, it has previously been shown that solving fluid intelligence test items recruits the parieto-frontal network in populations of average intelligence (Prabhakaran et al., 1997) and the ability to solve these kinds of tasks is impeded by rTMS stimulation over these areas (Boroojerdi et al., 2001). In the literature, the activity of parietal brain regions is associated with goal-directed attentional control (Corbetta & Shulman, 2002; Kelley, Serences, Giesbrecht & Yantis, 2008; Shulman et al., 2009) and task-related processing (Gevins & Smith, 2000; Rypma et al., 2006). More specifically, it has been suggested that the parietal lobe may be involved in directing spatial attention, visuo-spatial imagery, spatial object feature processing (such as size or orientation), visuo-spatial mental operations, and spatial stimuli selection, as it is essential for solving the geometric analogical reasoning task (Faillenot, Decety & Jeannerod, 1999; Cavanna & Trimble, 2006; Frings et al., 2006; Bledowski, Rahm & Rowe, 2009; Sack, 2009).

To summarise, stronger recruitment of parietal brain regions involved in spatial and visuo-spatial cognition is related to superior behavioural performance in the geometric analogical reasoning task in hi-fluIQ. Moreover, as the above-mentioned component processes of geometric analogical reasoning require executive control, parietal and prefrontal brain regions functionally interact during task solving (Cavanna & Trimble, 2006; Jung & Haier, 2007).

3.1.1 Executive functions and their relation to fluid intelligence

The cognitive processes controlling thought and action comprise a number of separate functions, such as information selection, working memory, information integration, cognitive flexibility, inhibition of inappropriate responses, and action initiation. This group of cognitive processes is termed 'executive functions' and has been associated with the involvement of prefrontal brain regions (Roberts, Robbins & Weiskrantz, 1998; Miller & Cohen, 2001). Previous research showed that executive functions are related to fluid intelligence, but the two concepts are not isomorph. Moreover, the various executive functions differentially relate to fluid intelligence (N. P. Friedman et al., 2006; Unsworth, Miller et al., 2009). Some researchers are of the opinion that specifically working memory and intelligence level are very closely related (Kyllonen & Christal, 1990; Engle, Tuholski, Laughlin & Conway, 1999; Süß, Oberauer, Wittmann, Wilhelm & Schulze, 2002; Kane, Hambrick & Conway, 2005;

Oberauer, Schulze, Wilhelm & Süß, 2005; Wilhelm & Oberauer, 2006; Salthouse & Pink, 2008). However, other studies and meta analyses alleviate this strong view by showing that fluid intelligence and working memory are only slightly yet statistically significantly correlated. Thus, the current and generally agreed upon view is that working memory and fluid intelligence may be related but are not identical (Conway, Kane & Engle, 2003; Ackerman, Beier & Boyle, 2005; Unsworth, Brewer & Spillers, 2009).

Differential involvement of executive functions may possibly account for the differential task-related involvement of the ACC in hi-fluIQ and ave-fluIQ in Study 2. However, please note, that there were no group differences in working memory capacity as assessed by the digit operation span. Therefore, there is reason to assume that the differential recruitment of the ACC may be related to interindividual differences in integration of (conflicting) information and inhibition of alternative but inappropriate responses when solving the geometric analogical reasoning task (M. Botvinick, Nystrom, Fissell, Carter & Cohen, 1999; Allman, Hakeem, Erwin, Nimchinsky & Hof, 2001; M. M. Botvinick, Cohen & Carter, 2004). This is in line with findings by Duncan et al. (2000) who reported that the involvement of prefrontal brain regions was increased in items that demanded intelligence (and hence information integration and cognitive control) more strongly.

In a nutshell, interindividual differences in fluid intelligence lead to interindividual differences in relative task difficulty and thus display interindividually different cognitive demands, which in turn elicit interindividually different cerebral activation. Furthermore, the increase of activation in frontal brain regions with increasing task difficulty that we showed in all three studies hints to an increasing demand of executive functions with increasing task difficulty. More precisely, the more difficult task conditions pose a stronger demand on the detection and selection of relevant information and information integration.

3.1.2 Task difficulty

Royer (1981) proposed that the geometric mirroring axes are represented hierarchically in the cognitive system and thus mirroring detection is carried out in a fixed order. He postulated that symmetry along the vertical axis is detected more easily than symmetry along the horizontal axis, which is detected more easily than symmetry along the left tilted diagonal, which again is detected more easily than symmetry along the right tilted diagonal. Our results from all three studies go in line with these postulates and also with the findings of Corballis und Roldan (1975) who reported that participants detected vertical symmetry much faster than diagonal symmetry. Even so, there is no conclusive evidence that can explain why this is the case. The advantage of the vertical over the other mirroring axes could possibly be explained by the direction of reading in German (left to right), which allows a certain advantage for detecting manipulations on the vertical mirroring axis, even if the geometry of the different mirroring conditions does not differ qualitatively. This assumption should be corroborated by future studies examining mirroring detection in the geometric analogical reasoning task in individuals with a different primary direction of reading (e.g., Hebrew or Arabic). Still, further research is needed to understand why individuals detect orthogonal mirrorings faster and more accurately than diagonal mirrorings.

3.1.3 Neural efficiency and flexibility in thinking

When solving the geometric analogical reasoning task, the extent of task-related brain activation was modulated by fluid intelligence; while hi-fluIQ showed stronger involvement of parietal brain regions, ave-fluIQ showed stronger involvement of frontal brain regions. These results partly run counter to the postulates of the neural efficiency hypothesis, which assumes lower overall brain activation in hi-fluIQ as a marker of cognitive efficiency. Instead, in the geometric analogical reasoning task, neural efficiency for the hi-fluIQ was restricted to frontal brain regions, while parietal brain regions showed the reverse of neural efficiency. There have been prior assumptions and research findings in the literature that neural efficiency may be specific to frontal brain regions (Neubauer & Fink, 2009). For instance, in an EEG study Neubauer et al. (2004) demonstrated neural efficiency exclusively for frontal recording sites and only after training in highly intelligent individuals carrying out a figural reasoning task. Likewise, Grabner et al. (2006) established neural efficiency in frontal brain regions for participants with higher figural intelligence when solving chess problems. Furthermore, our findings are partly in line with the findings of Rypma et al. (2006) who reported lower involvement of the Brodmann area 9 (the superior part of the dorsolateral PFC) in individuals who performed faster than the whole-group median in the digit-symbol substitution test. The same group of participants additionally showed stronger task-related involvement of the Brodmann area 46 (the middle and inferior part of the dorsolateral PFC), inferior frontal gyrus, and supramarginal gyrus than the sub-group performing below the median.

Moreover, other fMRI studies reported a positive brain activation-intelligence relationship (e.g., Gray et al., 2003; Geake & Hansen, 2005).

Our results as well as other findings from the literature thus contradict the hypothesis of a globally and unidirectionally negative brain activation-intelligence relationship. It can instead be assumed that neural efficiency is moderated by diverse variables. Although different brain regions have different characteristic signatures of brain activation, these are probably not independent of cognitive demands but may differ between tasks. Thus, when characterising the function of the human brain, rather than focusing on brain regions, research should strive to characterise brain function related to different cognitive demands or processes. It is conceivable that a brain region may show neural efficiency in one task and/or for a specific sample while it does not show neural efficiency in a different task or for a different sample. For example, Grabner, Stern und Neubauer (2003) found neural efficiency in high intelligence participants only when solving a task demanding intelligence but not in a memory task. Furthermore, task familiarity led to a decrease of brain activation in the memory task. Hence, neural efficiency may result from the interplay of task characteristics and individual ability regarding the cognitive demand. Our results are further corroborated by pupillometry findings on a similar sample of hi-fluIQ and ave-fluIQ by van der Meer et al. (2010) who reported greater pupil dilations in hi-fluIQ than in ave-fluIQ when solving the most difficult items of the geometric analogical reasoning task. This was interpreted as higher general availability of cognitive resources and more extensive task-related resource allocation in hi-fluIQ.

To understand the cerebral characteristics of fluid intelligence, the focus of research should not be restricted to frontal brain regions. Furthermore, the cerebral characteristics of fluid intelligence go beyond a negative brain activation-intelligence relationship. Thus, the concept of neural efficiency may need revision and extension. More specifically, as our results show, the interplay between different brain regions from the parieto-frontal network is characteristic of high fluid intelligence and thus crucial for performance on the geometric analogical reasoning task.

To conclude, it can be conjectured that the adaptive and flexible modulation of brain activation to task demands is characteristic of high fluid intelligence rather than general neural efficiency. Thus, Cattell's definition of fluid intelligence – adaptivity and flexibility in thinking and problem solving – can be expanded from the cognitive and behavioural levels to the cerebral level, and therefore is integratively valid psychologically and physiologically. On the one hand, this may explain hitherto contradictory results on neural efficiency (e.g., Gray et al., 2003; Geake &

Hansen, 2005; Neubauer & Fink, 2009); on the other hand, this opens up new perspectives for future research, which should investigate the influence of task characteristics and individual abilities on brain activation in more detail. Furthermore, as every neuroimaging method has its particular advantages and can thus contribute a different piece of the puzzle to elucidate a research question, future research should aim at collecting evidence from various methods and could, for example, include measures of cerebral connectivity or mechanisms of neurotransmitter action.

3.1.4 Temporal characteristics of high fluid intelligence

While little was known about the cerebral correlates of high fluid intelligence, still less was known about the cerebral correlates of high fluid intelligence during adolescence, an age at which fluid intelligence reaches its peak according to Cattell (Cattell, 1963; Horn & Cattell, 1966; Cattell, 1987). In the follow-up study with a sample of high fluid intelligence high-school students solving the geometric analogical reasoning task, which demands fluid intelligence, we demonstrated that behavioural performance improved at the follow-up measurement at age 18, and the same cerebral network of parieto-frontal regions was involved in geometric analogical reasoning at both time points. Since brain activation strength did not change over time, we concluded that more efficient use of the cerebral resources led to improvements in geometric analogical reasoning performance. As the geometric analogical reasoning task or other closely related tasks are not usually utilised outside laboratory settings, the results cannot be attributed to task-specific training effects but are related to increased task familiarity at the second measuring time point or processes of cognitive development.

Based on our findings from Study 1 and reports from the literature (e.g., Ansari & Dhital, 2006; Ischebeck et al., 2007; Wright et al., 2008), we had hypothesised improvements in behavioural performance along with decreased task-related brain activation, especially in frontal brain regions, owing to a more automatised processing of the task. Contrary to our expectations, there was no decrease in brain activation in frontal brain regions. This may be because the geometric analogical reasoning task was not sufficiently automatised to elicit both improvements in behavioural performance and decreases in brain activation at the same time. Furthermore, the time period between ages 17 and 18 might not be long enough to substantiate broader developmental changes in the function of the parieto-frontal network. The congruence of brain regions involved at both measuring time points suggests that development-related changes in the function of prefrontal brain regions might be worth investigating in an early adolescence sample (between ages 11 and 15) of varying fluid intelligence levels.

To summarise, in Study 3 we showed that hi-fluIQ were able to improve their behavioural performance in a one-year follow-up of the geometric analogical reasoning task while recruiting the same cerebral network. This can be interpreted as a variant form of neural efficiency induced by task familiarity. Study 3 is one of the few fMRI studies that report multiple measuring time points instead of pursuing a cross-sectional approach.

3.2 Limitations of the studies and directions for future research

The study results presented above need to be considered along with some limitations. Fluid intelligence is a theoretical construct. Its complement is crystallised intelligence. The two hardly appear in their pure form in everyday life. The research results from my dissertation project contribute a building block to our understanding of analogical reasoning and interindividual differences in fluid intelligence. As successful learning is always based on both the individual's world knowledge and the individual's ability to identify and manipulate relations, to think flexibly, and to acquire new knowledge, it will render fruitful for future research to build upon the results presented here and to examine the interplay between fluid and crystallised intelligence. Insights from such research might, for example, aid to understand interindividual differences in scholastic performance and learning.

The sample characteristics of Studies 2 and 3 need to be considered when transferring the study results to the general population. Study 2 examined ave-fluIQ and hi-fluIQ participants. Thus, the results might not be generalised to people with below-average fluid intelligence. For reasons not related to the research content, Study 3 only followed-up on hi-fluIQ. Thus, those results might not be generalised to ave-fluIQ. How the follow-up results would have looked like for ave-fluIQ and whether or not the cerebral characteristics of below-average fluid intelligence show patterns comparable to our findings remains speculative until future research with samples composed of participants with a wider spectrum of fluid intelligence provides further insights on the cerebral characteristics of below-average fluid intelligence and the temporal characteristics of behavioural and cerebral correlates of average fluid intelligence.

Being single time point measurements, Studies 1 and 2 catch only snapshots of the behavioural and cerebral correlates of geometric analogical reasoning and fluid intelligence. Even though Study 3 is one of the very few follow-up neuroimaging studies in the field, it only covers a short time frame of cognitive development. In order to build more comprehensive models of the cerebral correlates of cognitive abilities and their development, long-term studies are desirable, following-up people from very early childhood all through adolescence and even up to adulthood.

3.3 Conclusion

Our research showed that the parieto-frontal network is involved in solving the geometric analogical reasoning task which demands fluid intelligence very purely. Furthermore, by recruiting a sample with extraordinarily high fluid intelligence, we demonstrated that task-related activation of parietal and frontal brain regions is modulated differentially by fluid intelligence. This runs counter to the postulates of the neural efficiency hypothesis, which we thus suggest to revise. Instead, the results of the presented studies suggest an integrative model of fluid intelligence which on the one hand comprises Cattell's concept of flexible and adaptive information processing on the cognitive level, and on the other hand incorporates the flexible and adaptive modulation of brain activation to task demands on the cerebral level. Taken together, this allows superior performance in cognitive tasks.

Moreover, in a one-year follow-up study demonstrating the stability of the cerebral correlates of geometric analogical reasoning in high-fluIQ, we showed that the relevant brain network for geometric analogical reasoning is already in place at age 17 and that improvements in behavioural performance due to task familiarity are indicative of more efficient use of the cerebral resources available.

Bibliography

Ackerman, P. L., Beier, M. E. & Boyle, M. O. (2005). Working memory and intelligence: The same or different constructs? *Psychological Bulletin*, *131* (1), 30-60.

Allman, J. M., Hakeem, A., Erwin, J. M., Nimchinsky, E. & Hof, P. (2001). The anterior cingulate cortex. *Annals of the New York Academy of Sciences*, *935*, 107-117.

Ansari, D. & Dhital, B. (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: An event-related functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, *18* (11), 1820-1828.

Asendorpf, J. B. (2007). *Psychologie der Persönlichkeit*. Berlin: Springer Verlag.

Beckmann, C. F., Jenkinson, M. & Smith, S. M. (2003). General multilevel linear modeling for group analysis in fMRI. *NeuroImage*, *20* (2), 1052-1063.

Beckmann, J. F. (2001). *Zur Validierung des Konstrukts des intellektuellen Veränderungspotentials. Neuere Befunde zur Validität computergestützter adaptiver Kurzzeitlerntests*. Logos Berlin.

Bennett, C. M. & Miller, M. B. (2010). How reliable are the results from functional magnetic resonance imaging? *Annals of the New York Academy of Sciences*, *1191* (1), 133-155.

Bethell-Fox, C. E., Lohmann, D. F. & Snow, R. E. (1984). Adaptive reasoning: Componential and eye movement analysis of geometric analogy performance. *Intelligence*, *8* (3), 205-38.

Blair, C. (2006). How similar are fluid cognition and general intelligence? A developmental neuroscience perspective on fluid cognition as an aspect of human cognitive ability. *Behavioral and Brain Sciences*, *29* (2), 109-125.

Blakemore, S.-J. & Choudhury, S. (2006). Development of the adolescent brain: Implications for executive function and social cognition. *Journal of Child Psychology and Psychiatry*, *47* (3-4), 296-312.

Bledowski, C., Rahm, B. & Rowe, J. B. (2009). What "works" in working memory? Separate systems for selection and updating of critical information. *Journal of Neuroscience*, *29* (43), 13735-13741.

Boroojerdi, B., Phipps, M., Kopylev, L., Wharton, C. M., Cohen, L. G. & Grafman, J. (2001). Enhancing analogic reasoning with rTMS over the left prefrontal cortex. *Neurology*, *56* (4), 526-528.

Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S. & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex.

Nature, *402* (6758), 179-181.

Botvinick, M. M., Cohen, J. D. & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: an update. *Trends in Cognitive Sciences*, *8* (12), 539-546.

Bouchard, T. & McGue, M. (1981). Familial studies of intelligence: A review. *Science*, *212* (4498), 1055-1059.

Cabeza, R. & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12* (1), 1-47.

Carpenter, P. A., Just, M. A. & Shell, P. (1990). What one intelligence test measures: A theoretical account of the processing in the Raven Progressive Matrices Test. *Psychological Review*, *97* (3), 404-431.

Carroll, J. B. (1993). *Human cognitive abilities.* Cambridge: University Press.

Cattell, R. B. (1963). Theory of fluid and crystallized intelligence: A critical experiment. *Journal of Educational Psychology*, *54* (1), 1-22.

Cattell, R. B. (1987). *Intelligence: Its structure, growth, and action.* Amsterdam: Elsevier Science Publishers.

Cavanna, A. E. & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, *129* (Pt 3), 564-583.

Chiang, M.-C., Barysheva, M., Shattuck, D. W., Lee, A. D., Madsen, S. K., Avedissian, C. et al. (2009). Genetics of brain fiber architecture and intellectual performance. *Journal of Neuroscience*, *29* (7), 2212-2224.

Colom, R., Abad, F. J., García, L. F. & Juan-Espinosa, M. (2002). Education, Wechsler's full scale IQ, and g. *Intelligence*, *30* (5), 449-462.

Colom, R., Haier, R. J., Head, K., Linera, J. Álvarez, Quiroga, M. Ángeles, Chun Shih, P. et al. (2009). Gray matter correlates of fluid, crystallized, and spatial intelligence: Testing the P-FIT model. *Intelligence*, *37* (2), 124-135.

Colom, R., Jung, R. E. & Haier, R. J. (2006). Finding the g-factor in brain structure using the method of correlated vectors. *Intelligence*, *34* (6), 561-570.

Conway, A. R. A., Cowan, N., Bunting, M. F., Therriault, D. J. & Minkoff, S. R. B. (2002). A latent variable analysis of working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence. *Intelligence*, *30* (2), 163-183.

Conway, A. R. A., Kane, M. J. & Engle, R. W. (2003). Working memory capacity and its relation to general intelligence. *Trends in Cognitive Sciences*, *7* (12), 547-552.

Corballis, M. C. & Roldan, C. E. (1975). Detection of symmetry as a function of angular orientation. *Journal of Experimental Psychology: Human Perception and Performance*, *1* (3), 221-230.

Corbetta, M. & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3* (3), 201-215.

Crone, E. A., Wendelken, C., van Leijenhorst, L., Honomichl, R. D., Christoff, K. & Bunge, S. A. (2009). Neurocognitive development of relational reasoning. *Developmental Science*, *12* (1), 55-66.

Dehaene, S., Molko, N., Cohen, L. & Wilson, A. J. (2004). Arithmetic and the brain. *Current Opinion in Neurobiology*, *14* (2), 218-224.

Doppelmayr, M., Klimesch, W., Stadler, W., Pöllhuber, D. & Heine, C. (2002). EEG alpha power and intelligence. *Intelligence*, *30* (3), 289-302.

Duncan, J. (2003). Intelligence tests predict brain response to demanding task events. *Nature Neuroscience*, *6* (3), 207-208.

Duncan, J., Seitz, R. J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A. et al. (2000). A neural basis for general intelligence. *Science*, *289* (5478), 457-460.

Engle, R. W., Tuholski, S. W., Laughlin, J. E. & Conway, A. R. A. (1999). Working memory, short-term memory, and general fluid intelligence: A latent-variable approach. *Journal of Experimental Psychology: General*, *128* (3), 309-331.

Faillenot, I., Decety, J. & Jeannerod, M. (1999). Human brain activity related to the perception of spatial features of objects. *NeuroImage*, *10* (2), 114-124.

Feigenson, L., Dehaene, S. & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences*, *8* (7), 307-314.

Ferrer, E., O'Hare, E. D. & Bunge, S. A. (2009). Fluid reasoning and the developing brain. *Frontiers in Neuroscience*, *3* (1), 46-51.

Fisher, P. J., Turic, D., Williams, N. M., McGuffin, P., Asherson, P., Ball, D. et al. (1999). DNA pooling identifies QTLs on chromosome 4 for general cognitive ability in children. *Human Molecular Genetics*, *8* (5), 915-922.

French, R. (2002). The computational modeling of analogy-making. *Trends in Cognitive Sciences*, *6* (5), 200-205.

Friedman, L., Stern, H., Brown, G. G., Mathalon, D. H., Turner, J., Glover, G. H. et al. (2008). Test-retest and between-site reliability in a multicenter fMRI study. *Human Brain Mapping*, *29* (8), 958-972.

Friedman, N. P., Miyake, A., Corley, R. P., Young, S. E., DeFries, J. C. & Hewitt, J. K. (2006). Not all executive functions are related to intelligence. *Psychological Science*, *17* (2), 172-179.

Frings, L., Wagner, K., Quiske, A., Schwarzwald, R., Spreer, J., Halsband, U. et al. (2006). Precuneus is involved in allocentric spatial location encoding and recognition. *Experimental Brain Research*, *173* (4), 661-672.

Gazzaniga, M., Ivry, R. & Mangun, G. (2002). *Cognitive neuroscience. The biology of the mind.* New York: Norton & Company.

Geake, J. G. & Hansen, P. C. (2005). Neural correlates of intelligence as revealed by fMRI of fluid analogies. *NeuroImage*, *26* (2), 555-564.

Geake, J. G. & Hansen, P. C. (2010). Functional neural correlates of fluid and crystallized analogizing. *NeuroImage*, *49* (4), 3489-3497.

Gentner, D. (1983). Structure-mapping: A theoretical framework for analogy. *Cognitive Science*, *7* (2), 155-170.

Gentner, D. (1988). Metaphor as structure mapping: The relational shift. *Child Development*, *59*, 47-59.

Gevins, A. & Smith, M. E. (2000). Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style. *Cerebral Cortex*, *10* (9), 829-839.

Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A. et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, *2* (10), 861-863.

Goswami, U. (1991). Analogical reasoning: What develops? A review of research and theory. *Child Development*, *62*, 1-22.

Goswami, U. (1996). Analogical reasoning and cognitive development. *Advances in Child Development and Behavior*, *26*, 91-138.

Grabner, R. H., Ansari, D., Reishofer, G., Stern, E., Ebner, F. & Neuper, C. (2007). Individual differences in mathematical competence predict parietal brain activation during mental calculation. *NeuroImage*, *38* (2), 346-356.

Grabner, R. H., Fink, A., Stipacek, A., Neuper, C. & Neubauer, A. C. (2004). Intelligence and working memory systems: Evidence of neural efficiency in alpha band ERD. *Cognitive Brain Research*, *20* (2), 212-225.

Grabner, R. H., Neubauer, A. C. & Stern, E. (2006). Superior performance and neural efficiency: The impact of intelligence and expertise. *Brain Research Bulletin*, *69* (4), 422-439.

Grabner, R. H., Stern, E. & Neubauer, A. C. (2003). When intelligence loses its impact: Neural efficiency during reasoning in a familiar area. *International Journal of Psychophysiology*, *49* (2), 89-98.

Gray, J. R., Chabris, C. F. & Braver, T. S. (2003). Neural mechanisms of general fluid intelligence. *Nature Neuroscience*, *6* (3), 316-322.

Green, A. E., Fugelsang, J. A., Kraemer, D. J. M., Shamosh, N. A. & Dunbar, K. N. (2006). Frontopolar cortex mediates abstract integration in analogy. *Brain Research*, *1096* (1), 125-137.

Guthke, J., Beckmann, J. F., Stein, H., Vahle, H. & Rittner, S. (1995). *Adaptive Computergestützte Intelligenz-Lerntestbatterie (ACIL).* Mödlingen: Schuhfried.

Haier, R. J., Siegel, B. V., Nuechterlein, K. H. & Hazlett, E. (1988). Cortical glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography. *Intelligence*, *12* (2), 199-217.

Haier, R. J., Siegel, B. V., Tang, C., Abel, L. & Buchsbaum, M. S. (1992). Intelligence and changes in regional cerebral glucose metabolic rate following learning. *Intelligence*, *16* (3-4), 415-26.

Heeger, D. J. & Ress, D. (2002). What does fMRI tell us about neuronal activity? *Nature Reviews Neuroscience*, *3* (2), 142- 151.

Hofstadter, D. (2001). Analogy as the core of cognition. In D. Gentner, K. J. Holyoak & B. N. Kokinov (Hrsg.), *The analogical mind: Perspectives from cognitive science* (S. 504-537). Cambridge: MIT Press.

Hofstadter, D. & Mitchell, M. (1997). The copycat project: A model of mental fluidity and analogy-making. In D. Hofstadter (Hrsg.), *Fluid concepts and creative analogies: Computer models of the fundamental mechanisms of thought* (S. 205-267). London: Penguin Press.

Holyoak, K. J. & Morrison, R. (2005). *The Cambridge handbook of thinking and reasoning.* Cambridge: University Press.

Horn, J. L. (1968). Organization of abilities and the development of intelligence. *Psychological Review*, *75* (3), 242-259.

Horn, J. L. & Cattell, R. B. (1966). Refinement and test of the theory of fluid and crystallized general intelligences. *Journal of Educational Psychology*, *57* (5), 253-270.

Hosenfeld, B., van der Maas, H. L. J. & van den Boom, D. C. (1997). Indicators of discontinuous change in the development of analogical reasoning. *Journal of Experimental Child Psychology*, *64* (3), 367-395.

Houdé, O., Rossi, S., Lubin, A. & Joliot, M. (2010). Mapping numerical processing, reading, and executive functions in the developing brain: An fMRI meta-analysis of 52 studies including 842 children. *Developmental Science*, *13* (6), 876-885.

Huettel, S. A., Song, A. W. & McCarthy, G. (2009). *Functional magnetic resonance imaging*. Basingstoke: Palgrave Macmillan.

Hummel, J. E. & Holyoak, K. J. (2005). Relational reasoning in a neurally plausible cognitive architecture. *Current Directions in Psychological Science*, *14* (3), 153-157.

Ischebeck, A., Zamarian, L., Egger, K., Schocke, M. & Delazer, M. (2007). Imaging early practice effects in arithmetic. *NeuroImage*, *36* (3), 993-1003.

Jausovec, N. (1998). Are gifted individuals less chaotic thinkers? *Personality and Individual Differences*, *25* (2), 253-267.

Jausovec, N. (2000). Differences in cognitive processes between gifted, intelligent, creative, and average individuals while solving complex problems: An EEG study. *Intelligence*, *28* (3), 213-237.

Jezzard, P., Matthews, P. M. & Smith, S. M. (2003). *Functional MRI: An introduction to methods*. Oxford University Press.

Jung, R. E., Brooks, W. M., Yeo, R. A., Chiulli, S. J., Weers, D. C. & Sibbitt, W. L. (1999). Biochemical markers of intelligence: A proton MR spectroscopy study of normal human brain. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266* (1426), 1375-1379.

Jung, R. E. & Haier, R. J. (2007). The parieto-frontal integration theory (P-FIT) of intelligence: Converging neuroimaging evidence. *Behavioral and Brain Sciences*, *30* (2), 135-154; discussion 154-87.

Jäger, A., Süß, H.-M. & Beauducel, A. (1997). *Test für das Berliner Intelligenzstrukturmodell (BIS)*. Göttingen: Hogrefe.

Kane, M. J. & Engle, R. W. (2002). The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psychonomic Bulletin & Review*, *9* (4), 637-671.

Kane, M. J., Hambrick, D. Z. & Conway, A. R. A. (2005). Working memory capacity and fluid intelligence are strongly related constructs: Comment on Ackerman, Beier, and Boyle (2005). *Psychological Bulletin*, *131* (1), 66-71.

Kelley, T. A., Serences, J. T., Giesbrecht, B. & Yantis, S. (2008). Cortical mechanisms for shifting and holding visuospatial attention. *Cerebral Cortex*, *18* (1), 114-125.

Kelly, A. M. C. & Garavan, H. (2005). Human functional neuroimaging of brain changes associated with practice. *Cerebral Cortex*, *15* (8), 1089-1102.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, *29* (2-3), 169-195.

Kyllonen, P. C. & Christal, R. E. (1990). Reasoning ability is (little more than) working-memory capacity?! *Intelligence*, *14* (4), 389-433.

Larson, G. E., Haier, R. J., LaCasse, L. & Hazen, K. (1995). Evaluation of a "mental effort" hypothesis for correlations between cortical metabolism and intelligence. *Intelligence*, *21* (3), 267-278.

Levinson, P. J. & Carpenter, R. L. (1974). An analysis of analogical reasoning in children. *Child Development*, *45* (3), 857-861.

Liu, T., Shi, J., Zhao, D. & Yang, J. (2008). The relationship between EEG band power, cognitive processing and intelligence in school-age children. *Psychological Science Quarterly*, *50* (2), 259-268.

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature*, *453* (7197), 869-878.

Logothetis, N. K., Pauls, J., Augath, M., Trinath, T. & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, *412*, 150-157.

Luders, E., Narr, K. L., Thompson, P. M. & Toga, A. W. (2009). Neuroanatomical correlates of intelligence. *Intelligence*, *37* (2), 156-163.

Luo, Q., Perry, C., Peng, D., Jin, Z., Xu, D., Ding, G. et al. (2003). The neural substrate of analogical reasoning: An fMRI study. *Cognitive Brain Research*, *17* (3), 527-534.

Miller, E. K. & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167-202.

Mulholland, T. M., Pellegrino, J. W. & Glaser, R. (1980). Components of geometric analogy solution. *Cognitive Psychology*, *12* (2), 252-284.

Neubauer, A. C. (1990). Speed of information processing in the Hick paradigm and response latencies in a psychometric intelligence test. *Personality and Individual Differences*, *11* (2), 147-152.

Neubauer, A. C. & Fink, A. (2003). Fluid intelligence and neural efficiency: Effects of task complexity and sex. *Personality and Individual Differences*, *35* (4), 811-827.

Neubauer, A. C. & Fink, A. (2009). Intelligence and neural efficiency. *Neuroscience & Biobehavioral Reviews*, *33* (7), 1004-1023.

Neubauer, A. C., Fink, A. & Schrausser, D. G. (2002). Intelligence and neural efficiency: The influence of task content and sex on the brain-IQ relationship. *Intelligence*, *30* (6), 515-536.

Neubauer, A. C., Freudenthaler, H. H. & Pfurtscheller, G. (1995). Intelligence and spatiotemporal patterns of event-related desynchronization (ERD). *Intelligence*, *20* (3), 249-266.

Neubauer, A. C., Grabner, R. H., Fink, A. & Neuper, C. (2005). Intelligence and neural efficiency: Further evidence of the influence of task content and sex on the brain-IQ relationship. *Cognitive Brain Research*, *25* (1), 217-225.

Neubauer, A. C., Grabner, R. H., Freudenthaler, H. H., Beckmann, J. F. & Guthke, J. (2004). Intelligence and individual differences in becoming neurally efficient. *Acta Psychologica*, *116* (1), 55-74.

Neubauer, A. C., Riemann, R., Mayer, R. & Angleitner, A. (1997). Intelligence and reaction times in the Hick, Sternberg and Posner paradigms. *Personality and Individual Differences*, *22* (6), 885-894.

Neubauer, A. C., Sange, G. & Pfurtscheller, G. (1999). Psychometric intelligence and event-related desynchronisation during performance of a letter matching task. In G. Pfurtscheller & F. Lopes da Silva (Hrsg.), *Event-related desynchronization (ERD) and related oscillatory EEG-phenomena of the awake brain* (S. 219-230). Amsterdam: Elsevier.

Newman, S. D. & Just, M. A. (2005). The neural bases of intelligence: A perspective based on functional neuroimaging. In J. Sternberg & J. Pretz (Hrsg.), *Cognition and intelligence: Identifying the mechanisms of the mind* (S. 88-103). Cambridge: University Press.

Oberauer, K., Schulze, R., Wilhelm, O. & Süß, H.-M. (2005). Working memory and intelligence–their correlation and their relation: Comment on Ackerman, Beier, and Boyle (2005). *Psychological Bulletin*, *131* (1), 61-65.

Olesen, P. J., Westerberg, H. & Klingberg, T. (2004). Increased prefrontal and parietal activity after training of working memory. *Nature Neuroscience*, *7* (1), 75-79.

Orrison, W. W., Lewine, J. D., Sanders, J. A. & Hartshorne, M. F. (1995). *Functional brain imaging.* St. Louis: Mosby.

Pfurtscheller, G. & Lopes da Silva, F. (2005). Event-related desynchronization (ERD) and event-related synchronization (ERS). In E. Niedermeyer & F. Lopes da Silva (Hrsg.), *Electroencephalography: Basic principles, clinical applications, and related fields* (S. 1003-1016). Philadelphia: Lippincott, Williams & Wilkins.

Poldrack, R. A. (2000). Imaging brain plasticity: Conceptual and methodological issues - A theoretical review. *NeuroImage*, *12* (1), 1-13.

Prabhakaran, V., Smith, J. A., Desmond, J. E., Glover, G. H. & Gabrieli, J. D. (1997). Neural substrates of fluid reasoning: An fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test. *Cognitive Psychology*, *33* (1), 43-63.

Preusse, F., van der Meer, E., Deshpande, G., Krueger, F. & Wartenburger, I. (2011). Fluid intelligence allows flexible recruitment of the parieto-frontal network in analogical reasoning. *Frontiers in Human Neuroscience*, *5* (22), 1-14.

Preusse, F., van der Meer, E., Ullwer, D., Brucks, M., Krueger, F. & Wartenburger, I. (2010). Long-term characteristics of analogical processing in high-school students with high fluid intelligence: An fMRI study. *International Journal* *on Mathematics Education (ZDM)*, *42* (6), 635-647.

Prieto-Corona, B., Rodríguez-Camacho, M., Silva-Pereyra, J., Marosi, E., Fernández, T. & Guerrero, V. (2010). Event-related potentials findings differ between children and adults during arithmetic-fact retrieval. *Neuroscience Letters*, *468* (3), 220-224.

Rae, C., Scott, R. B., Thompson, C. H., Kemp, G. J., Dumughn, I., Styles, P. et al. (1996). Is pH a biochemical marker of IQ? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *263* (1373), 1061-1064.

Raichle, M. E. & Mintun, M. A. (2006). Brain work and brain imaging. *Annual Review of Neuroscience*, *29*, 449-476.

Rammsayer, T. H. & Troche, S. J. (2010). Effects of age and the relationship between response time measures and psychometric intelligence in younger adults. *Personality and Individual Differences*, *48* (1), 49-53.

Raven, J., Court, J. & Raven, J. J. (1980). *RAVEN-Matrizen-Test. Advanced Progressive Matrices*. Weinheim: Beltz Test Gesellschaft.

Richland, L. E., Morrison, R. G. & Holyoak, K. J. (2006). Children's development of analogical reasoning: Insights from scene analogy problems. *Journal of Experimental Child Psychology*, *94* (3), 249-273.

Risberg, J., Maximilian, A. V. & Prohovnik, I. (1977). Changes of cortical activity patterns during habituation to a reasoning test: A study with the 133Xe inhalation technique for measurement of regional cerebral blood flow. *Neuropsychologia*, *15* (6), 793-798.

Roberts, A., Robbins, T. & Weiskrantz, L. (1998). *The prefrontal cortex: Executive and cognitive functions*. Oxford: University Press.

Royer, F. L. (1981). Detection of symmetry. *Journal of Experimental Psychology: Human Perception and Performance*, *7* (6), 1186-1210.

Rypma, B., Berger, J. S. & D'Esposito, M. (2002). The influence of working-memory demand and subject performance on prefrontal cortical activity. *Journal of Cognitive Neuroscience*, *14* (5), 721-731.

Rypma, B., Berger, J. S., Prabhakaran, V., Bly, B. M., Kimberg, D. Y., Biswal, B. B. et al. (2006). Neural correlates of cognitive efficiency. *NeuroImage*, *33* (3), 969-979.

Sack, A. T. (2009). Parietal cortex and spatial cognition. *Behavioural Brain Research*, *202* (2), 153 - 161.

Salthouse, T. A. & Pink, J. E. (2008). Why is working memory related to fluid intelligence? *Psychonomic Bulletin & Review*, *15* (2), 364-371.

Schweizer, K., Goldhammer, F., Rauch, W. & Moosbrugger, H. (2007). On the validity of Raven's matrices test: Does spatial ability contribute to performance? *Personality and Individual Differences*, *43* (8), 1998-2010.

Shaw, P., Greenstein, D., Lerch, J., Clasen, L., Lenroot, R., Gogtay, N. et al. (2006). Intellectual ability and cortical development in children and adolescents. *Nature*, *440* (7084), 676-679.

Shulman, G. L., Astafiev, S. V., Franke, D., Pope, D. L. W., Snyder, A. Z., McAvoy, M. P. et al. (2009). Interaction of stimulus-driven reorienting and expectation in ventral and dorsal frontoparietal and basal ganglia-cortical networks. *Journal of Neuroscience*, *29* (14), 4392-4407.

Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H. et al. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage*, *23 Suppl 1*, S208-S219.

Sodian, B. (2008). Entwicklung des Denkens. In R. Oerter & L. Montada (Hrsg.), *Entwicklungspsychologie* (S. 436-461). Weinheim: Psychologie Verlags Union.

Sternberg, R. J. (1977). Component processes in analogical reasoning. *Psychological Review*, *84* (4), 353-378.

Sternberg, R. J. & Rifkin, B. (1979). The development of analogical reasoning processes. *Journal of Experimental Child Psychology*, *27* (2), 195-232.

Süß, H.-M. (2003). Intelligenztheorie. In K. D. Kubinger & R. S. Jäger (Hrsg.), *Schlüsselbegriffe der Psychologischen Diagnostik* (S. 217ff.). Weinheim: Psychologie Verlags Union.

Süß, H.-M., Oberauer, K., Wittmann, W. W., Wilhelm, O. & Schulze, R. (2002). Working-memory capacity explains reasoning ability–and a little bit more. *Intelligence*, *30* (3), 261-288.

Unsworth, N., Brewer, G. A. & Spillers, G. J. (2009). There's more to the working memory capacity-fluid intelligence relationship than just secondary memory. *Psychonomic Bulletin & Review*, *16* (5), 931-937.

Unsworth, N., Miller, J. D., Lakey, C. E., Young, D. L., Meeks, J. T., Campbell, W. K. et al. (2009). Exploring the relations among executive functions, fluid intelligence, and personality. *Journal of Individual Differences*, *30* (4), 194-200.

van der Meer, E., Beyer, R., Horn, J., Foth, M., Bornemann, B., Ries, J. et al. (2010). Resource allocation and fluid intelligence: Insights from pupillometry. *Psychophysiology*, *47* (1), 158-169.

Vernon, P. A. (1983). Speed of information processing and general intelligence. *Intelligence*, *7* (1), 53-70.

Villringer, A. & Dirnagl, U. (1995). Coupling of brain activity and cerebral blood flow: Basis of functional neuroimaging. *Cerebrovascular and Brain Metabolism Reviews*, *7* (3), 240-276.

Vosniadou, S. & Ortony, A. (1989). *Similarity and analogical reasoning.* Cambridge: University Press.

Wartenburger, I., Heekeren, H. R., Preusse, F., Kramer, J. & van der Meer, E. (2009). Cerebral correlates of analogical processing and their modulation by training. *NeuroImage*, *48* (1), 291-302.

Wharton, C. M., Grafman, J., Flitman, S. S., Hansen, E. K., Brauner, J., Marks, A. et al. (2000). Toward neuroanatomical models of analogy: A positron emission tomography study of analogical mapping. *Cognitive Psychology*, *40* (3), 173-197.

Wilhelm, O. & Oberauer, K. (2006). Why are reasoning ability and working memory capacity related to mental speed? An investigation of stimulus-response compatibility in choice reaction time tasks. *European Journal of Cognitive Psychology*, *18* (1), 18-50.

Wright, S. B., Matlen, B. J., Baym, C. L., Ferrer, E. & Bunge, S. A. (2008). Neural correlates of fluid reasoning in children and adults. *Frontiers in Human Neuroscience*, *1*, 1-8.

Zacks, J. M. & Michelon, P. (2005). Transformations of visuospatial images. *Behavioral and Cognitive Neuroscience Reviews*, *4* (2), 96-118.

Selbstständigkeitserklärung

Ich erkläre hiermit, dass ich die vorliegende Dissertationsschrift selbstständig und ohne unerlaubte Hilfe angefertigt sowie nur die angegebene Literatur verwendet habe. Jede Mitwirkung von anderen mit mir zusammen arbeitenden Personen an den Forschungsergebnissen ist explizit gekennzeichnet.

Ich besitze keinen Doktorgrad und habe mich nicht bereits anderwärts um einen solchen beworben. Mir ist die Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät II der Humboldt-Universität zu Berlin (veröffentlicht im Amtlichen Mitteilungsblatt Nr. 34/2006) bekannt.

Berlin, den 28. Juli 2011

Franziska Preusse