The Development and Relation of Working Memory and Fluid Intelligence in Middle and Late Childhood: A Neurocognitive Developmental Perspective

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Eva Aurelia Aeschlimann

Rüderswil (BE)

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Prof. Dr. Thomas H. Rammsayer (ZweitgutachterIn) angenommen.
Bern, den 24. Mai 2018 Die Dekanin: Prof. Dr. Tina Hascher

To all children

This cumulative dissertation includes an umbrella paper and the following two scientific studies:

Study 1:

Aeschlimann, E. A., Voelke, A. E., & Roebers, C. M. (2017). Short-term storage and executive working memory processing predict fluid intelligence in primary school children. *Journal of Intelligence, 5*, 1-17. doi:10.3390/jintelligence5020017

Study 2:

Aeschlimann E. A., Witmer J. S., Metz A. J., Rammsayer T. H., Roebers C. M. Effects of age and mental ability on verbal working memory in children: A functional near-infrared spectroscopy study. *Manuscript submitted to the Journal Developmental Neuropsychology*.

Umbrella Paper

The Development and Relation of Working Memory and Fluid Intelligence in Middle and Late Childhood:

A Neurocognitive Developmental Perspective

Eva A. Aeschlimann

University of Bern

Abstract

Working memory (WM) und fluid intelligence (Gf) are both key abilities in many cognitive development areas. Previous studies showed that both constructs are substantially related. However, WM consists of different aspects and it is not clear which of these aspects underlies this relation. Moreover, previous studies investigating the development of the neural basis of verbal WM have neglected the fact that WM and Gf are related. Accordingly, the main goal of the two studies presented in this dissertation was to gain a deeper understanding of the relation between WM and Gf. In addition, we aimed to investigate how age and Gf combine to affect WM performance and WM-related brain activity in middle and late childhood. The main question addressed in this umbrella paper was driven by the question of how Gf and WM develop, which was incorporated in both studies. The results revealed that WM and Gf improve with increasing age. Moreover, results showed that different WM aspects promote the development of WM as well as of Gf. However, also individual differences in Gf seem to foster the development in WM. Hence, the relation between WM and Gf seems to go in both directions. In addition, neural results revealed an age-by-Gf interaction effect on WM-related brain activation, indicating that also functional brain differences contribute to the development of WM and Gf. The results are discussed in terms of neural efficiency and in terms of theoretical and practical implications.

Content

1. General Introduction

Many daily tasks and especially demands at school challenge working memory (WM). For example, solving a mathematical task requires to remember while simultaneously processing the numbers. Moreover, WM is essential for further cognitive abilities such as language, reading, problem solving and reasoning (Archibald & Gathercole, 2006; Bjorklund, 2012; Cowan & Alloway, 2009). Hence, the questions how WM develops with age and how individual differences emerge are central topics in child developmental research. An important factor explaining individual differences in WM is intelligence. Namely, WM and intelligence are positively related (Conway, Getz, Macnamara, & Engel de Abreu, 2011). Intelligence itself is also essential for developmental outcomes, especially for educational achievements (Deary, 2012; Deary, Strand, Smith, & Fernandes, 2007).

The relation between WM and intelligence has been widely investigated. However, explanations for the relation between WM and intelligence are still being discussed. In study 1, we investigated whether different WM aspects are cognitive mechanisms underlying the WM-intelligence relation. Moreover, to gain a better understanding of the development of WM, its neural basis has been increasingly investigated (Jolles, Kleibeuker, Rombouts, & Crone, 2011; Vogan, Morgan, Powell, Smith, & Taylor, 2016). Despite WM and intelligence being related, no prior study investigated developmental changes in the neural basis of WM while simultaneously controlling for intelligence. Hence, this topic was addressed in a further project, study 2.

A better understanding of the development of WM and intelligence is of special interest when considering for example their contribution for education (see above). Education in turn is central for the life of an individual in a Western culture (e.g., health, income and social status; Becker, 2017). Moreover, a better understanding of the development of WM and intelligence will influence theories and in the longer term, this may serve to support children with lower abilities in these constructs. Therefore, the overall question of the present umbrella paper is “how do WM and intelligence develop?”. This question also comprises the topics how individual differences emerge and how both constructs are related.

1.1. Working Memory

The term *working memory* (WM) refers to the ability to keep information in a highly accessible state while simultaneously processing it in mind. WM is positively related to social and emotional abilities but also to various cognitive developmental domains (e.g., language, reading, mathematics; Archibald & Gathercole, 2006; Cowan & Alloway, 2009; de Wilde, Koot, & van Lier, 2016; Zelazo & Cunningham, 2007).

Various theories and models describe WM differently. What all theories have in common is the assumption of a limited WM capacity. This means that only a small amount of information can be maintained during a restricted period of time, while processing this or additional information (Baddeley, 2012; Cowan & Alloway, 2009; Engle, Tuholski, Laughlin, & Conway, 1999; Friedman & Miyake, 2000; Oberauer, Süß, Wilhelm, & Wittman, 2003). Hence, WM seems to comprise two aspects: Firstly, a more passive storage aspect (also denoted as maintenance of information, short-term memory capacity or scope of attention). Secondly, a higher ordered executive processing aspect (also denoted as manipulation, control of attention or central executive; Baddeley, 2012; Cowan & Alloway, 2009; Engle et al., 1999; Jarrold, 2016).

WM theories differentiate in distinct points from one another: (a) Some theories differ whether they take more a domain-specific or domain-general view of WM. More precisely, whether WM can be divided into verbal and visual-spatial subcomponents or not (Alloway & Alloway, 2013; Baddeley, 2012; Chow & Conway, 2015; Swanson, 2017). (b) WM theories also differ whether they see WM as containing a unitary mechanism or as a multi-faceted construct (Cowan, 2005; Jarrold, 2016; Unsworth, 2016). (c) WM theories further differ in terms of their relation between WM and long-term memory (LTM). More precisely, WM theories differ whether WM and LTM are two different interacting systems, or separate but related aspects of one system, or whether WM represents activated information of LTM (Baddeley, 2012; Cowan, 2005; Swanson, 2017). As most authors of the WM theories also considered the relation to intelligence, WM theories will be discussed again later when introducing the relation between WM and intelligence.

Further theories considering WM are executive function (EF) theories. Together with inhibition and flexibility, WM directly guides the goal-directed behavior, as it formulates and maintains the action-oriented rules (Diamond, 2013; Miyake et al., 2000). Inhibition refers to the ability to keep back dominant, automatic responses. Flexibility refers to the ability to switch attention between mental sets, rules or tasks (Diamond, 2013; Miyake et al., 2000). Consequently, these three EF processes are interacting with each other, meaning that WM most of the time does not operate alone (Miyake et al., 2000; Zelazo, 2015).

From a developmental neurocognitive perspective, *the Iterative-Reprocessing (IR) model of self-regulation* (i.e., EF) is of special interest, because it integrates WM and further neurocognitive skills to explain effective learning (see Figure A in Appendix A; Zelazo, 2015). The model will be described more precisely due to its importance to the studies described in this umbrella paper. In the IR model of self-regulation, effective learning and adaptation (or problem solving) occurs via goal-directed modulation of attention and behavior. For the goal-directed modulation of behavior, different interrelated neurocognitive skills are essential: (a) EF represent the set of regulatory skills which guide behavior, (b) the use of explicit action-oriented rules serve the EF to guide the goal-directed behavior. In addition, (c) reflection (i.e., metacognition) monitors the events. Reflection is reinforced by the detection of conflict or uncertainty and provides an important basis for the EF and therefore also for the maintenance and formulation of more complex rules. These neurocognitive skills, in turn, depend on the iterative reprocessing of information. The iterative reprocessing via neural circuits, which coordinate hierarchically arranged regions of the prefrontal cortex (PFC), allows the reflective formulation and maintenance of more complex action-oriented rules. Hence, in this model, WM represents an important construct. Together with inhibition and flexibility, WM directly guides the goal-directed behavior, as it formulates and maintains the action-oriented rules.

The most popular tasks to assess WM are the so-called complex span tasks, in which a participant has to keep some information in mind while simultaneously processing the same or additional information (Alloway, Gathercole, & Pickering, 2006; Conway et al., 2005).

Consequently, a complex span task measures the WM capacity, which includes the storage and processing aspects of WM (i.e., the number of items one can hold in mind while processing them). To isolate the executive processing aspect, the storage aspect is statistically controlled for in complex span tasks (Colom, Rebollo, Abad, & Shih, 2006). So-called simple span tasks—in which participants have to recall stimuli in order, immediately after presentation—are used to assess the storage aspect (Colom et al., 2006; Conway et al., 2005).

How the developmental curve of WM runs and at which age WM peaks is still unclear (Swanson, 2017). Some studies have revealed that children's WM performance increases more or less linearly during childhood until adolescents (Gathercole, Pickering, Ambridge, & Wearing, 2004; McAuley & White, 2011; Pelegrina et al., 2015). Other studies found that the increase already levels off at the age of 9 until 11 and then WM increases only slowly until young adulthood (Gathercole, 1999; Huizinga, Dolan, & van der Molen, 2006; Swanson, 2017). However, other studies found that WM develops until the age of 30 and 40 (Alloway & Alloway, 2013; Swanson, 1999).

1.2. Intelligence

Intelligence (Latin: *understand*) is a widely used term and denoted in various ways. One group of experts defined it as follows:

> Intelligence is a very general mental capability that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience. (….) it reflects a broader and deeper capability for comprehending our surroundings-"catching on," " making sense" of things, or "figuring out" what to do (Gottfredson, 1997, p. 13).

Hence, it is not surprising that intelligence plays a central role in many areas of live. For example, individuals who perform better on an intelligence task live a healthier and longer life (Deary, 2012). Furthermore, it has been found that already childhood intelligence is a powerful predictor of developmental outcomes, especially for educational achievement. Approximately 60 % of variance in mathematics and 50 % in linguistic disciplines are explained by intelligence

(Calvin, Fernandes, Smith, Visscher, & Deary, 2010; Christopher et al., 2012; Deary et al., 2007; Green, Bunge, Briones Chiongbian, Barrow, & Ferrer, 2017).

Intelligence has been a subject of research for more than a century (Galton, 1869). Since the first decade of the twentieth century, various theories and models have been proposed (Sternberg & Kaufman, 2011). The most influential theories—also for the construction of intelligence tests—have been psychometric theories of intelligence. These theories describe the structure of intelligence based on hierarchically ordered factors (Willis, Dumont, & Kaufman, 2011).

At the highest level, psychometric intelligence theories contain either one or more broad factors. These broad factors represent general abilities. Lower levels represent more specialized factors. For example, at the highest level of the extended Gf-Gc theory, there are two broad factors, the *fluid intelligence* (Gf) and *crystalized intelligence* (Gc; Horn & Blankson, 2005). Gf refers to the reasoning ability and describes the ability to flexibly adapt our thinking to a new cognitive problem. It is viewed as inherent and relatively culture-free. In contrast, Gc describes the ability to make use of acquired knowledge and learned skills to answer questions or solve problems and is therefore dependent on education and culture (Cattell, 1963; Horn & Cattell, 1966). Further theories like Carroll’s (1993) three-striatum theory and Cattell-Horn-Carroll theory contain at the highest level one broad factor, the so-called *g*-factor or Spearman’s *g*. In these theories, Gf and Gc represent more specific factors both underlying the *g*-factor (McGrew, 2005; McGrew, 2009).

The studies of the present dissertation focus on Gf. This is because Gf is highly related to general intelligence (i.e., *g*-factor), relatively culture-free and can be assessed reliably and economically (Hunt, 2011; Weiß, 2006). Gf is assessed with tests in which individuals are typically faced with unfamiliar figural problems, so called matrices (Raven, Raven, & Court, 2001; Weiß, 2006). In such figural problems, a matrix has to be completed or continued, which requires inductive and deductive reasoning abilities (Hunt, 2011).

In addition to psychometric intelligence theories, further theories like system theories, culture theories and biology theories have been proposed (Davidson & Kemp, 2011; Sternberg, 2012). Biological theories consider the central role of genes and the brain for intelligence. One important theory is the Parieto-Frontal Integration Theory (P-FIT) of Intelligence (Jung & Haier, 2007). The theory proposes that brain regions responsible for individual differences in intelligence are distributed throughout the brain, but mostly in parietal and frontal areas. In addition, the P-FIT proposes that any differences within the parieto-frontal network can lead to individual differences in intelligence. Thus, individual differences in intelligence can emerge due to differences in the structural characteristics of any brain region within the network, but also due to differences in the efficiency of the processing of information within the network (Haier, 2011; Jung & Haier, 2007). A current meta-analysis confirmed the P-FIT. The authors of the meta-analysis even proposed to extend the theory and integrate also the posterior cingulate cortex and subcortical structures (Basten, Hilger, & Fiebach, 2015).

The idea that brains of individuals with higher intelligence are more efficient in information processing is also part of the neural efficiency hypothesis of intelligence proposed by Haier et al. (1988). This initially proposed efficiency hypothesis claimed that higher intelligent individuals showed a lower and more specifically localized glucose metabolic rate (Haier, Siegel, Tang, Abel, & Buchsbaum, 1992). Today, it is beyond debate that neural efficiency is much more complicated and depends on various factors, like the method applied to asses brain activation, the investigated brain area or the task difficulty (Neubauer & Fink, 2009). For example, regarding task difficulty, previous findings showed that the neural efficiency hypothesis was confirmed for simple tasks and for moderately difficult tasks, but not for highly demanding tasks. In highly demanding tasks, brains of more intelligent individuals were less neurally efficient compared to brains of less intelligent individuals (Neubauer & Fink, 2009; Zhang, Gan, & Wang, 2015). Note, the term neural efficiency is also used independently of differences in intelligence (Jäncke, 2014). For example, neural efficiency can be related to differences in experience or in performance (Gimenez et al., 2014; Jäncke, 2014). Hence, all differences in the strength of brain activation evoked by a cognitive task can be interpreted in terms of neural efficiency (Basten et al., 2015). Consequently, it could also be investigated how neural efficiency relates to differences in age.

Coming back to Gf, the developmental curve of Gf increases rapidly during early and middle childhood, increases slower during adolescence and levels off into young-adulthood (Fry & Hale, 2000; McArdle, Ferrer-Caja, Hamagami, & Woodcock, 2002). An important developmental factor of Gf is WM (Žebec, Demetriou, & Kotrla-Topić, 2015). WM has even been described as the information processes that best predicts Gf (Bayliss, Jarrold, Baddeley, Gunn, & Leigh, 2005; Conway, Kane, & Engle, 2003; Oberauer, Süß, Schulze, Wilhelm, & Wittmann, 2000).

1.3. The Relation Between Working Memory and Fluid Intelligence

WM and Gf are substantially related. Indices for this relation are the similar developmental curves of both constructs, but also neurodevelopmental disorders like the Down-Syndrome, in which individuals are impaired in WM and Gf (Jarrold, Purser, & Brock, 2006; Silverman, 2007; Žebec et al., 2015). Furthermore, both WM and Gf tasks involve activation in the frontal-parietal brain network (Bunge & Wright, 2007; Haier, 2017; Jog et al., 2016). Hence, it is not surprising that some authors have suggested that WM and Gf represent the same construct (Ackerman, Beier, & Boyle, 2005; Kyllonen, 2002). However, specific developmental disorders, like math disability or specific language disorders in which an individual has deficits in WM but not in Gf indicate that both seem to represent separable constructs (Bjorklund, 2012; Swanson, 2005).

Indeed, studies directly investigating the relation between WM and Gf in adults found that although both constructs relate highly (between r = .50 and r = .85), they are separable (Ackerman et al., 2005; Oberauer, Schulze, Wilhelm, & Süß, 2005). In recent studies with children, the relation shows a similar strength and results indicate that WM and Gf are already separable (Giofrè, Mammarella, & Cornoldi, 2013; Kuhn, 2016; Shahabi, Abad, & Colom, 2014).

Different reasons explain why WM and intelligence are substantially related. For example, environmental and genetic factors may play a role (Beckett, Castle, Rutter, & Sonuga-Barke, 2010; Luciano et al., 2001). However, also the maturation of the brain, the shared neural basis and shared cognitive information processes seem to contribute to the relation (Clark, Lawlor-Savage, & Goghari, 2017; Colom et al., 2013; Conway & Kovacs, 2013; Wendelken, Ferrer, Whitaker, & Bunge, 2015).

Different theories describe the WM-intelligence relation from an information-processing approach. Because in study 1, we investigated whether different WM aspects (i.e., information processes) are mechanisms underlying the WM-intelligence relation, these theories will be shortly discussed. One of these theories is the popular multi-component WM model of Baddeley and Hitch (1974). The authors of this model proposed that a fixed pool of general resources has to be shared between the storage components (i.e., visuospatial sketchpad and phonological loop) and the processing of information. The authors assumed that individual differences in the *ability to share resources* account for the relation between WM and higher order cognition, like intelligence. In a further theory, by Engle et al. (1999) and Engle and Kane (2003), authors proposed that individual differences in executive processing, or as they call it the *control of attention*, explain the relation between WM and intelligence. In another model, the embedded process model by Cowan et al. (2005), authors assume that individual differences in the storage capacity, or as they call it the *scope of attention*, account for the relation between WM and intelligence. More recent WM theories take a multi-faceted view of WM. They suggest that individual differences in different WM aspects underlie the WM-intelligence relation (Jarrold, 2016; Unsworth, Fukuda, Awh, & Vogel, 2014).

1.4. Functional Near-Infrared Spectroscopy

In study 2, WM-related brain activity was assessed with functional near-infrared spectroscopy (fNIRS). Functional NIRS was used because this method has different advantages. Compared to functional magnetic resonance imaging (fMRI), fNIRS is relatively inexpensive and has a better temporal resolution. Essentially, for research with children, fNIRS is less sensitive to movement artefacts. Children do not need to lie in a loud tube, but can for example sit in a chair. Hence, cortex activity can be assessed in a more naturalistic setting. The use of verbal WM tasks—where individuals reply orally—is possible, in contrast to fMRI where face movement may render the measurements useless (Gervain et al., 2011; Wilcox & Biondi, 2015).

Functional NIRS is a non-invasive technique. It measures the brain activity of the superior layers of the cortex indirectly by the cerebral blood flow (similar to the BOLD signal of fMRI; Scholkmann et al., 2014). This is possible because neural activity is coupled with changes in local cerebral blood flow (called the neurovascular coupling; Leithner et al., 2010). More precisely, fNIRS measures the changes of the oxygenated and deoxygenated hemoglobin concentrations ([O_2Hb], [HHb]) which are related to neural activity (Scholkmann et al., 2014). As the near-infrared light (650-950 nm) passes through skin, skull and brain tissue, it gets absorbed and scattered by tissue. Light detectors measure the intensity of the exiting light at multiple wavelengths. The relative [O_2Hb] and [HHb] can be calculated from the changes in absorbance (Scholkmann et al., 2014). Typically, during cortical activation, local concentrations of O_2Hb increase and those of HHb decrease (Gervain et al., 2011; Huppert, Hoge, Diamond, Franceschini, & Boas, 2006; Scholkmann et al., 2014; Tachtsidis & Scholkmann, 2016; Wilcox & Biondi, 2015).

Simultaneous use of fNIRS with fMRI or positron emission tomography (PET) demonstrated that fNIRS is a reliable measure of brain functions (Huppert et al., 2006; Sato et al., 2013; Wijeakumar, Huppert, Magnotta, Buss, & Spencer, 2017). Furthermore, several previous studies showed that cortex activity evoked by a WM task can be measured with fNIRS (Buss, Fox, Boas, & Spencer, 2014; Gu et al., 2017; Matsuura et al., 2014; Perlman, Huppert, & Luna, 2015; Schecklmann et al., 2010; Tsujii, Yamamoto, Masuda, & Watanabe, 2009; Tsujii, Yamamoto, Ohira, Takahashi, & Watanabe, 2010; Tsujimoto, Yamamoto, Kawaguchi, Koizumi, & Sawaguchi, 2004; Zhu, Wang, & Wu, 2012). As in the fMRI field, also in the field of fNIRS, previous studies included mainly visual WM tasks and only few used a non-spatial or a verbal WM task. These few studies found that verbal WM-related brain activity can be assessed with fNIRS (Gu et al., 2017; Zhu et al., 2012). Further previous work found that fNIRS is able to detect differences in cortex activity due to differences in age and intelligence (Buss et al., 2014;

Di Domenico, Rodrigo, Ayaz, Fournier, & Ruocco, 2015; Perlman et al., 2015; Tsujii et al., 2009). Consequently, fNIRS is a potential technique to investigate the question of study 2, namely how age and Gf combine to affect verbal WM-related brain activity in children.

However, previous studies investigating cognitive tasks (incl. WM tasks) in children or adults also showed methodical drawbacks, hampering the interpretation of the results. For example, in WM research, only few studies controlled for the hemodynamic responses in the extra-cerebral space. In most fNIRS devices, the signal from the cortex is superimposed by these extra-cerebral responses, therefore adding a contamination (see Scholkmann et al., 2014 for a review). Moreover, only few studies included an active control task (Sanefuji et al., 2011; Sato, Dresler, Haeussinger, Fallgatter, & Ehlis, 2014; Schecklmann et al., 2010). The inclusion of an active control task aims at controlling for other task features, which are induced by the WM task in addition to the intended WM stimulation (e.g., visual, auditory inputs or movements). Furthermore, only few studies considered the relative time dynamics of [O_2Hb] and [HHb] and analyzed only [O_2Hb] (Buss et al., 2014; Perlman et al., 2015). Consequently, it is impossible to conclude if the [O_2Hb] changes are associated with cortical activation or if they are due to other blood flow processes (Matsuura et al., 2014; Schecklmann et al., 2010; Tsujii et al., 2009; Tsujimoto et al., 2004). Thus, one of the aims in study 2 was to overcome the methodical disadvantages of previous studies and to examine whether fNIRS is a sensible tool for measuring WM-related cortex activity in children.

Note that study 2 was the first fNIRS study released by the department of Psychology of the University of Bern. Hence, before the project could be started, fNIRS specific knowledge had to be acquired and different methodical challenges had to be faced. Most of these challenges were related to the headgear (forehead fiber holder from Shimadzu Corporation, 2010) which held the glass fiber light emitters and detectors (called optodes). Among these challenges were: (a) the optodes caused pressure on the forehead which started to hurt after a few minutes, (b) the headgear did not fit all participant’s head shapes, and (c) the headgear did not include short-distance channels for the optodes. Note, short-distance channels (e.g., an emitter-detector distance of 15 mm instead of 30 mm) were necessary in order to be able to control for the hemodynamic responses in the extra-cerebral space (Saager & Berger, 2005). Because of these points, the headgear had to be modified and was completely re-manufactured using laser cut (see study 2, Figure S1, Supplemental Material 1, picture of the headgear). Among others, further challenges were the handling of movement artefacts. Although fNIRS is less sensitive to movement compared to fMRI, movement also causes artefacts in fNIRS data. Therefore, the laboratory was furnished by a special chair with head-, arm- and a footrest. Despite of these furnishings, our fNIRS data showed many movement artefacts, especially in the younger children (mainly caused by movement of the eyebrows). As a result, a time-consuming movement artefact removal method was conducted (Scholkmann, Spichtig, Muehlemann, & Wolf, 2010). Despite the aforementioned challenges and difficulties, the fNIRS method was successfully applied in study 2, which enabled us to leverage the advantages of this method to gain new insight in the field of how age and Gf affect WM-related cortex activity.

2. The Projects

2.1. Study 1

Study 1, entitled “Short-term storage and executive working memory processing predict fluid intelligence in primary school children”, aimed to investigate the interrelation between different WM aspects and their relation to Gf. To investigate this issue, Gf and the four WM aspects verbal storage, visual-spatial storage, verbal processing and visual-spatial processing were assessed in children between the age of 9 (*M* = 9.5 years; *SD* = 0.3 years; range: 9–10 years) and 11 years (*M* = 11.5 years; *SD* = 0.25 years; range: 11–12 years).

Results revealed positive correlations between age and the WM tasks as well as between age and the Gf task (see study 1: Table 3, p. 7 or Figure 1, p. 8). Moreover, all WM tasks correlated positively with the Gf task (see study 1: Table 3, p. 7). After controlling for age, inter-correlations between the four WM aspects revealed small to large positive correlations among each other including two exceptions (verbal storage did not correlate with both visual-spatial aspects; see study 1: Figure 1, p. 8). These inter-correlations indicate that the WM aspects share common processes. Especially, visual-spatial storage seems to demand, along with storage, also the processing aspect. Because of these inter-relations, the relation between WM and Gf was analyzed with the method of structure equation modeling (SEM). This method has the advantage to control for common variance. A first SEM was built to analyze the relation between a general WM factor (i.e., all WM aspects loaded on this factor) and Gf while controlling for age (see study 1: Figure 2, p. 9 and Figure A1 in Appendix A, p. 13). Results showed that age explained 5 to 18 % of the WM aspects and 31 % of Gf (Figure A1). In addition, the general WM factor was a strong predictor of Gf (60 % in Figure A1; 90 % in Figure 2). A second SEM was built to analyze the relations between the four WM aspects and Gf while not only controlling for common variance among all WM tasks but also controlling for age (see study 1: Figure 3, p. 10 and Figure A2 in Appendix A, p. 14). Results revealed again that age explained 5 to 18 % of the WM aspects, however, this time only 5 % of Gf (Figure A2). Moreover, verbal and visual-spatial storage and verbal processing were predictive for Gf (5-15 %), while visual-spatial processing was not predictive for Gf.

2.2. Study 2

Study 2, entitled “Effects of age and mental ability on verbal working memory in children: A functional near-infrared spectroscopy study” was part of a larger project called “The impact of mental ability on sensory discrimination and working memory functioning in children and young adults: A cognitive-neuroscience approach to neural efficiency”. The overall aim of this project was to investigate intelligence-related individual differences in the developmental progression of information processing. Thereby, performance and brain activity of auditory and visual sensory discrimination and verbal and visual-spatial WM were measured.

The developmental progression was assessed cross-sectionally with three age groups: (1) young adults with a mean age of 21.3 years (*SD* = 1.9 years; range: 18-24 years), (2) older children with a mean age of 12.1 years (*SD* = 0.5 years; range: 11.3-13.0 years) and (3) younger children with a mean age of 9.8 years (*SD* = 0.5 years; range: 8.8-10.5 years). To assess the intelligence-related differences, there were two intelligence subgroups (i.e., lower vs. higher) for each age group. In the lower intelligence group, adults had an IQ of 112 or lower and children an IQ of 96 or lower. In the higher intelligence group, adults had an IQ of 130 or higher and children an IQ of 115 or higher.

To obtain these intelligence groups, in a first session, an IQ screening was implemented (approx. 295 adults and 500 children were screened). In the second session, participants performed four tasks: an auditory and a visual sensory discrimination task and a verbal and a visual-spatial WM task, each with increasing difficulty levels. With the data acquired in these tasks, group differences in performance were analyzed and the *relative task difficulty* was defined. The relative task difficulty was defined for each participant as follows: (a) for the sensory discrimination tasks, the smallest threshold with an accuracy of 75 %, and (b) for the WM tasks, the highest span at which the participant had at least three of four trials correct. Finally, in a third session, participants solved again the same sensory discrimination and WM tasks while brain activity was recorded. This time, however, the tasks were presented on the relative task difficulty and in a block design alternating with the corresponding active control task. The relative task difficulty was implemented to achieve the same processing workload among all participants. Hence, we controlled for task difficulty which is essential, as previous studies observed that task difficulty affects brain activity (Den Bosch et al., 2014; Dix, Wartenburger, & van der Meer, 2016).

For study 2, a subsample of the data was used[1], namely data from the verbal WM task of the younger and older children with higher and lower IQ (see study 2: Table 1, p. 1 for more details of the sample). The specific aim of study 2 was to investigate how age and Gf combine to affect verbal WM performance and verbal WM-related brain activity in children. However, before investigating this question, we examined whether fNIRS is able to measure WM-evoked cortex

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[1] Data from the visual sensory discrimination task and the visual WM task of the adults and older children are analyzed by Joëlle S. Witmer and are in preparation for submission.

activity, even after considering the mentioned methodological requirements (see section 1.4. Functional Near-Infrared Spectroscopy with more details).

Behavioral results of the WM performance (assessed in the second session) revealed the following (study 2: Table 3, p. 3): (a) independent of Gf, older children outperformed younger ones and (b) independent of age, children with higher Gf outperform children with lower Gf. During fNIRS data recording, the mentioned WM performance group differences disappeared based on the relative task difficulty among the participants (study 2: Table 3, p. 3). Therefore, we can exclude that performance differences led to differences in brain activity and in neural efficiency, respectively. Among all children, the average WM task accuracy was 90.73 % (range: 67.50-100 %; study 2: Table 2, p. 2). Additional analysis only presented in this umbrella paper revealed that in both Gf groups, older children reached higher raw scores in the Culture Fair Test (i.e., Gf test) compared to younger children [lower Gf group, younger children: $M = 22.31$, $SE = 0.52$, older children: $M = 27.33$, $SE = 0.85$, $t(48) = -5.30$, $p < .001$, $r = .61$; higher Gf group, younger children: $M = 36.12$, $SE = 0.44$, older children: $M = 41.69$, $SE = 0.60$, $t(57) = -7.65$, $p < .001$, $r = .71$].

Neurophysiological results revealed that fNIRS is a sensitive method to measure hemodynamic concentration changes in children due to verbal WM stimulation (see study 2: Figure 3, p. 3 and Table D in Appendix D, p. 42). Namely, four channels were exclusively activated during the WM task but *not* during the control task: channels 9 and 14, located in the left Brodmann area (BA) 10, which belongs to the rostrolateral PFC. Channel 11 located in the left BA 9 and channel 16, located in the left BA 46. BAs 9 and 46 belong both to the dorsolateral PFC. Note, these mentioned channels showed significant WM-evoked hemodynamic increases only in [O_2Hb], but not significant changes in [HHb]. Because only channels 9, 11, 14 and 16 were exclusively activated during the WM task but not in the control task, these channels were included in the analysis investigating the effects of age and Gf on WM-related cortical activity.

Children’s [O_2Hb] responses, evoked by the verbal WM task, differed because of an age-by-Gf interaction effect, which was found in the left BAs 9 and 46 (see study 2: Table 3, p. 3;

Table 4, p. 4 and Figure 4, p. 4). The interaction revealed that within the younger age group, children with higher Gf showed a stronger WM-related brain activation compared to their age-matched peers with lower Gf. In contrast, within the older age group, children with lower Gf showed a stronger WM-related brain activation compared to their age-matched peers with higher Gf. To gain a better understanding of the interaction effects, subsequent tests [multivariate analysis of variances (MANOVAs) with follow-up analyses of variances (ANOVAs) and t-tests] were performed (see study 2: results of MANOVAs and ANOVAs are on Table 6, p. 6; results of the t-tests are in the second paragraph on p. 21). See Figure B (in Appendix B of this umbrella paper) with an illustration of the age-by-Gf interaction effects. Figure B also includes the significant results of the subsequent tests, which are illustrated by stars.

3. Discussion of Main Findings

3.1. The Development of Working Memory

Findings of both presented studies revealed that children’s WM performance improved with increasing age. In study 2, results of the WM task showed that independent of Gf, older children outperformed younger ones. Furthermore, in study 1, age explained variance in each of the WM aspects. Combining the results from study 1 and 2 indicates that based on the improvement of the WM aspects storage and processing, each in both modalities (i.e., verbal and visual-spatial), WM improves with age. The findings that older children outperformed younger ones and that both storage and executive processing increase with age correspond to results from previous studies (Bayliss et al., 2005; Gathercole et al., 2004; Huizinga et al., 2006; Kuhn, 2016).

In study 1, correlations revealed that independent of age, higher Gf ability is related to higher WM abilities and vice versa. Differences in Gf affecting WM performance was also confirmed in study 2. More precisely, independent of age, children with higher Gf outperformed children with lower Gf on the WM task. Our findings showing that WM performance is affected by differences in Gf are in line with previous studies (Duan, Shi, & Wu, 2009).

In study 1, age did not explain all the variance in the WM aspects. This indicates that further factors not investigated in study 1 affect WM development and lead to individual differences in the WM aspects. Examples for such possible factors are other information processes, environmental factors or mere brain maturation. At the same time, these factors also provide an explanation why in the presented studies, age influenced WM performance.

In addition to age, further information processes explain variance in WM. For example, individual differences in strategy use (e.g., rehearsal or chunking), in the forgetting rate and in speed of processing could all explain variance in WM (Bayliss & Jarrold, 2015; Bayliss et al., 2005; Jarrold & Hall, 2013; Kail, Lervåg, & Hulme, 2015; Schneider, 2015b). Since all these processes improve with age, they may also explain the positive relation between WM and age (Jarrold, 2016).

Because previous studies observed that schooling and the socio-economic status predict WM, also environmental factors might explain individual differences in WM (Brod, Bunge, & Shing, 2017; Noble, McCandliss, & Farah, 2007). This shows that like all neurocognitive skills, WM development depends on experience (Zelazo, 2015).

The brain develops substantially during childhood (Zelazo & Lee, 2010). Hence, it is clear that also the age-related maturation of the brain and individual differences in the brain development contribute to age effects and individual differences in WM (Bathelt, Gathercole, Johnson, & Astle, 2017; Tamnes et al., 2013; Wierenga, Langen, Oranje, & Durston, 2014). In study 2, we observed a verbal WM-evoked brain activation in the left dorsolateral PFC (BAs 9 and 46) and the left rostrolateral PFC (BA 10). Already previous studies associated these areas with verbal WM (Ciesielski, Lesnik, Savoy, Grant, & Ahlfors, 2006; Finn, Sheridan, Hudson Kam, Hinshaw, & D’Esposito, 2010; Jog et al., 2016; Jolles et al., 2011; Thomason et al., 2009). However, in study 2, only brain activation in the left dorsolateral PFC differed as a function of age interacting with Gf. This indicates that in the investigated age range, especially the left dorsolateral PFC seems to undergo a functional brain maturation. More precisely, the age-by-Gf interaction indicates that chronological and mental age both interactively influence WM functional brain development. Relating this neural finding with the behavioral data from study 1 and 2 leads to the following speculation: WM performance improves with age and is affected by

Gf because of differences in the functional brain development in the left dorsolateral PFC. This is a preliminary conclusion because in study 2, we did not directly investigate the relations between performance differences in WM or Gf and brain activity.

The fact that brain activity differed as an age-by-intelligence interaction effect in the left PFC is in line with a previous study using a verbal generation task (Schmithorst & Holland, 2006). Moreover, our finding that especially the left dorsolateral PFC was sensitive to age conforms to previous studies (Jolles et al., 2011; Klingberg, Forssberg, & Westerberg, 2002a; Vogan et al., 2016). In addition, our finding that the left rostrolateral PFC was not sensitive to age is in line with most previous studies (Ciesielski et al., 2006; Jolles et al., 2011; Klingberg et al., 2002a; Thomason et al., 2009) and contradicts only few studies (Desco et al., 2011; Vogan et al., 2016). However, in general, it has to be said that today, little is known at which age and where exactly within the PFC, age affects verbal WM-related brain activity. What we know today is that in verbal WM tasks, older groups compared to younger groups show a stronger activity in the bilateral frontal-parietal cortex (Ciesielski et al., 2006; Crone, Wendelken, Donohue, van Leijenhorst, & Bunge, 2006; Jolles et al., 2011; Thomason et al., 2009; Vogan et al., 2016). Consequently, for verbal WM tasks, a stronger activation in the frontal-parietal cortex is an indication of a more mature brain. This may explain why in study 2, the results obtained in the lower Gf group showed that older children revealed a stronger activation in the left PFC (BA 46) compared to younger ones. However, it contradicts the results obtained in the higher Gf group showing that younger children revealed a stronger activation in the left PFC (BA 46) compared to older ones.

Of course, WM functional brain differences not only depend on the brain development due to an age-intelligence interaction, but also on environmental factors, such as experience (Bjorklund, 2012; Brod et al., 2017; Jäncke, 2014; Zelazo, 2015). This shows that age differences in WM-related brain activity seem to be due to reciprocal influences of experience and brain development.

3.2. The Development of Fluid Intelligence

Results of study 1 and 2 replicated previous findings showing that Gf improves with age (Fry & Hale, 2000; McArdle et al., 2002). Moreover, results of study 1 revealed that after controlling for age, WM explained 61 to 90 % (depending on the model) of the variance in Gf. Hence, this confirms that WM is a powerful factor underlying the development of Gf (Conway et al., 2011; Voelke, Troche, Rammsayer, Wagner, & Roebers, 2014). Additionally, study 1 showed that different mechanisms underlie the strong relation between WM and Gf. Namely, independent from each other, verbal storage, visual-spatial storage and verbal processing explained variance in Gf.

The finding that verbal and visual-spatial storage as well as verbal processing contribute to the relation between WM and Gf is consistent with previous studies (Hornung, Brunner, Reuter, & Martin, 2011; Shahabi et al., 2014; Tillman, Nyberg, & Bohlin, 2008). Visual-spatial processing did not predict variance in Gf over and above verbal storage, visual-spatial storage and verbal processing. This finding contradicts the only previous study investigating visual-spatial processing independently of the verbal modality (Tillman et al., 2008).

Our finding that visual-spatial processing did not predict Gf is surprising because, in the figural Gf test, children operated with visually overlapping features. It is possible that because visual-spatial storage also required the processing aspect of WM, visual-spatial processing could not explain variance over and above visual-spatial "storage". An alternative explanation could be that domain-general processing variance underlies the WM-intelligence relation. Therefore, visual-spatial processing could not explain variance over and above verbal processing (Swanson, 2017). Hence, these possible reasons show that the interpretations of the results are ambiguous. Additionally, it is not clear what the variances of the WM aspect—after controlling for the common variance among all WM aspects—represent exactly. Especially for visual-spatial storage, it is not clear whether this factor actually represents visual-spatial storage variance or rather visual-spatial processing variance. Therefore, all interpretations of the WM aspects should be drawn cautiously (see study 1, last paragraph on page 12 with a detailed description of this limitation).

As already discussed in section 3.1. The development of Working Memory, results of study 2 revealed that WM-evoked brain activity differed as a function of age interacting with Gf. Hence, this shows that WM and Gf are also related on the neural level, which is in line with previous studies investigating adult samples (Basten, Stelzel, & Fiebach, 2013; Nussbaumer, Grabner, & Stern, 2015). The finding that WM and Gf are also related on the neural level, in turn, could serve as a potential explanation for the relation between WM and Gf observed on the behavioral level in study 1 and 2.

Moreover, the fact that in our study, Gf affected brain activity, indicates that the brains of children with higher and lower Gf function differently while solving WM tasks. This interpretation dovetails with previous findings showing that children's brain responses also differ between children with higher and lower intelligence in various cognitive tasks (e.g., reasoning tasks, flanker task or visual choice reaction task; Desco et al., 2011; Lee et al., 2006; Liu, Xiao, Shi, Zhao, & Liu, 2011; Zhang et al., 2007). Consequently, the fact that intelligence affects brain activity in various tasks indicates that brains of children with higher and lower Gf function differently in general. The assumption that brains of children with higher and lower Gf seem to function differently is also in line with the P-FIT. This theory suggests that individual differences in intelligence can be due to any differences within the parieto-frontal network (Haier, 2011; Jung & Haier, 2007).

Importantly, neural results of study 2 did not reveal a main effect for Gf. However, the age-by-Gf interaction effect on WM-related brain activity was significant. As already discussed, this age-by-Gf interaction effect indicates that chronological and mental age both interactively influence WM functional brain development. Consequently, it seems that brain development differs between children with higher and lower Gf. On a scale of things, previous studies found that in WM tasks, a stronger PFC activation is associated with a functionally more mature brain (see section 3.1. The Development of Working Memory). Beyond, that in WM tasks, individuals with higher intelligence seem to have a stronger PFC activation compared to their age-matched peers with lower intelligence (Basten et al., 2013; Desco et al., 2011). Hence, combining these two findings suggests that children with higher intelligence show a stronger PFC activation compared to their age-matched peers with lower intelligence, because their brains are functionally more mature. Results of study 2 support this suggestion. Namely, results obtained in the younger age group (in BAs 9 and 46) revealed that children with higher Gf had a stronger brain activation and a higher WM capacity compared to their age-matched peers with lower Gf. In addition, brain responses and WM capacity of the younger children with higher Gf were comparable to those of the two year older children with lower Gf. However, the result that older children with higher Gf did not show a stronger left PFC activation compared to all other groups contradicts the assumption of Gf being related to functional brain maturation. Consequently, the suggestion that individual Gf differences are related to functional brain maturation should be treated cautiously.

In study 1, WM and age together did not explain all the variance in Gf. This indicates that Gf develops also due to further factors not investigated in the presented studies. Possible factors could be environmental factors and further information processes. These factors will be briefly mentioned in the following paragraph.

Also for Gf, research revealed that environmental factors like schooling and the socio-economic status explain individual differences (Bates, Lewis, & Weiss, 2013; Ceci, 1991). Moreover, previous findings show that particularly the speed of information processing predicts Gf (Kail et al., 2015; Nettelbeck, 2011). However, also the use of strategies or secondary memory retrieval processes seem to be essential (Bailey, Dunlosky, & Kane, 2011; Gonthier & Thomassin, 2015; Schneider, 2015a; Unsworth, 2016; Vigneau, Caissie, & Bors, 2006).

3.3. Neural Efficiency

Results of study 2 can also be interpreted in terms of neural efficiency. Neural efficiency is moderated by task difficulty (Neubauer & Fink, 2009). Therefore, it should be mentioned that during the fNIRS recording, depending on the group, the WM accuracy was from 67.5 to 100 %.

Consequently, for all groups, the relative WM task difficulty ranged from simple to moderate. In addition, the children of all groups solved the WM task equally well on the relative task difficulty.

In study 2 (in BAs 9 and 46), results obtained in the younger age group showed that children with higher Gf had a stronger brain activation compared to their age-matched peers with lower Gf. Hence, compared to brains of children with lower Gf, brains of children with higher Gf were neurally less efficient. This result contradicts the initially proposed neural efficiency hypothesis and also a more recent review (Haier et al., 1992; Haier et al., 1988; Neubauer & Fink, 2009). This review showed that most studies using electroencephalography (EEG) confirmed the neural efficiency hypothesis if task difficulty was simple or moderate. However, in the EEG studies of this review, all participants solved the simple or moderately difficult tasks on the same difficulty level. In contrast, in our study, participants solved the task on a relative simple to moderate task difficulty and brain activity was assessed with fNIRS. These differences between our study and the review hamper their comparison. Consequently, it seems more sensible to compare our results with fMRI studies, because fMRI measures hemodynamic changes, as does fNIRS.

Interestingly, the result obtained in the younger age group is in line with a recent fMRI meta-analysis investigating adult samples (Basten et al., 2015). This meta-analysis revealed that in brain regions where a significant relation between intelligence and hemodynamic changes was found, this relation was mostly positive. The same relation was also observed in fMRI studies investigating adolescents (Desco et al., 2011; Lee et al., 2006). To the best of the authors' knowledge, there is no fMRI or fNIRS study investigating this topic in children. Furthermore, a fMRI study using a verbal WM task observed that adults' neural efficiency depended on whether the investigated brain area was associated with the task or not (independently of task difficulty; Basten et al., 2013). Namely, in contrast to brains of less intelligent adults, brains of more intelligent adults were neurally less efficient in areas positively associated with the task, but neurally more efficient in areas negatively associated with the task. In our study, differences in neural efficiency were found in the left BAs 9 and 46, which are associated with verbal WM

(Jolles et al., 2011; Vogan et al., 2016). Therefore, it is plausible that in study 2 in the left BAs 9 and 46, brains of younger children with higher Gf put more energy on task-relevant brain regions compared to brains of their age-matched peers with lower Gf. Also in the left BA 46, the result obtained in the lower Gf group, namely that older children had a significant stronger brain activation compared to younger ones, can be interpreted in the same way. However, contrary to this interpretation is the following finding obtained in the left BA 46 of the higher Gf group: The brains of the younger children put more energy on task-relevant brain regions compared to brains of the older children. Furthermore, it is an open question why in the left BAs 9 and 46, brains of the older children did not differ in neural efficiency with regard to Gf. In addition, further research is needed to clarify why in the left BA 9, brains of the children with higher Gf and brains of the children with lower Gf did not differ in neural efficiency with regard to age.

In summary, study 2 indicates that while solving a verbal WM task, neural efficiency differs as a function of age interacting with Gf. To the best of the authors' knowledge, study 2 is the first one showing that differences in neural efficiency are also apparent while participants solved the task on a relative task difficulty. However, concerning the interpretations of neural efficiency, study 2 revealed inconsistent findings. In addition, because of the relative task difficulty, children solved the WM task on different task difficulties from an objective point of view (e.g., younger age group: higher Gf: 3.7 items on average per trial vs. lower Gf: 3.3 items on average per trial). Therefore, we cannot be certain that both groups activated the same cognitive processes. For example, it is feasible that the children with higher Gf used strategies additionally to WM processes (Jolles et al., 2011). Furthermore, current biophysical knowledge indicates that neural efficiency is much more complicated than initially assumed, so any interpretation should be treated with caution (Poldrack, 2015).

3.4. Summary

Going back to the initially proposed question "how do WM and Gf develop?", the discussion of the main findings showed that multiple interacting factors are involved. In summary, results of the presented studies showed that WM as well as Gf improve with age. The fact that

WM improves with age seems to be due to the development of different WM aspects (i.e., verbal and visual-spatial storage, as well as verbal and visual-spatial processing).

Moreover, results of both studies confirmed the relation between WM and Gf. On the one hand, study 2 indicates that WM develops by means of individual differences in Gf. On the other hand, study 1 shows that Gf develops by means of individual differences in WM. Consequently, the development of WM and Gf seems to influence each other bidirectionally. But why are WM and Gf related? Study 1 revealed that the WM-Gf relation is caused by different mechanisms, namely verbal storage, visual-spatial storage and verbal processing. In addition, study 2 leads one to suspect that the relation on the behavioral level is due to a relation on the neural level.

A further factor influencing the development of WM and Gf seems to be the development of the left PFC. At the same time, this factor provides an explanation why WM and Gf improve with increasing age. More precisely, study 2 revealed an age-by-Gf interaction effect in the left dorsolateral PFC. This interaction effect indicates that from middle to late childhood, especially the left dorsolateral PFC seems to undergo a functional brain development. Moreover, the age-by-Gf interaction indicates that chronological and mental age both interactively influence WM functional development. Furthermore, a closer look at the interaction together with previous studies (see above) leads to the two following assumptions: Firstly, a stronger activation in the frontal-parietal cortex seems to be an indication of a more mature brain. Secondly, brains of children with higher and lower intelligence seem to differ in their functional brain maturation. Moreover, results indicate that also further factors not investigated in the present studies foster the development of WM and Gf. In this context, literature shows that also further information processes and environmental factors boost the development of WM and Gf.

All the mentioned differences in the WM-related brain activity can also be interpreted in terms of neural efficiency. These interpretations revealed that in study 2, while solving a verbal WM task, neural efficiency differs as a function of age interacting with Gf. Noteworthy, our results obtained in the younger age group indicate that brains of children with higher Gf put more energy on task-relevant brain regions compared to the brains of their age-matched peers with lower Gf. Furthermore, results obtained in the lower Gf group indicate that brains of older children put more energy on task-relevant brain regions compared to the brains of younger ones. Hence, the development of WM and Gf seems to be reflected in the neural basis of WM by differences in neural efficiency.

4. Outlook and Conclusion

Results of the studies presented in this dissertation have theoretical and practical implications. These implications will be discussed in the remaining part of the umbrella paper, followed by a discussion of limitations and suggestions for improvements and future research.

4.1. Theoretical Implications

Results of study 1 give a better understanding of the mechanisms underlying the WM-intelligence relation. When linking our results to the WM-intelligence relation theories, the following conclusions can be drawn: The finding that storage as well as executive processing explained unique variance in Gf indicates that both WM aspects account for the relation between WM and Gf. This is contrary to Engle et al. (1999) and Engle and Kane (2003), who proposed that only the executive processing aspect explains the WM-intelligence relation. It is also contrary to Cowan et al. (2005) who suggested that only the storage aspect underlies the WM-intelligence relation. The resources sharing ability as proposed by Baddeley and Hitch (1974) cannot account for the relation either. This is because storage and processing explained variance in Gf independently of each other. However, the finding that storage as well as executive processing predicted Gf indicates that multiple aspects underlie the WM-intelligence relation. This is in line with recent WM theories which propose that WM is a concept with multiple aspects (Jarrold, 2016; Unsworth et al., 2014).

Moreover, the findings that verbal and visual-spatial storage predicted Gf independently of each other indicate that domain-specific storage variance contributes to the WM-intelligence relation. This interpretation is also supported by literature (Hornung et al., 2011; Jarrold, 2016). The finding that only verbal processing but not visual-spatial processing predicted Gf over and above the other WM aspects is difficult to interpret. Because of the inter-relations between the

WM aspects, it is not clear whether domain-general variance or solely domain-specific verbal variance of processing underlies the WM-intelligence relation. In this context, literature indicates that, rather than domain-specific variance, general processing variance underlies this relation (Swanson, 2017).

The finding that different WM aspects underlie the WM-intelligence relation favors a WM model with different aspects. However, this conclusion should be treated cautiously. Because in study 1, only one task per WM aspect was included, the structure of WM was not investigated. The finding that different WM aspects underlie the WM-intelligence relation indicates that Gf requires the coordination of several basic processes (Swanson, 2008).

To gain a better understanding of the relation between WM and Gf, it is essential to understand the direction of the relation. In the SEMs of study 1, the path between the general WM factor and Gf as well as the paths between each WM aspect and Gf were drawn pointing from WM to Gf. The paths were drawn in this direction because in psychometric intelligence theories, WM is on a lower, more specialized level then Gf. Therefore, WM is considered to be a more basic process underling Gf (Schneider & McGrew, 2012).

However, study 2 showed that WM-related brain activity is affected by Gf (interacting with age). In addition, children with higher Gf outperformed children with lower Gf in the WM task. This leads one to suspect that not only WM influences Gf, but, that the relation goes in both directions. This suspicion is supported by longitudinal studies. More precisely, longitudinal studies investigating the relation between WM and Gf in both directions found: (a) In each study, earlier WM abilities were positively related to later Gf ability. (b) In contrast, *not* every study found that earlier Gf ability are positively related to later WM abilities (Demetriou et al., 2002; Kail, 2007; Kail et al., 2015; Žebec et al., 2015).

In addition, all existing training studies investigated only whether WM training affects Gf, but not the other way. A recent WM training meta-analysis study showed that WM trainings do not improve Gf ability (Melby-Lervåg, Redick, & Hulme, 2016). Therefore, it would be premature to conclude that increases in WM necessarily lead to improved Gf ability.

Alternatively, it is also possible that WM trainings did not improve Gf because WM trainings—as currently implemented—are ineffective (Melby-Lervåg et al., 2016). In summary, with the present state of knowledge, we can only speculate that the relation is bidirectional.

Results of the presented studies revealed that WM and Gf are related on the behavior and neural level. In addition, WM and Gf are both essential for educational achievements (see sections 1.1. Working Memory and 1.2. Intelligence). Therefore, a neurocognitive developmental model including WM as well as Gf should be developed. Since the *developmental neurocognitive IR model of self-regulation* already explains effective learning (via goal-directed modulation of attention and behavior), the IR model could serve as a starting point for a revised developmental model (Zelazo, 2015). Our results strongly support including Gf into the IR model.

In the IR model, WM plays an essential role. WM is responsible for the maintenance and manipulation of action-oriented rules, which in turn are important for the goal-directed modulation of attention and behavior. Furthermore, iterative reprocessing and reflection are necessary for the formulation of more complex rules and „as rules become more complex, they also become more abstract (i.e., abstracted away from the exigencies of a situation)“ (Zelazo, 2015, p. 61).

However, the model cannot explain how a person deduces rules and how rules get more abstract. This question is essential, because in learning and adaptation processes, one is often presented with new cognitive problems or situations and rules have to be reasoned. Therefore, Gf (i.e., reasoning) would complete this model. Gf is essential for educational achievements, but also for social and emotional cognition (De Stasio, Fiorilli, & Di Chiacchio, 2014; Franco, Beja, Candeias, & Santos, 2017; Ibanez et al., 2013). This implies that Gf is involved in reasoning rules directly related to the learning material but also involved in reasoning more general rules, like rules related to social aspects of the school setting. An example for such a general rule could be: *If I make a focused facial expression, the teacher thinks that I am motivated and she/he will give me better grades*. With more experience and reasoning processes, such a rule may get more abstract and perhaps resulting in the following shortened rule: *Whenever I show interest, people judge me positively*.

The examples of the rules imply that a person with higher Gf ability is more talented in abstracting rules and therefore also more talented in reducing information to the most essential points. The reduction of information, in turn, may facilitate maintaining and manipulating information in WM and lead to higher WM abilities. Consequently, higher Gf ability seems to lead to higher WM abilities. Considering the role of WM in the IR model of self-regulation, results of study 1 showed that verbal storage, visual-spatial storage and verbal processing are all fundamental to Gf. This is probably because these three WM aspects maintain and process the information while the reasoning processes deduce the rules. Thus, higher WM abilities may facilitate Gf processes. Consequently, the proposed revised model favors a bidirectional relation between WM and Gf.

Considering reflection (i.e., metacognitive processes), the IR model of self-regulation proposes that these processes are necessary for the formulation of more complex rules. Because metacognition and Gf are related (see Roebers, 2017 for an overview), it seems that reflection monitors reasoning processes along with rule use and EF (incl. WM). Moreover, the iterative reprocessing of information in neural circuits constitutes the neural basis of all neurocognitive skills of the model (Bunge & Zelazo, 2006; Zelazo, 2015). Zelazo (2015) proposed that the efficiency of the neural circuits depends on age and experience. In study 2, the WM-related brain activity differed due to an age-by-Gf interaction. This finding leads one to suspect that the efficiency of the neural circuits not only depends on age and experience, but also on an interaction between age and Gf. Hence, this finding indicates that Gf should be included into the model.

4.2. Practical Implications

WM seems to be a construct with multiple aspects (Jarrold, 2016). In addition, study 2 showed that multiple WM aspects are related to Gf. Consequently, individual differences in WM and Gf could origin in all these different WM aspects. Moreover, the proposed IR model of self-regulation complemented with Gf shows that WM and Gf seem to operate together with further neurocognitive skills. Therefore, if a child has lower WM or lower Gf abilities, a detailed diagnostic should be performed. Only if the reasons for the lower abilities are profoundly understood, an intervention can be adjusted to the needs of the child. Thus, it is justified that not only for intelligence, but also for WM, whole test batteries are performed and successively extended.

In this context, the intervention investigated the most is probably the WM training. The idea of WM trainings is to produce transfer effects from the increased WM abilities to untrained cognitive functions such as reading comprehension, arithmetic and Gf (Dunning, Holmes, & Gathercole, 2013; Klingberg, Forssberg, & Westerberg, 2002b; Melby-Lervåg et al., 2016). However, a recent meta-analysis demonstrated that WM trainings are not effective to improve cognitive abilities like Gf or mathematics (Melby-Lervåg et al., 2016). Current WM trainings implement mainly practicing simple memory tasks (such as n-back tasks) repetitively on a computer (Melby-Lervåg et al., 2016). Such tasks require solely one WM aspect, namely storage (Conway et al., 2005). However, recent WM theories and the results of study 1 indicate that WM and Gf ability depend on different WM aspects (Jarrold, 2016). Accordingly, WM trainings might be more effective if multiple aspects are trained. Whether this is the case should be investigated in future research.

As long as the effectivity of WM trainings is not confirmed, it is important to consider other interventions in order to support children’s WM and therewith also Gf. Possible interventions are strategy training (e.g., rehearsal or self-explanation) or reducing the WM demands in the classroom (Alloway, 2006; Loomes, Rasmussen, Pei, Manji, & Andrew, 2008; McCabe, Redick, & Engle, 2016; Miller, McCulloch, & Jarrold, 2015; Richey & Nokes-Malach, 2015).

4.3. Limitations and Suggestions for Improvement and Future Research

Some limitations were already mentioned. Nevertheless, some limitations will be re-discussed throughout the next paragraphs together with further open limitations. In addition, suggestions for improvements and future research will be discussed.

A limitation concerning both studies is the fact that age was investigated cross-sectionally and “only” with two age groups. Because of the cross-sectional design, we cannot draw conclusions about the directions of the investigated relations. Hence, future research using a longitudinal design and investigating the relation in both directions may contribute to a better understanding of WM, Gf and their relation.

Noteworthy, due to the inclusion of two age groups, all conclusions concerning the development with age represent the development from middle to late childhood. Including a broader age range in the future would allow investigating developmental changes in the WM-intelligence relation. Furthermore, it would allow investigating whether different brain regions are affected by age and Gf in different phases of development. In addition, it would allow investigating when most changes in WM functional activation occur. This would contribute to a better understanding of the development of the neural basis of WM and individual differences in intelligence. In addition, if the phase of most brain changes is known, we also know when the period of relatively high plasticity is and when interventions should be implemented (Huttenlocher, 2009).

Two further limitations, specific to study 1, were the inclusion of only one task per WM aspect and the inter-relations between most of these tasks. Because of these inter-relations, it is not clear what exactly the variances of the WM aspect represent after controlling for the common variance among all WM aspects. The question what the remaining variance represents after controlling for storage in complex span tasks is in general an open question in WM research (Jarrold, 2016). Hence, future research needs to clarify the structure of WM first. This should be done with purer tasks for each WM aspect. Additional aspects such as attention control and secondary memory retrieval should be considered too (Unsworth et al., 2014). In a second step, the relation between these WM concept, further information processes (which relate to WM and Gf, e.g., speed of processing) and Gf should be investigated (Bayliss et al., 2005). In a third or in an additional step, the revised IR model of self-regulation including Gf should be investigated. To the best of the authors’ knowledge, there is no study investigating all the model’s neurocognitive skills in one sample. Therefore, future research with a longitudinal design, investigating the inter-relations of these neurocognitive skills and their relations to school achievements is needed. Such an approach would provide a unique opportunity to examine whether the proposed model, complemented with Gf, can be empirically confirmed.

The remaining limitations and suggestions for improvement concern the neural data from study 2. In fNIRS data, the relative hemodynamic changes (i.e., [O_2Hb] and [HHb]) are calculated by subtracting the hemodynamic concentration of the preceding baseline from the one of the task. In addition, fNIRS data are always contaminated by physiological responses like respiration (Scholkmann et al., 2014). Therefore, only if enough blocks are included, influences of confounders can be averaged out of the hemodynamic changes (Moosbrugger & Kelava, 2011). In addition, the changes in [O_2Hb] and [HHb] are rather weak. Hence, several blocks are also required in order to be able to detect changes between the baseline and the task in [O_2Hb] and especially in [HHb] (Note that changes in [HHb] are even weaker; Lloyd-Fox, Blasi, & Elwell, 2010). In study 2, only four blocks per task were included. This may be the reason why only in [O_2Hb] but not in [HHb], significant task-evoked changes were detected. Moreover, the inclusion of only four blocks per task may be an explanation for the contradicting results of the interaction effect in study 2. Thus, future neuro-functional research with more blocks per tasks is needed, comparing children with regard to their chronological and mental age.

Furthermore, in such a future study, it would be interesting to consider not only the left PFC, but also further brain regions. To investigate WM-related brain activity of further regions (e.g., the whole cortex) would clarify whether already in children, the neural efficiency depends on the investigated brain regions (whether the brain reagion is associated with the task or not; Basten et al., 2015; Basten et al., 2013). In addition, it would allow examining whether the investigated groups also differ in further brain regions.

4.4. Conclusion

Despite the mentioned limitations and several questions remaining open, the presented studies contribute to a deeper understanding of the development of WM and Gf and their relation.

Furthermore, study 2 is the first study investigating the effects of age and Gf on WM-related brain activity. Results showed an age-by-Gf interaction effect on WM-related brain activity. Consequently, this result emphasizes that the development of the neural basis of WM should be investigated together with Gf at all times. Moreover, the presented studies have theoretical and practical implications. The results favor a model with multiple WM aspects underlying the WM-intelligence relation and give reason to suspect that the relation between WM and Gf is bidirectional. In addition, results prefer a model including WM as well as Gf. The IR model of self-regulation from Zelazo (2015) was proposed as a starting point but should be revised by adding Gf. Such a model has the advantage of explaining the development of WM and Gf and their relation in the context of further neurocognitive skills. In addition, it gives a deeper understanding how goal-directed behavior and effective learning emerge. Regarding practical implications, results indicate that if a child has lower WM or lower Gf ability, a detailed diagnostic should be performed. Furthermore, results indicate that WM trainings might be more effective if multiple aspects were trained.

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Selbstständigkeitserklärung

Ich erkläre hiermit, dass ich diese Arbeit selbstständig verfasst und keine andern als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche kenntlich gemacht. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36, Absatz 1, Buchstabe o des Gesetzes vom 5. September 1996 über die Universität zum Entzug des aufgrund dieser Arbeit verliehenen Titels berechtigt ist.

Bern, im Februar 2018 Eva Aeschlimann

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Appendix A

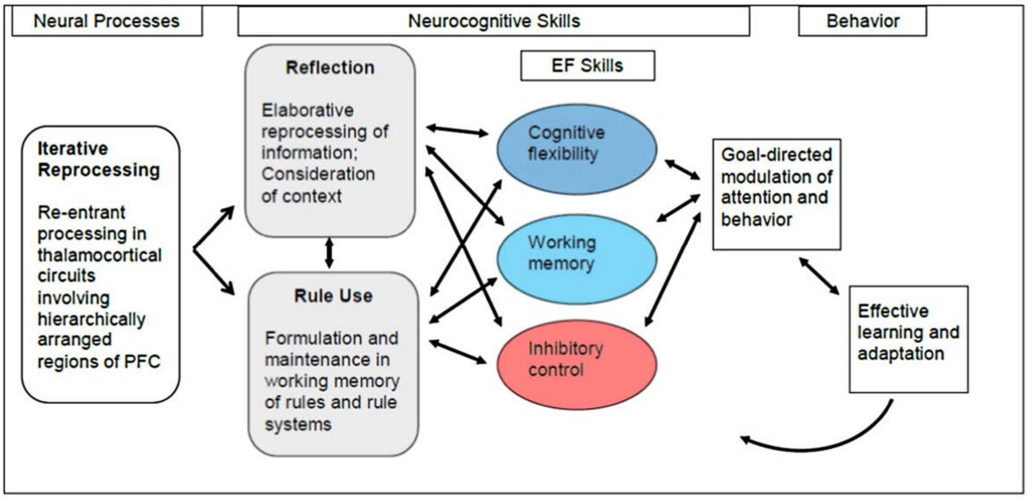

Figure A. The “Iterative-Reprocessing model of self-regulation“ by Zelazo (2015).

Appendix B

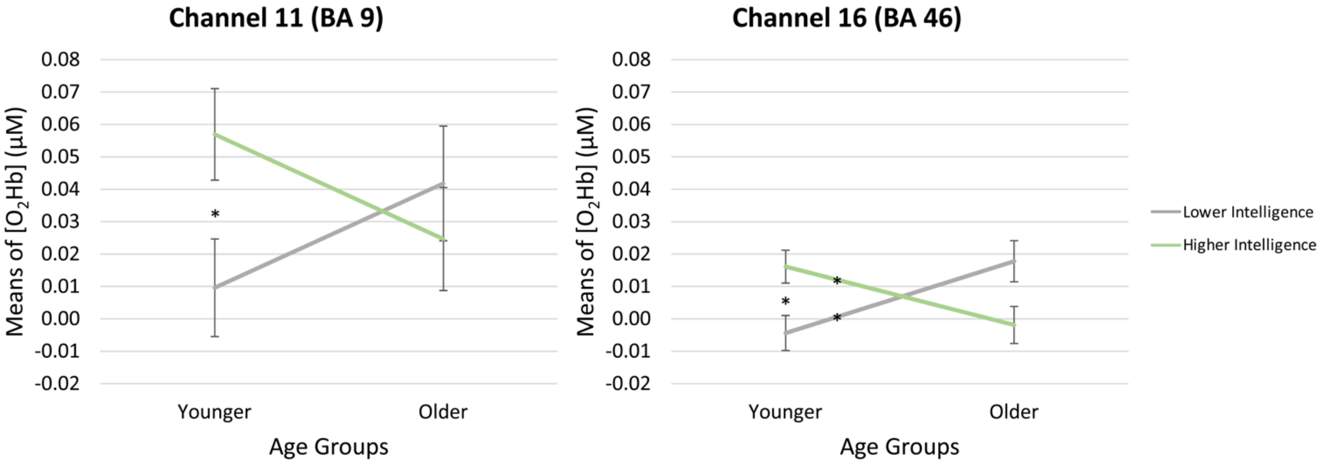

Figure A. Illustration of the interaction effects found in channels 11 and 16. Error bars represent the standard error of the mean. BA = Brodmann area. * = significant differences between the corresponding groups.

Appendix C

Study 1:

Aeschlimann, E. A., Voelke, A. E., & Roebers, C. M. (2017). Short-term storage and executive working memory processing predict fluid intelligence in primary school children. *Journal of Intelligence, 5*, 1-17. doi:10.3390/jintelligence5020017

Study 2:

Aeschlimann E. A., Witmer J. S., Metz A. J., Rammsayer T. H., Roebers C. M. Effects of age and mental ability on verbal working memory in children: A functional near-infrared spectroscopy study. *Manuscript submitted to the Journal Developmental Neuropsychology*.

Study 1

Short-Term Storage and Executive Working Memory Processing Predict Fluid Intelligence in Primary School Children

Eva A. Aeschlimann, Annik E. Voelke and Claudia M. Roebers

University of Bern

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Article

Short-Term Storage and Executive Working Memory Processing Predict Fluid Intelligence in Primary School Children

Eva A. Aeschlimann *, Annik E. Voelke and Claudia M. Roebers

Department of Psychology, University of Bern, 3012 Bern, Switzerland;
avoelke@gmx.ch (A.E.V.); claudia.roebers@psy.unibe.ch (C.M.R.)
* Correspondence: eva.aeschlimann@psy.unibe.ch; Tel.: +41-31-631-47-25

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Abstract: Working memory (WM) includes short-term storage and executive processing of information. WM has been suggested to be one of the key concepts to explain individual differences in fluid intelligence (Gf). However, only a few studies have investigated the association of the two different aspects of WM in relation to Gf. Furthermore, even fewer studies have included children. Therefore, we first investigated the inter-relations between the WM aspects (verbal and visual-spatial storage, verbal and visual-spatial executive processing). Second, we explored the relation between a general WM factor and Gf. Third, we analyzed the relations between the different WM aspects and Gf while we controlled for common variance among all WM tasks. Nine- to 11-year olds had to solve simple and complex span tasks. Correlations and structural equation modeling techniques were used to examine these relations. Most inter-relations among simple and complex spans were found to be substantial and positive. The general WM factor was related to Gf. Furthermore, after controlling for common variance among all WM tasks, individual differences in verbal storage, visual-spatial storage and verbal processing still uniquely related to Gf. Visual-spatial processing, however, was not related to Gf. Results are discussed in terms of underlying mechanisms.

Keywords: intelligence; fluid intelligence; verbal and visual-spatial working memory; executive processing; short-term storage; children; cognitive development

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1. Introduction

Children and adults performing better on intelligence tests are typically also more successful in school- and work-related settings and live healthier and longer [1]. Because of its importance in many domains, researchers have been interested in the study of intelligence for more than a century. One topic that has been addressed is cognitive correlates of intelligence such as processing speed, attention, inhibition and working memory (WM). This is done to shed light on the underlying information processes of intelligence, both in children and in adults, as intelligence is a very broad construct [2–8].

WM has been investigated intensively in relation to intelligence, regarding its relation with fluid intelligence (Gf). Previous studies consistently report that higher WM performance is associated with higher intelligence [9–12]. The reasons for this substantial relation, however, are still being discussed. A better understanding of the underlying information processes contributing to the WM–intelligence link appears to be of special significance in the context of cognitive development. On the one hand, this is because WM is not only related to intelligence but also to cognitive performance in many domains, including school achievement. On the other hand, WM is also found to contribute to growth in various areas of cognitive development such as language, reading and mathematics [13–17].

Against this background, understanding the information processes involved in the WM–intelligence link in children seems to be of great theoretical and practical importance.

WM is a complex theoretical construct. While conceptualizations of WM differ strongly, most researchers agree that WM contains a short-term storage aspect and an executive processing aspect [18,19]. The distinction between these two aspects of WM may in fact be crucial for understanding the WM–intelligence relation. Unfortunately though, this has only rarely been addressed and existing results are inconsistent [12]. While some studies suggest that the individual's capacity to store a certain amount of information for a short time drives the relation to intelligence, other studies found a predominance of executive processing in the WM–intelligence link [8,12,20]. Especially in young samples, evidence concerning the specific contribution of short-term storage and executive processing is scattered and inconsistent, a fact that constitutes the starting point for the present approach. We will explore the relations among WM short-term storage, WM executive processing and Gf in a sample of elementary school children.

1.1. Definition of Key Concepts

In the present work, we focused on *fluid intelligence* (Gf). Gf is a complex ability that allows us to adapt our thinking to a new cognitive problem or situation [21]. Compared to other intelligence constructs, Gf is sought widely independent of experience and unrelated to culture and language [22,23]. Furthermore, Gf explains around 80% of variance in general intelligence in children [23]. Typically, Gf is measured with tests in which individuals are confronted with figural problems. To solve such problems, inductive and deductive reasoning is needed [23].

There are different theories that vary in their definitions of *WM*. Despite this heterogeneity, what all the theories have in common is that they provide a description of how individuals temporarily store information during cognitive processing. Moreover, experts agree that WM is a capacity-limited system. Hence, within this system, only a fair amount of information can be maintained during a very limited period of time [19,24–27]. Thus, WM comprises different aspects of information processing and is viewed as a multifaceted construct with interacting *storage* and *executive processing* [28–30].

The *storage* aspect describes the maximum amount of information an individual can possibly store for a short time. It is also called short-term memory or short-term memory capacity and is required when a small amount of information must be held in an active state. Short-term storage facilitates the processing of task relevant information [6,28] and has been found to be of special importance for first and second language learning [31].

The *executive processing aspect* is much more difficult to define as it is heterogeneously denoted by different researchers, including terms like "control of attention", "executive control", "cognitive control", "controlled processing" or "executive attention" [6,8,25]. As an exhaustive review of these denotations is beyond the scope of the present paper, we focus on the most typical operationalization. Namely, executive processing is defined as the residual variance left in WM after variance of storage has been controlled for. In other words, executive processing subsumes all the mental processes that are left when storage is held constant. Thus, this residual executive processing variance contains mental operations that go beyond passive storage, including attention and cognitive control processes [6,25]. In the present work, when using the term *WM*, we refer to the whole WM system including storage and executive processing aspects. With the term *storage*, we refer to the short-term storage aspect. With the term *processing*, we refer to the executive processing aspect.

1.2. Measurement Challenges in WM

Storage and processing are measured by means of differing tasks. To assess the storage aspect, so-called *simple span tasks* are typically used. For example, an individual is presented with a sequence of digits and is asked to recall them in the same order as presented after a minimal delay. Thus, to solve a simple span task, mainly short-term storage is required. To assess the processing aspect of WM, so-called *complex span tasks* are typically used [32]. In these tasks, individuals are asked to keep some information in mind while simultaneously processing the same or additional information [18,33]. For example, an individual is presented with a sequence of digits and is asked to recall them in reversed order after a minimal delay. Thus, the executive processing aspect of WM can only be assessed indirectly because complex span tasks also trigger short-term memory processes. Hence, it is difficult to interpret WM task results [34].

As simple and complex span tasks both contain the storage aspect, it is not surprising that typically they substantially correlate. When aiming to establish the involved information processes, that contribute to the WM–intelligence link, in isolation (i.e., storage and processing), high correlation among constructs leads to the problem of multicollinearity [20,35]. It implies that the unique contributions of the single predictors are likely to be either under- or overestimated, because, shared variances are attributed to either one of the included inter-correlated predictors. Typically, one way to solve this problem is to control for storage variance in complex span tasks and thereby capture the "pure" processing variance [20]. It is important to note that the problem of multicollinearity does not only occur because complex span tasks demand storage. It additionally occurs because simple span tasks also demand executive processing. Specifically, visual-spatial simple span tasks demand executive processing [36,37]. Such findings also challenge the classical measurement of the storage aspect of WM and implicate that common variance between simple and complex span tasks may differ between the verbal and visual-spatial modality. In fact, in the verbal modality, common variance seems to be storage. In contrast, for the visual-spatial modality, evidence is rare but suggests that, besides storage, common variance is also mirrored in the processing aspect of WM [33,36,37].

In the next sections, we will discuss previous studies examining the relation between WM and Gf. Note that, in all discussed studies, authors controlled for common variance among simple and complex span tasks. They controlled for common variance either with the use of hierarchical regression analyses or by using structural equation modeling techniques (SEM).

1.3. Relationship between WM and Gf

In literature, it has been emphasized that WM is the concept that best predicts individual differences in Gf [38,39]. Some authors have even suggested that WM and Gf represent the same construct [40,41]. However, most experts consider them separable constructs, both in adults and children [8–10,12,42,43]. Meta-analyses with adult data estimated the correlation between WM and Gf to vary between $r = .72$ and $r = .85$ [9,10]. In recent studies with children, WM has been found to correlate with Gf as high as $r = .77$ [44].

Given this strong overlap, is it the storage or processing aspect that is the basic mechanism driving the relation between WM and Gf? Inconsistent results have been reported so far. Studies with adults revealed that the relation between WM and Gf is mainly driven by executive processing [25,45], while more recent research suggested that storage also explains substantial amounts of variance in Gf [20,28,46,47].

Studies including children produced a mixed pattern of results: while some findings suggest that only processing is a predictor of Gf [6,7,48], other findings indicate that storage and processing are equally strong predictors [49]. Further findings indicate that either storage or processing is the stronger predictor of Gf [4,8,12,50]. In summary, existing findings suggest that processing is certainly one substantial mechanism underlying the connection between WM and Gf. For storage, however, findings are inconsistent. Explanations for these different results vary strongly, including the nature of the WM system itself, the analyzed samples, developmental changes as well as the modality (verbal or visual-spatial) of the included tasks [8,12,18,35].

In fact, an important issue within the literature on the WM–intelligence link concerns the modality of the to-be-recalled material [18,35,49]. In other words, the question arises whether processing and storage are both related to Gf when analyzed separately for the verbal and visual-spatial modality. This is essential because it provides a more detailed understanding of the mechanisms underlying the connections between WM and Gf [43]. Especially for storage, findings suggest that it should be analyzed separately for the verbal and visual-spatial modality. For example, results from individual differences approaches with children point out that storage is modality-specific [30]. Further studies analyzing individuals with atypical development revealed selective deficits for the verbal storage aspect of WM, but not for the visual-spatial storage aspect [51]. For the processing aspect, in contrast, previous studies suggest that the link to intelligence is likely to generalize for both the verbal and the visual-spatial modality [33,43]. Taken together, these findings imply that individual differences in WM have diverse sources that may all contribute to the WM–intelligence link. However, only a few studies analyzed the relation between storage and processing and Gf separately for the verbal and visual-spatial modality. In the next section, findings of these studies including children will be discussed.

Studies investigating the predictive power of the WM processing aspect for the verbal modality indicate that verbal processing, in fact, predicts significant amounts of variance in Gf [7,8,48,50]. However, to the best of our knowledge, only one study explored the relation between the WM processing aspect and Gf separately for the verbal and visual-spatial modality [49]. The authors found that verbal and visual-spatial processing are equally important for Gf. This result is in line with findings showing that WM processing is modality-general [33,43]. In summary, findings indicate that verbal processing predicts Gf. However, because of the small number of studies, the question whether visual-spatial processing predicts Gf over and beyond verbal processing is yet to be thoroughly investigated, especially in young samples.

Studies investigating the predictive power of the WM storage aspect for the verbal modality indicate that verbal storage does not predict variance in Gf [6,7,48]. In contrast, the few studies that explored the relation between the WM storage aspect and Gf separately for the verbal and visual-spatial modality indicate conflicting results. Namely, two studies found that verbal and visual-spatial storage both predict variance in Gf [49,50], whereas another study found that only visual-spatial storage was related to Gf, but not verbal storage [52]. Together, these findings indicate that visual-spatial storage predicts Gf. However, the question whether verbal storage predicts Gf over and beyond visual-spatial storage in children remains open.

1.4. The Present Study

The main aim of the present work was to investigate the relations between the four WM aspects (verbal storage, visual-spatial storage, verbal processing and visual-spatial processing) and Gf. For this purpose, the storage and processing aspect of WM were measured with tasks that were—within their modality—as similar as possible, and differed only with respect to the additional processing demand. Due to the problem that simple and complex span tasks always share variance, we firstly analyzed the inter-relations among these tasks [20]. Secondly, we studied the relation between a general WM factor and Gf. Thirdly, relations between the different WM aspects and Gf were examined. To calculate relations among WM (respectively, WM aspects) and Gf, we used SEM, hence taking the inter-relations among the storage and processing tasks and among the modalities into account. The method of SEM has different advantages. Particularly, it enables controlling for common variance of the simple and complex span tasks when exploring the relations between different WM aspects and Gf.

To get a more detailed understanding of the mechanisms underlying the connections between WM and Gf, we studied the relations between Gf and the WM aspects separately for both the verbal and visual-spatial modality. To the best of our knowledge, there is only one study that investigated the connection between storage, processing and Gf separately for verbal and visual-spatial tasks [49]. Especially for young samples, our study will thus make a unique contribution to illuminating the WM information processes involved in Gf.

As for the present work, simple and complex span tasks were very similar within the modality (i.e., verbal vs. visual-spatial). However, across modalities, they differed greatly, hence why we assumed a stronger link between the two tasks within one modality than between the two tasks of comparable complexity. Furthermore, we examined whether the visual-spatial simple span task would not only demand the storage aspect of WM, but also the executive processing aspect of WM, something that has been suggested by very few previous studies.

Concerning the WM–intelligence link, we predicted that the general WM factor would explain substantial variance in Gf. When analyzing the relations between the different WM aspects and Gf, we assumed the following: verbal processing predicts unique variance in Gf, over and beyond the common variance that is captured by the WM factor. Because only few studies explored the relation between visual-spatial processing and Gf, we had no firm hypothesis as to visual-spatial processing predicting variance in Gf. As for the storage aspects, previous research is also rare, and our study is explorative in nature. For both verbal and visual-spatial storage, we aimed to explore whether storage explains significant amounts of variance in intelligence, over and beyond the processing aspects.

2. Materials and Methods

2.1. Participants

The sample consisted of 127 children between the age of 9 ($N = 57$; 51% girls; mean age = 114 months; $SD = 4$; age range: 108–122 months) and 11 years ($N = 70$; 49% girls; mean age = 138 months; $SD = 3$; age range: 132–144 months). Participants were recruited from public schools in the vicinity of a University town. In addition, 69% of the children had Swiss German or German as the first language, 25% were bilingual with Swiss German or German and a second language as the first language. The remaining children had sufficient German language skills as to understand the instructions. Written consent was obtained from the main caregiver of the participating children; children gave oral consent.

The study was conducted in accordance with the Declaration of Helsinki, and the protocol was approved by the local ethics committee of the faculty (project identification code: 2011-06-103). The intelligence quotient (IQ) was normally distributed in the sample (skewness = -0.22; kurtosis = -0.48) with a mean only slightly above 100 ($M = 102.39$; $SD = 12.15$; range = 75–128). This is important to note because homogenous IQ samples are not supposed to show the same relations between Gf and WM as normally distributed samples do [35].

2.2. Tasks

2.2.1. Assessment of Gf

Fluid intelligence (Gf) was assessed with the short version of the German adaptation of Cattel's Culture Fair Test (CFT 20-R; reliability of.92; [53]). The CFT 20-R is a paper–pencil task and consists of four subtests (Series Completion, Classification, Matrix Completion, and Topological Reasoning). All subtests have a time limit. For the descriptive statistics and the correlations, we used the sum of correct answers across all four subtests as dependent variable of Gf. For the SEM, the sum of correct answers for each subtest was used separately.

2.2.2. Assessment of WM Aspects (Simple and Complex Span Tasks)

An overview of the span tasks used to measure the WM aspects is shown in Table 1. To control for storage in a complex span task, we applied tasks in which the same information per modality had to be stored across different levels of complexity (digits in the verbal tasks and blackened squares in the visual-spatial tasks). For measures of storage, we included forward versions; for measures of executive processing, backward versions were used. The forward versions represent simple span tasks. Because the sequences are immediately reproduced, the processing load is assumed to be minimal. In contrast, for reproducing the sequences backwards (i.e., complex span tasks), additional executive processing is needed [25,33,54].

Table 1. Simple and complex span tasks used in the present study to assess the WM aspects.

Simple Span Tasks		**Complex Span Tasks**	
Verbal	**Visual-Spatial**	**Verbal**	**Visual-Spatial**
Digit Forward Task (Digit-FW)	Matrix Forward Task (Matrix-FW)	Digit Backward Task (Digit-BW)	Matrix Backward Task (Matrix-BW)
Digit Recall task from the Working Memory Test Battery for Children (WMTB-C; [55]).	Adapted version of the *Matrix subtest* from the Arbeitsgedächtnistest-batterie für Kinder von 5 bis 12 Jahren (AGTB 5–12; [56]).	*Backward Digit Recall task* from the WMTB-C [55].	Adapted version of the *Matrix subtest* from the AGTB 5–12 [56].

In the present study, span tasks consisted of six trials per block and sequence length, respectively. Each task started with a training block of four trials. Note that a training trial was repeated if recall was inaccurate. After the training block, each participant started with the length of two digits or two blackened squares, respectively. A trial was considered correct when all digits or squares were reproduced in the correct order. With four correct trials out of the six trials within one sequence length, the next block was administered, including trials of one additional digit or blackened square, respectively. If less than four trials were reproduced correctly, the task was terminated. Before a new block started, children were informed about the length of the next trials. While instructions were given orally, stimuli were presented computer-based in order to increase standardization and to attain a higher reliability (Computer: Acer W700 with a 26.0 cm × 14.4 cm and 1920 × 1080 pixel touch-screen; Software: E-Prime [57,58]).

In the verbal span tasks, digits were played by headphones (Sennheiser HD 201, Wedemark, Germany) at a rate of one digit per second. Children had to respond orally after the last digit and were thereby being protocolled by the experimenter.

In the visual-spatial tasks, blackened squares were presented in a 4 × 4 matrix (size of the matrix: 13.2 cm × 13.2 cm; size of each field within the matrix: 3.3 cm × 3.3 cm). Every blackened square appeared for 1.2 s and disappeared when the next blackened square showed up. Every last blackened square was first followed by a screen with an interrogation mark for 1 s and then by an empty 4 × 4 matrix. Children had to type their answers directly into this empty matrix on the touch-screen, with the computer recording the answers. When finished, children were asked to put back their hand onto a pad in front of the computer.

For all of the span tasks, there was no time limit. Hence, the next trial started whenever the child indicated to be ready. For each span task, the dependent variable was the total number of correctly answered trials.

2.3. Procedure

During normal school hours, participants solved the tasks in two sessions. In one of these sessions, participants solved the CFT 20-R task in small groups of four to seven children (duration: max. 45 min). In the other session, participants completed the span tasks individually in a separate and quiet room with their experimenter (duration: max. 40 min). Every child started with the simple span tasks and ended with the complex span tasks, while verbal and visual-spatial tasks alternated. The starting modality was counterbalanced among the children. At the end of the last session, participants received a small gift.

2.4. Data Analysis

Data was analyzed using the software SPSS statistics 23 and Amos 23 [59,60]. Partial correlations were used to examine the inter-relations among the simple and complex span tasks, and SEM was used to examine the relation among the WM aspects and Gf. For the SEM, fits were considered good if the chi-square probability was greater than .05, the normed χ^2 was below 2, the comparative fit index (CFI) was greater than .95, the root mean square error of approximation (RMSEA) was smaller or equal to .06, and the standardized root mean square residual (SRMR) was smaller than .10 [61,62].

3. Results

Results are organized in three sections. Firstly, we provided descriptive statistics and compared performances in the four span tasks. Secondly, we examined the inter-relations among the simple and complex span tasks. Thirdly, we investigated the relation between WM and Gf. For this, we (a) analyzed the prediction of one general WM factor onto Gf; and (b) we explored the prediction of each WM aspect onto Gf.

3.1. Descriptive Statistics

Descriptive statistics of performance level of simple and complex span tasks and Gf are displayed in Table 2. Kurtosis and skewness were within the range of ±1.0. Thus, data may be assumed to be normally distributed [61].

Table 2. Descriptive statistics of raw scores for all variables included in the study.

Variables	*Mean*	*SD*	Range	Skewness	Kurtosis
Digit Forward (verbal)	20.23	3.30	13–27	0.07	−0.67
Matrix Forward (visual-spatial)	15.65	4.11	3–24	−0.32	−0.43
Digit Backward (verbal)	13.98	3.69	6–24	0.21	−0.26
Matrix Backward (visual-spatial)	14.48	3.91	7–24	0.23	−0.24
Series Completion	10.09	2.31	3–14	−0.61	−0.20
Classification	7.26	2.23	2–13	0.09	−0.50
Matrix Completion	9.10	2.37	1–14	−0.66	0.28
Topological Reasoning	4.46	1.82	0–9	−0.05	−0.34
Age (in years)	10.63	1.02	9–12	−0.21	−1.66

To get a better understanding of the simple and complex span tasks, we analyzed performance differences between them. Results of the analysis of variance revealed that children achieved higher scores in the forward tasks (simple span tasks) compared to the backward tasks (complex span tasks), $F(1,126) = 307.51$, $p < .001$, and $\eta_p^2 = .71$. Furthermore, children achieved higher scores in the verbal span tasks compared to the visual-spatial span tasks, $F(1,126) = 36.54$, $p < .001$, and $\eta_p^2 = .22$. It is important to note that the interaction between the modality (verbal vs. visual-spatial), and the order/complexity (forward vs. backward) was also significant: in both modalities, children achieved higher scores in the simple span tasks (forward versions) compared to the more complex ones. However, the effect was greater for the verbal simple span than for the visual-spatial simple span, $F(1,126) = 131.35$, $p < .001$, and $\eta_p^2 = .51$.

Pearson correlations (Table 3) showed that all tasks are positively related to each other. Age correlated positively with all variables from $r = .22$ until $r = .45$. Previous studies found that storage and processing predict Gf differently depending on age [8,12,63]. Furthermore, previous studies found that age is related to storage, processing and/or Gf [4,6,12,34,64,65]. Because of these reasons, we controlled for age in all model analysis and computed additional models to examine the predictive power of age onto Gf. For further analysis, all variables were *z*-standardized.

Table 3. Pearson correlations and partial correlations controlling for age between span tasks and Gf.

Variables	Simple Span Tasks		Complex Span Tasks		Intelligence
	Digit-FW	**Matrix-FW**	**Digit-BW**	**Matrix-BW**	**CFT Score**
Digit Forward (Digit-FW)	-	.16	.47 ***	.12	.38 ***
Matrix Forward (Matrix-FW)	.24 **	-	.28 **	.58 ***	.43 ***
Digit Backward (Digit-BW)	.50 ***	.38 ***	-	.21 *	.44 ***
Matrix Backward (Matrix-BW)	.19 *	.64 ***	.31 ***	-	.30 **
Intelligence Composite Score (CFT Score)	.43 ***	.54 ***	.52 ***	.42 ***	-
Age (in years)	.22 *	.43 ***	.34 ***	.36 ***	.45 ***

Note: Pearson correlations below the diagonal; partial correlations controlling for age (in months) above the diagonal; * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$.

3.2. Inter-Relations between Simple and Complex Span Tasks

To analyze inter-relations among the WM aspects, partial correlations were calculated with age as control variable (see Table 3 or Figure 1 with an illustration of the correlations). Results showed that all correlations were significant and positive (all $p < .05$), except for two; namely, the correlations between the verbal simple span and the two visual-spatial spans. As expected, correlations among modalities (verbal vs. visual-spatial) were stronger (correlation between simple and complex spans within the modalities: verbal $r = .47$; visual-spatial $r = .58$) than among task complexities (simple vs. complex; correlation between the complex spans: $r = .21$; correlation between the simple spans: $r = .16$, non-significant).

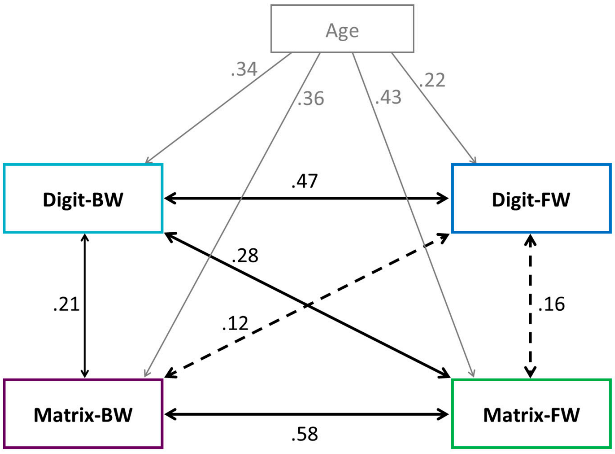

Figure 1. Correlations between age and the four WM aspects as well as partial correlations after controlling for age between the four WM aspects. Digit-FW = digit forward; Digit-BW = digit backward; Matrix-FW = matrix forward; and Matrix-BW = matrix backward. *Solid lines* represent significant correlations ($p < .05$), *dashed lines* represent non-significant correlations ($p > .05$).

Next, we explored whether the visual-spatial simple span task not only demanded the storage aspect of WM, but also the executive processing aspect of WM. Hence, we looked at the correlations between the visual-spatial simple span task and the two complex span tasks. Results revealed that visual-spatial simple span correlated with visual-spatial complex span ($r = .58$). Additionally, visual-spatial simple span correlated with verbal complex span ($r = .28$). Surprisingly, the strength of these correlations was moderate to large [66]. Consequently, we can assume that visual-spatial simple span demands not only storage, but also processing. This indicates that, above storage, shared variance between visual-spatial simple span and visual-spatial complex span mirrors mainly processing.

3.3. Relationship between WM and Gf

A SEM was performed to investigate first the relation among a common WM factor and Gf, and second, to investigate the relations between the different WM aspects and Gf. We used a two-step modeling approach. In the first step, we tested the measurement model. After a good fit of the measurement model was confirmed, the second step of testing the structural model followed [61,62].

The measurement model was built as follows: all four WM tasks were to load on one WM factor, and all Gf tasks loaded on one Gf factor. The WM factor correlated with the Gf factor. Additionally, we controlled for age by regressing each WM task and each Gf task onto age. The model generated a good fit [χ^2 (18) = 16.63, $p = .55$, normed χ^2 = 0.92; CFI = 1.00; RMSEA = .00; SRMR = .04]. Next, we built the SEM (Model 1a). This model was built as the measurement model, except that Gf was regressed onto WM. See Figure 2 with the results of this model. The model generated an excellent fit to the data and explained 79% of the variance in Gf [χ^2 (18) = 16.63, $p = .55$, normed χ^2 = .92; CFI = 1.00; RMSEA = .00; SRMR = .04]. All regression coefficients of the model were significant at $p < .05$.

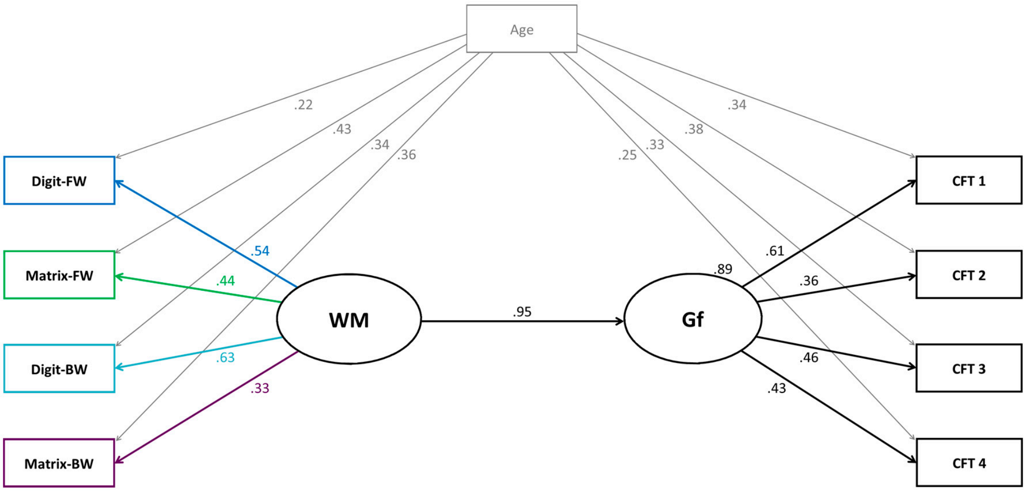

Figure 2. Structural equation model (Model 1a) testing the relation between one working memory (WM) factor and fluid intelligence (Gf). Age (in months) was included as control variable. Digit-FW = digit forward; Digit-BW = digit backward; Matrix-FW = matrix forward; Matrix-BW = matrix backward; CFT 1–4 = subtests of the CFT 20-R. All paths were significant ($p < .05$).

In a next model, we investigated the predictive power of WM and age onto Gf. For this, we built a further model (Model 1b). Model 1b was computed equally as Model 1a, except that each Gf task was no longer regressed onto age. Instead, the Gf factor was regressed onto age to determine the direct and overall effect of age on Gf. In addition, Model 1b generated an excellent fit [χ^2 (21) = 19.48, $p = .55$, normed $\chi^2 = .93$; CFI = 1.00; RMSEA = .00; SRMR = .04]. Together, WM and age explained 84% of the variance in Gf (see Figure A1 in Appendix A with further results of Model 1b). Because there was only one task per WM aspect, we were not able to further analyze the structure of WM [35].

In the next step, we built a model (Model 2a) testing the assumption that each WM aspect (and each task, respectively) uniquely contributes to the prediction of Gf. As mentioned above, simple and complex span tasks both measure storage, at least to some extent. Knowing this, several previous studies built nested models to test if processing still has a predictive value for Gf after controlling for storage. In these nested models, storage was controlled for by having all simple span tasks load on the processing factor [8,12,20,43,47,50]. However, none of the studies considered that in children, visual-spatial simple span tasks also demand processing [36,37]. Consequently, in the visual-spatial modality, common variance of simple span and complex span tasks seems to be mainly executive processing. As this proved to be the case in our data (see above), we built a model in which we regressed Gf onto the WM aspects while controlling for common variance among all WM tasks.

Model 2a was computed as Model 1a, except that Gf was not regressed onto the WM factor. Instead, Gf was separately regressed onto each WM aspect. See Figure 3 with the results of Model 2a. The model resulted in a very good fit and explained 42% of the variance in Gf [$\chi^2(15) = 6.95$, $p = .96$, normed $\chi^2 = .46$; CFI = 1.00; RMSEA = .00; SRMR = .02]. All regression coefficients in the model were significant at $p < .05$, except for three; namely, the coefficients from age onto two Gf subtests (CFT-1 and CFT-4), and from visual-spatial processing (respectively, matrix backward) onto Gf.

In the next model, we investigated the predictive power of each WM aspect and age onto Gf. This model (Model 2b) was similar to Model 2a, except that each Gf task was not regressed onto age. Instead the Gf factor was regressed onto age. Furthermore, Model 2b generated an excellent fit [χ^2 (18) = 9.88, $p = .94$, normed $\chi^2 = .55$; CFI = 1.00; RMSEA = .00; SRMR = .03]. The WM aspects (after controlling their common variance) and age explained 51% of the variance in Gf (see Figure A2 in Appendix A with further results of Model 2b).

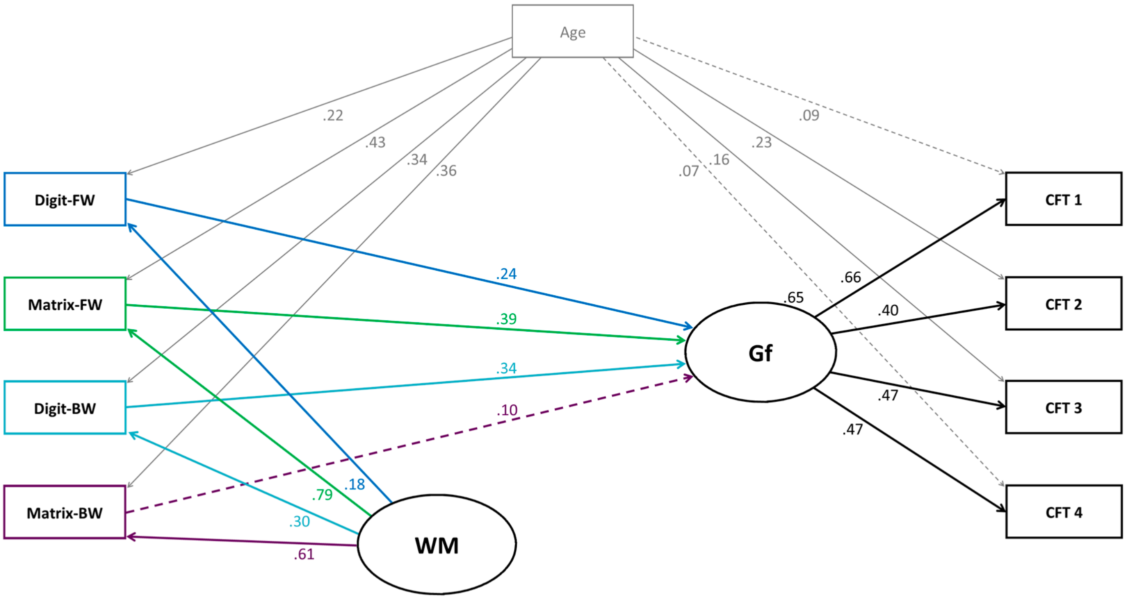

Figure 3. Structural equation model (Model 2a) testing the relations between working memory (WM) aspects and fluid intelligence (Gf). Age (in months) was included as control variable. Digit-FW = digit forward; Digit-BW = digit backward; Matrix-FW = matrix forward; Matrix-BW = matrix backward; CFT 1–4 = subtests of the CFT 20-R. *Solid lines* represent significant paths ($p < .05$), *dashed lines* represent non-significant paths ($p > .05$).

4. Discussion

In the present work, firstly, we investigated the inter-relations between simple and complex span tasks in elementary school children. Secondly, we explored the relation between one WM factor and Gf, and thirdly, we examined the relations between the different WM aspects (i.e., verbal storage, visual-spatial storage, verbal processing and visual-spatial processing) and Gf. In order to get "purer" estimations of the contribution of storage and processing, we analyzed the relations between WM aspects and Gf by controlling for the common variance among simple and complex span tasks.

In short, the inter-relations revealed that—in general—simple and complex span tasks correlated positively and substantially, with a differential pattern across the two modalities: in the verbal modality, common variance seemed to mirror mainly storage. In contrast, in the visual-spatial modality, common variance seemed to mirror mainly executive processing. Loading all span tasks on one WM factor revealed a significant relation between the corresponding WM factor and Gf. However, when examining the unique contribution of the four WM aspects separately for Gf, results revealed that verbal storage, visual-spatial storage and verbal processing predicted unique variance in Gf. For visual-spatial processing, this was not the case. In the remainder of this discussion, we consider some limiting conditions on this evidence and discuss our findings in the context of prior work.

There are limits to drawing firm conclusions of our results. First, our data are not longitudinal. A longitudinal design would allow analyzing the directions of the relations between the WM aspects and Gf. In addition, development differences in the relations among the WM aspects and Gf could be explored. The latter issue would be important because our results indicate that age explains a substantial amount of variance in Gf. Furthermore, Demetriou et al. [67] showed that the strength of the relation between WM and Gf varies with age. They found that Gf is strongly linked to WM in the age ranges 9–11 and 14–16. In the age ranges of 6–8 and 11–13, in contrast, WM appears to be less closely linked to Gf. A second limitation of the present study is that we included only one task per concept. Consequently, we cannot draw very firm conclusions about the theoretical structure of the WM system. For this purpose, more tasks per latent variable would be necessary [35]. Therefore, we interpret our data more on the task- than on the construct-level. Future studies might want to investigate if our results generalize to other and to more tasks per WM aspect. For example, a previous study with older adults showed that backward span tasks are easier compared to other complex span tasks [68]. Thus, it might be good to include additional and more difficult complex span tasks. Having said that, however, the construction of very similar tasks (forward and backward span) in two distinct modalities in fact constitutes a strength of our approach. A third limitation of the present study is that WM is a multi-faceted construct that comprises several information processes (e.g., attention, inhibition, primary memory, secondary memory and speed of processing; [28–30,34]). With our selection and construction of tasks, we were not able to capture all these processes but aimed—for theoretical reasons—at focusing on the distinction between storage and processing as a first step. Future research will address the remaining open issues.

4.1. Inter-Relations between Simple and Complex Span Tasks

Because one of the aims of our approach was to better understand the inter-relations between the simple and complex span tasks used, we will discuss those results in more detail. The inter-relations between simple and complex span variables revealed significant correlations among each other including two exceptions (verbal simple span did not correlate with both visual-spatial spans). These otherwise substantial correlations among simple and complex spans indicate that the complex span tasks also demand storage. However, it is also possible that simple span tasks demand executive processing, at least as from a certain degree of complexity [37,69].

Furthermore, our data showed that simple and complex span tasks share a substantial amount of variance within each modality (within the verbal and visual-spatial modality, respectively). This is most likely due to a similar kind of representation of this information [70]. In line with this interpretation, the relation between the two complex span variables was much weaker, and the relation between the two simple span variables was not significant. This may point to different kinds of information representations in memory [70].

The substantial links between simple and complex span tasks within each modality raise the question if our simple and complex span tasks measured different concepts (storage and WM), or if they possibly tapped the same basic processes. On the one hand, Unsworth and Engle [71], for example, argue that simple and complex span tasks do not represent different concepts like short-term storage (respectively, short-term memory) and WM (storage and processing). They argue that these tasks differ only from each other in terms of the relative emphasis in which basis information processes are involved, at least in adults. On the other hand, other authors argue that storage and executive processing represent different concepts, at least in children [12,43,48,50]. Together, therefore, findings concerning the question of whether or not simple and complex span tasks measure different concepts are inconsistent. As for the present study, we did not include enough different tasks per concept to answer this question. However, we can state that inter-relations (within the modalities: verbal r = .47; visual-spatial r = .58) indicate simple and complex span tasks to share a substantial amount of variance within each modality. However, the magnitudes of the correlations still indicate that the two tasks are not identical.

A closer look at the visual-spatial simple span variable revealed that it correlates with both complex span tasks. The strength of these correlations was moderate to large (correlation with verbal complex span: r = .28; with visual-spatial complex span: r = .58), and therefore stronger than expected. This led us to conclude that, in our study, the visual-spatial simple span task also demanded processing. Consequently, this indicates that the shared variance between both visual-spatial variables mirrors a substantial amount of processing in addition to storage.

Our interpretation is in line with van der Ven et al. [72], who analyzed a giant database (Math Garden). They found that, within the visual-spatial modality, item difficulty was very similar when forward and backward span tasks were compared. They assume that visual-spatial simple span tasks require active executive processing. This assumption was confirmed by Ang and Lee [36,37], who directly analyzed the cognitive processes underlying spatial simple span tasks (Corsi Blocks and Visual Patterns Test) in children. They found that both simple span tasks demanded executive processes, yet to a different extent.

Taken together, results regarding the inter-relations indicate that simple and complex spans share common processes. This emphasizes the necessity to control for common variance between simple and complex spans, when the relation between WM aspects and Gf shall be analyzed.

4.2. Relationship between WM and Gf

As expected, mapping all span tasks on one general WM factor revealed a significant relation among the resulting WM factor and Gf. This finding is in line with several other studies showing that WM explains a large proportion of variance in Gf [11,73]. Including age into the model as a predictor of Gf resulted in even more variance of Gf being explained. However, when the four WM aspects were separately related to Gf, only three of the four WM aspects explained unique variance in Gf. The WM aspects that substantially contributed to the WM–intelligence link in children were verbal storage, visual-spatial storage and verbal processing. However, visual-spatial processing did not explain additional variance in Gf over and beyond the other WM aspects. It is noteworthy that the three WM aspects explaining variance in Gf had a comparable predictive power. These findings suggest that there is no predominance of any of the three tasks in the prediction of Gf, but rather that each of them contributes uniquely. This indicates that the different tasks trigger distinct information processes, all of which seem to be involved in Gf. In the next paragraphs, we will interpret these findings in the context of previous studies. First, we will consider the relations between verbal and visual-spatial storage and Gf. Second, we will discuss the relations between verbal and visual-spatial processing and Gf.

The finding that verbal and visual-spatial storage explained unique variance in Gf confirms results from Hornung et al. [50] as well as Tillman et al. [49]. These authors investigated storage separately for the verbal and visual-spatial modality and also found that verbal and visual-spatial storage to predict variance in Gf. At the same time, Gray et al. [52], who also investigated storage separately for both modalities, found that only visual-spatial storage was related to Gf, but not verbal storage. This underlines that visual-spatial storage involves processes shared with Gf (for similar findings, see: [6,7,48]). Therefore, our results, together with previous findings, indicate that visual-spatial storage is a predictor of Gf.

The finding that only verbal processing but not visual-spatial processing explained unique variance in Gf is surprising. In particular because of the following two reasons: first, in the figural Gf test, children had to operate with visually overlapping features. This led to the expectation that better visual-spatial processing abilities would yield better results in the Gf test. Second, previous studies suggest that verbal as well as visual-spatial processing explain variance in Gf [33,43,49].

The result that verbal processing explained variance in Gf is in line with Tillman et al. [49] and other studies investigating processing only for the verbal modality [7,8,48,50]. However, the finding that visual-spatial processing did not explain variance in Gf contradicts previous findings [49]. Looking at the inter-relations among the four WM aspects included in the present approach provides one possible explanation why visual-spatial processing did not explain variance in Gf: the inter-relations indicate that in the visual-spatial modality, simple and complex span tasks trigger both storage and executive processing. Hence, it is feasible that visual-spatial processing could not explain additional variance in Gf over and beyond visual-spatial "storage". Consequently, visual-spatial "storage" has to be interpreted with caution. We controlled for the common variance among simple and complex span tasks in order to get "purer" estimations of the contribution of storage and processing. However, it is not clear what variance is captured with this common WM factor, while we regressed Gf on each WM task. Was it storage or was it processing variance, or both? As all four WM tasks significantly loaded on this common factor, it is possible that common variance represented mainly storage [20]. Thus, the question arises if the variance left in visual-spatial "storage" actually represents more processing than storage variance. Therefore, even if the path from visual-spatial processing onto Gf was not significant, we cannot rule out the possibility that visual-spatial processing variance does not predict variance in Gf. The question of what represents the remaining variance after controlling for shared variance between WM span tasks is a general, yet open question in WM research, a question that has to be addressed in future research [30].

Taken together, our results indicate that individual differences in verbal storage, visual-spatial "storage" (or whatever the Matrix forward task measures) and verbal processing predict unique individual differences in Gf. However, future research needs to investigate if our findings are replicable with "purer" storage and processing tasks.

5. Conclusions

In the present study, inter-relations among simple and complex span tasks were examined. In addition, the relation between one general WM factor and Gf was analyzed. Lastly, relations between different, more circumscribed WM aspects and Gf were explored. Results concerning the inter-relations revealed that simple (forward) and complex (backward) span tasks share common processes. More precisely, the visual-spatial simple span task used also demands executive processes. Results concerning the relations between WM and Gf revealed the following: (a) loading all WM tasks on one factor explained substantial variance in Gf; (b) regressing Gf onto each WM aspect separately revealed that verbal and visual-spatial storage and verbal processing predicted unique variance in Gf, when holding the other effects constant. Thus, we are tempted to conclude that children who perform better in intelligence tests have better WM abilities such as better verbal storage, visual-spatial "storage" and more efficient verbal processing abilities.

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Author Contributions: C.M.R., E.A.A., and A.E.V. conceived and designed the experiments; E.A.A. performed the experiments; and C.M.R. and E.A.A. analyzed the data and wrote the paper.

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Appendix A

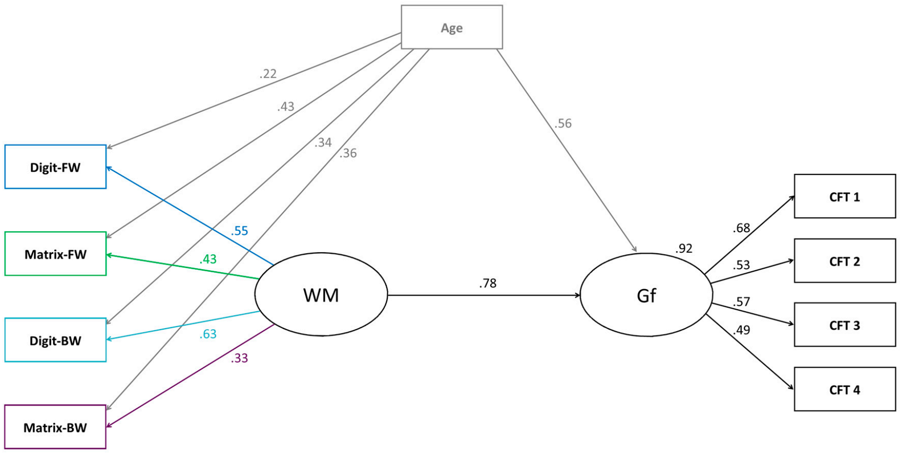

Figure A1. Structural equation model (Model 1b) testing the relation between one working memory (WM) factor, age and fluid intelligence (Gf). Digit-FW = digit forward; Digit-BW = digit backward; Matrix-FW = matrix forward; Matrix-BW = matrix backward; CFT 1–4 = subtests of the CFT 20-R. All paths were significant ($p < .05$).

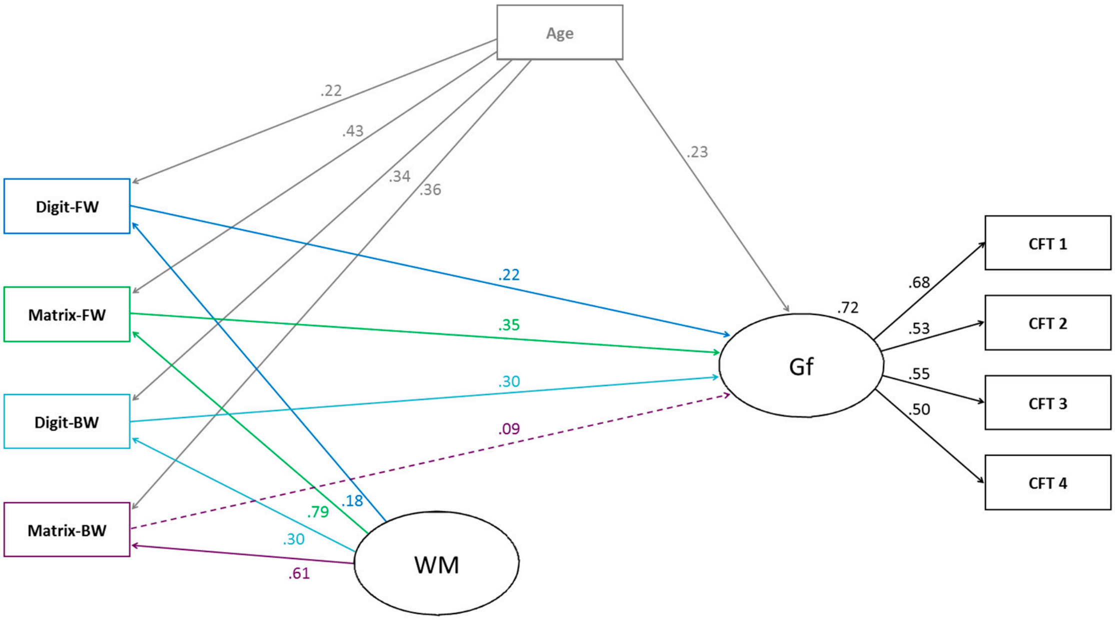

Figure A2. Structural equation model (Model 2b) testing the relations between working memory (WM) aspects, age and fluid intelligence (Gf). Digit-FW = digit forward; Digit-BW = digit backward; Matrix-FW = matrix forward; Matrix-BW = matrix backward; CFT 1–4 = subtests of the CFT 20-R. *Solid lines* represent significant paths ($p < .05$), *dashed lines* represent non-significant paths.

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Study 2

Effects of Age and Mental Ability on Verbal Working Memory in Children: A Functional Near-Infrared Spectroscopy Study

Eva A. Aeschlimann, Joëlle S. Witmer, Andreas J. Metz, Thomas H. Rammsayer,

Claudia M. Roebers

University of Bern, Bern, Switzerland

Abstract

Working memory (WM) is considered to be a driving force for cognitive development. This study investigated how age and MA interact to affect verbal WM performance and verbal WM-related brain activation. Using functional near-infrared spectroscopy, cortical responses were recorded, while keeping the relative task difficulty similar for all the children. Results showed that children's WM-related cortical responses differed in the left dorsolateral prefrontal cortex as a function of chronological age and mental ability. The findings offer new insights for a better understanding of individual differences in WM and the functional brain activation underlying cognitive development in children.

Keywords: verbal working memory, intelligence, reasoning, cognitive development, functional near-infrared spectroscopy

Individual differences in working memory (WM) play a central role in many everyday life situations. They also have been found to contribute to growth in domains such as first and second language acquisition, reading, mathematics, reasoning and problem solving (Cowan & Alloway, 2009; Verhagen & Leseman, 2016). Understanding individual differences in WM is therefore of central interest. At any given time point in development, WM performance is substantially influenced by age and mental ability (MA, i.e., intelligence; Kail, Lervåg, & Hulme, 2015; Tourva, Spanoudis, & Demetriou, 2016). WM has been investigated with neuroimaging studies, which have contributed to a better understanding of its neural correlates (Bunge & Wright, 2007; Yang et al., 2015). In the present study, we investigated neural activity associated with verbal WM performance using functional near-infrared spectroscopy (fNIRS), and examined both age- and MA-related differential effects on WM in elementary school children.

Working memory (WM) refers to the cognitive system with which individuals temporarily store information during cognitive processing. It is viewed as capacity-limited, that is, only a small amount of information can be maintained, and only a limited number of mental operations can be conducted within a limited period of time (Cowan & Alloway, 2009). WM increases from infancy until adolescence and reaches a plateau by young adulthood (Swanson, 2017).

The second central concept, *mental ability* (MA), is used in the present paper synonymously with the term *fluid intelligence*. It describes the ability to flexibly adapt mental processing to a new cognitive problem or situation (Cattell, 1963). MA increases rapidly during early and middle childhood and peaks around the age of 25 years (McArdle, Ferrer-Caja, Hamagami, & Woodcock, 2002). Like WM, MA has been found to be a powerful predictor of diverse developmental outcomes, including school achievements (Deary, 2012; Deary, Strand, Smith, & Fernandes, 2007).

WM performance and fluid intelligence are substantially related. In adults, the two constructs show correlations as high as r = .50 to .85 with each other (Ackerman, Beier, & Boyle, 2005; Oberauer, Schulze, Wilhelm, & Süß, 2005). The relation is already substantial in childhood, during which WM shares about 50 % of its variance with fluid intelligence (Gignac & Watkins, 2015; Hornung, Brunner, Reuter, & Martin, 2011; Swanson, 2008; Voelke, Troche, Rammsayer, Wagner, & Roebers, 2014). It is therefore not surprising that children with higher MA perform better on WM tasks compared to their age-matched peers with lower MA (Duan, Shi, & Wu, 2009b). Moreover, WM and MA are also associated on the neural level in that both evoke brain activity in the frontal-parietal network. This was observed in adults as well as in children (Blair, 2010; Colom et al., 2013; Constantinidis & Klingberg, 2016; Desco et al., 2011).

Unfortunately, little is known about MA effects on children`s brain activity during a WM task. Two electroencephalography (EEG) studies using a numerical n-back task indicate that neural responses of children with higher MA differ from those of their age-matched peers with lower MA (Duan, Shi, Sun, Zhang, & Wu, 2009a; Duan et al., 2009b). Functional magnetic resonance imaging (fMRI) studies using reasoning tasks and comparing adolescents with regard to their MA (high versus low) revealed greater cortical activity for adolescents with high MA. This was observed most strongly in the parietal cortex, but also in the frontal and postcentral gyri (Desco et al., 2011; Lee et al., 2006). In one of these studies, adolescents additionally solved a Tower of London task (Desco et al., 2011). The results showed that compared to adolescents with lower MA, adolescents with higher MA showed more clusters of activation that were bilateral (not only on the left, but also on the right side) and more areas were activated in frontal and intraparietal regions.

With regard to age differences in brain activity during the processing of verbal WM tasks, fMRI studies showed a stronger activation in the bilateral frontal-parietal cortex in older compared to younger age groups (Ciesielski, Lesnik, Savoy, Grant, & Ahlfors, 2006; Crone, Wendelken, Donohue, van Leijenhorst, & Bunge, 2006; Jolles, Kleibeuker, Rombouts, & Crone, 2011; Thomason et al., 2009; Vogan, Morgan, Powell, Smith, & Taylor, 2016). Thus, addressing the effects of MA on brain activity during WM processing calls for studies that use homogenous age groups.

Taken together, these studies indicate that neural activity during WM processing is qualitatively different, both as a function of chronological *and* mental age (i.e., MA; Bunge & Wright, 2007; Jung & Haier, 2007). However, to our knowledge, no functional neuroimaging study investigated age and MA effects on WM-related brain activity simultaneously. Given the intertwining of WM and MA (outlined above), MA should be controlled for when investigating specific WM-related cortical activity. Therefore, in the present study we compared WM-related brain activity between younger and older elementary school children (10 and 12 years old) with lower and higher MA, respectively.

Unfortunately, in the above-mentioned EEG and fMRI studies investigating MA effects, task difficulty was not considered. This is methodologically problematic, because although MA and WM are interrelated, the relation is far from perfect (Kyllonen & Christal, 1990). Consequently, even when MA is homogenous in a group, the individual task difficulty is not. This typically impedes the interpretation of the obtained results, as task difficulty affects brain activity (Den Bosch et al., 2014; Dix, Wartenburger, & van der Meer, 2016). Hence, in the present study, prior to the fNIRS measurement we determined children’s relatively equal task difficulty of the verbal WM task. This estimated task difficulty was then used during fNIRS data recording of WM-associated neural activity, so that each individual was presented with a relatively equally difficult task.

Most functional neuroimaging studies investigated developmental changes in visual WM, but only a few in verbal WM. These few verbal WM studies mainly implemented n-back tasks or the Sternberg item recognition task (Ciesielski et al., 2006; Den Bosch et al., 2014; Finn, Sheridan, Hudson Kam, Hinshaw, & D’Esposito, 2010; Thomason et al., 2009; Vogan et al., 2016). However, these tasks require mainly the storage aspect of WM, and only minimally the executive processing aspect. Thus, in the present study we implemented a complex-span task to investigate the neural basis of the executive processing aspect of WM. We used fNIRS, as this method has the advantage of resilience against movement artifacts (Gervain et al., 2011; Vanderwert & Nelson, 2014; Wilcox & Biondi, 2015).

Functional NIRS is a non-invasive technique that measures the activity of the superior layers of the cerebral cortex indirectly via cerebral blood flow (Scholkmann et al., 2014). In detail, fNIRS measures changes in [O_2Hb] and [HHb]. Local concentrations of O_2Hb increase and those of HHb decrease during neural activation (see Scholkmann et al., 2014, p. 17 for an illustration; Tachtsidis & Scholkmann, 2016).

Functional NIRS is an established method of measuring cortical activity triggered by cognitive tasks (e.g., WM tasks) in infants and children (Arredondo, Hu, Satterfield, & Kovelman, 2017; Buss, Fox, Boas, & Spencer, 2014; Buss & Spencer, 2017; Edwards, Wagner, Tager-Flusberg, & Nelson, 2017; Gu et al., 2017; May, Gervain, Carreiras, & Werker, 2015; Perlman, Huppert, & Luna, 2015). However, recent methodological studies have uncovered three essential requirements: First, in participants aged older than the age at infancy, hemodynamic changes in the extra-cerebral space are also recorded by most fNIRS devices. These contaminate the signals from the cortex, and need to be controlled for (see Scholkmann et al., 2014, for a review). Second, an active control task should be included to control for other task features, which are also triggered by the targeted task but—in our case—unrelated to WM (e.g., visual/auditory inputs and motor responses; Sato, Dresler, Haeussinger, Fallgatter, & Ehlis, 2014; Tachtsidis & Scholkmann, 2016). Third, the relative time dynamics of both [O_2Hb] and [HHb] should be analyzed (Meek, 2002; Tachtsidis &

Scholkmann, 2016). These methodological requirements for a fNIRS approach were met in the present study. Thus, it allowed us to examine whether—under these strict criteria—fNIRS is still a sensible tool for measuring cortical activity in the developing brain during performance on a verbal WM task.

The present study addresses the question of whether there are differences in verbal WM performance and cortical activation between younger and older children with lower or higher MA. Thus, it is of central interest to explore the possibility that age and MA may interact. For example, younger children with higher MA may not only perform similarly to older children with lower MA on a WM task, but their brain activation might also be similar. This would point to differences in the brain maturation leading to differences in MA, at least in the course of development and within a certain age range.

To investigate this possibility, we constructed a 2 (age groups) by 2 (levels of MA) factorial design enabling comparison of the influences of age and MA on WM performance and WM-related brain activation. During the brain imaging, we kept the relative task difficulty the same for all children. Following the suggestion of Vanderwert and Nelson (2014), multiple fNIRS channels (i.e., measurement paths) were used, and in the first step of the analyses, the differentially and specifically responding channels (i.e., WM experimental task vs. active control task) were identified and used for further analyses.

On the behavioral level, we expected that (a) older children would outperform younger children on the WM task and (b) children with higher MA would outperform their age-mates with lower MA. Including measures of WM-related brain activity allowed us to explore whether there are similar age and MA effects on the neural level. To the best of our knowledge, there is no previous study analyzing the effect of age and MA on WM-related brain activity, and thus, no specific hypothesis was considered in this respect. Consequently, for fNIRS data, the present study was exploratory in nature.

Method

Participants

Over 500 children were recruited from public schools in the vicinity of the university town and screened for IQ. Of these screened children, only those children with higher or lower IQs (see below) were individually invited to attend further sessions (2nd session: assessment of the WM abilities; 3rd session: fNIRS data recording). Finally, a sample of 109 (55 % girls) healthy right-handed children participated in the present fNIRS study. An additional eight children participated, but their data were excluded for various reasons [epilepsy (*n* = 2), suspicion of attention deficit hyperactivity disorder (*n* = 1), too many movement artefacts (*n* = 2), postnatal heroin withdrawal (*n* = 1), low language abilities (*n* = 1) and age not in our selected range (*n* = 1)].

The details of the final fNIRS sample are presented in Table 1. The sample consisted of four groups: two age groups (younger/approx. 10 years and older/approx. 12 years), each of which in turn contained two MA groups (lower: IQ $\leq$ 96; higher: IQ $\geq$ 115). Seventy percent had Swiss German or German as first language; 16 % were bilingual with two distinct mother tongues, of which one was Swiss German or German. The remaining participants had sufficient German language skills to understand the instructions.

As blood sugar concentration influences blood flow (Gagnon et al., 2012), parents were asked to make sure their child did not consume sweets or soft drinks (including fruits and juice) two hours before the fNIRS session. The study was conducted in line with the American Psychiatric Association's ethical principles, and had been approved by the local ethics committee of the faculty. Written consent was obtained from the main caregivers of the participating children. The children gave oral consent. Participants were rewarded for participating (1st and 2nd sessions: 30 to 50 CHF per school class; 3rd session: 30 CHF for the child and 70 CHF reimbursement for the parents).

Procedure

Each child participated in three measurement sessions. In the first session, IQ was screened in small groups, with an average group size of 10 children (*SD* = 4.9; range: 1–23 children). Secondly, WM abilities and handiness were assessed (Oldfield, 1971). In the third session, fNIRS data were recorded while participants solved a WM experimental task and an active control task. The 1st and 2nd sessions took place in rooms of the schools and were performed by trained research assistants. The 3rd session was performed in the university laboratory by one of two fNIRS experts.

Material and Tasks

Intelligence Screening (1st session). Intelligence (fluid intelligence, respectively) was quantified with the short version of the *Culture Fair Test 20-R* (CFT 20-R; Weiß, 2006). As a measure of MA, and as a basis for deciding whether a child was included in one of the IQ groups, the normalized IQ was computed according to the manual (Weiß, 2006).

Working memory tasks and active control task. All tasks were computerized using E-prime software (Bailey, 2012; Psychology Software Tools, PST, Pittsburgh). Items were presented at a rate of one per second. The children were instructed to respond orally after the last item; the experimenter wrote down their recall. There was no time limit for answering in any of the tasks described below.

Assessment of working memory ability and calculation of relatively equal task difficulty (2nd session). WM ability was measured with the *letter-number-sequencing span task* from the Wechsler Intelligence Scale for Children (Petermann & Petermann, 2011). Participants heard a mixed sequence of letters and numbers (e.g., “D-8-M-1”) and were asked to repeat them, with the numbers in numerical order first and the letters in alphabetical order second (e.g., “1-8-D-M”). The span task had increasing difficulty levels (i.e., span levels = number of items), with each level consisting of four trials. After the training block, each participant started with a sequence of two items. A trial was considered correct if all items were recalled in the correct order. With at least two correct trials out of the four trials within one difficulty level, the next block was administered, consisting of trials of one additional item. Otherwise, the task was terminated. With the letter-number-sequencing span task two variables were calculated: a) *accuracy of the letter-number-sequencing span task* (sum of correctly completed trials), and (b) the *relatively equal WM task difficulty* was determined for each child as the highest level (i.e., span) at which the child was correct on at least three of four trials.

Working memory experimental task and active control task assessed during the fNIRS data recording (3rd session). During the fNIRS data recording, participants solved two tasks, the WM experimental task and the active control task. The *WM experimental task* was the same task as described above (letter-number-sequencing), except that each child solved trials only at the relatively equal task difficulty. During the *active control task* children heard trials with a sequence of only letters (from A-K) or only numbers (from 1-9). The sequences were already in the correct order and participants were asked to repeat them orally. Participants were told that they should repeat without sorting, because the elements were already sorted. The number of items per trial was the same as in the WM experimental task. This control task was designed to match the WM experimental task in terms of visual and auditory inputs and motor responses, but with less WM load.

The experiment started with instructions, followed by seven practice trials. The tasks were then presented in a block design, consisting of 16 blocks altogether (see Figure 1). In the baseline blocks, the screen was blanked, and the children were asked to relax as much as possible. To reduce Mayer waves (i.e., spontaneous oscillations in blood flow that confound the fNIRS signal; Yücel et al., 2016) and to prevent entrainment or habituation of blood flow changes due to rhythmic changes, the duration of the baseline blocks were varied ranging from 25 to 45 s.

The accuracy was calculated separately for the WM experimental task and for the active control task. Because individuals completed different numbers of trials and each of these trials were at the relatively equal task difficulty, the percentage of correct items was used as the dependent variable {[(correct items / relatively equal WM task difficulty)/total solved items] × 100}.

Functional NIRS measurement. Data from the fNIRS were collected at a sampling rate of 7.69 Hz with a FOIRE 3000/8 multi-channel device (Shimadzu Corporation, 2010). The device uses three continuous wavelengths (780 nm, 805 nm and 830 nm) and contains eight light emitters and eight glass fiber light detectors, also called optodes. Optodes were secured by customized headgear, which was attached as described by Tsuzuki et al. (2007; see the Supplemental Figure S1 for more details about the headgear and optode placement). Optodes were localized in the Montreal Neurological Institute space (MNI) using a 3D-digitizer [FASTRAK, Pholemus; see Table A in Appendix A with the MNI coordinates and corresponding Brodmann areas (BA)].

As can be seen in Figure 2, twenty channels were defined by specific emitter and detector pairs. We focused our measures on the left prefrontal cortex (PFC), because verbal WM typically triggers greater involvement of the left compared to the right PFC (Barbey, Colom, Paul, & Grafman, 2014; Jolles et al., 2011; Thomason et al., 2009; Vogan et al., 2016).

Data Analysis and Statistics

Functional NIRS signal processing. Functional NIRS data of the FOIRE 3000/8 were exported as $\log_{10}$-based optical density data and processed further in MATLAB (version

2015b, The Mathworks, Natick, MA, USA). The $\log_{10}$-based optical density data were converted to natural logarithm-based absorbance data (see Appendix B for the Formula B1).

The high-frequency noise in the absorbance data was removed by a 3rd order Savitzky-Golay low-pass moving average filter (window length: 1.5 s; cut-off frequency: 0.66 Hz; Savitzky & Golay, 1964; Schafer, 2011). Each 60 time series was smoothed separately.

[O_2Hb] and [HHb] were calculated using the molar absorption coefficients α of Prahl (1998). The age-dependent differential path length factor was calculated according to Scholkmann and Wolf (2013). Changes of [O_2Hb] and [HHb] were calculated according to the modified Beer-Lambert law (see Appendix B for the Formula B2; Delpy et al., 1988).

To overcome contamination from superficial hemodynamic changes of the [O_2Hb] and [HHb] measurements, short channel regression was applied (Saager & Berger, 2005). In this approach, each long channel is regressed with the closest short channel (see Table C in the Appendix C with details). The regression was only applied if the correlation between the time series of the two signals (i.e., [O_2Hb] and [HHb]) was sufficient, i.e., $R^2 > 0.1$ (Gagnon et al., 2011).

To remove movement artefacts, the movement artefact removal algorithm from Scholkmann, Spichtig, Muehlemann, and Wolf (2010) was used with a slightly different interpolation method, as described in Metz, Klein, Scholkmann, and Wolf (2017; parameters for window length L and threshold T were individually selected, parameter p set to 0.7). Across all channels, signals and blocks, the averaged percentage of corrected data was 3.70.

Next, the data were low-pass filtered with a 2nd order Chebyshev infinite-impulse-response filter (cut-off frequency: 0.2 Hz) to reduce the impact of respiration and heart-beat frequencies. To calculate the average response for each block, a general linear model (GLM) was then applied (Gagnon et al., 2011). We used a set of 129 Gaussian base functions with a standard deviation of 0.5 s, which were separated by 0.5 s. The 129 base functions covered a time range of 65 s. The tasks (i.e., WM experimental task or control task) took place from 5 to 45 s. The preceding 5 s were defined as baseline. Blocks were excluded from the GLM if the task accuracy of a block was below 50 % in the WM experimental task, or below 80 % in the control task. This resulted in an exclusion of altogether four blocks of the WM experimental task (each from a different child), and one block of the control task.

Each time series was segmented into 5 s intervals. This resulted in one baseline interval and eight task intervals for each signal, task, and channel. Next, to reduce the amount of data for the statistical analysis, the sampling frequency was reduced to 0.2 Hz by averaging over 5 s intervals. The intervals were normalized by subtracting the mean value of the 5-s baseline from the mean value in each task interval. This removed the intra-individual variance of the starting values, causing the data to reflect concentration changes from the baseline to the task (positive values = increase, negative values = decrease). For further analyses, intervals 1 and 8 were excluded (interval 1 because of the delayed reaction of the hemodynamic response; interval 8 because the signals were already decreased at this time point (Scholkmann et al., 2014). We also excluded channels 4 and 6, because they were located over the *fissura longitudinalis cerebri* and did not reach the underlying cortex (Augustine, 2017). Next, intervals 2 and 3 were averaged as the *early time-window*, intervals 4 and 5 were averaged as the *middle time-window,* and intervals 6 and 7 were averaged as the *late time-window*. For the fNIRS data analyses, the total number of dependent variables was 168, resulting from 2 hemodynamic concentration changes ([O_2Hb] and [HHb]) x 14 channels (1–16, excluding 4 and 6) x 3 time-windows (early, middle and late) x 2 tasks (WM experimental and control).

Statistical Analyses. Analyses were performed with SPSS (IBM Corp. Released 2016. IBM SPSS Statistics for Windows, Version 24.0. Armonk, NY: IBM Corp.) All variables were checked for outliers separately within the four groups. Data were defined as outliers when they deviated > 3 *SD* from the corresponding group mean. Outliers were corrected to the corresponding group mean ± 3 *SD* (Field, 2013). Across all groups this resulted of the following percentage of corrected data: 3.4 % of the control task data (all other performance variables had no outliers) and 1.36 % of the fNIRS data (calculated across all channels, signals and tasks).

Age and MA effects on the WM performance variables were calculated using two-way analyses of variance (ANOVAs). Age (younger vs. older) and MA (lower vs. higher) were included as between-subject factors. The fNIRS data were investigated in two steps. First, we examined in which channels we had a neural hemodynamic change uniquely evoked by the manipulation in WM. Second, we analyzed age and MA group effects.

To examine in which channels we had a neural hemodynamic change uniquely evoked by the manipulation in WM, we performed three steps: First, we tested whether the hemodynamic concentration changes were significantly evoked by the tasks (WM experimental and control), and were not spontaneous (Scholkmann et al., 2014). For this step, one-sample *t*-tests were applied across all participants separately for each variable (checks whether a mean is significantly different from zero, the baseline). The results were corrected for multiple comparisons by the Benjamini and Hochberg (1995) false discovery rate correction across all 168 variables. Second, we checked if the hemodynamic responses could be interpreted as cortical activity, by examining the relative time dynamics of [O_2Hb] to [HHb]. Hemodynamic changes were only interpreted as neural if (a) [O_2Hb] increased significantly (i.e., significantly task-evoked) and [HHb] decreased significantly ([O_2Hb] > 0 and [HHb] < 0), or (b) [O_2Hb] increased significantly and [HHb] showed no change ([O_2Hb] > 0 and [HHb] = 0). The latter criteria was also interpreted as neural responses, because concentration changes of HHb are much weaker than those of O_2Hb. Therefore,

[HHb] changes are often not significantly different from zero (Lloyd-Fox, Blasi, & Elwell, 2010; Scholkmann et al., 2014; Vrana, Meier, Hotz-Boendermaker, Humphreys, & Scholkmann, 2016). However, when both [O_2Hb] and [HHb] show a strong increase or a strong decrease, these indicate concentration changes due to systemic influences (Tachtsidis & Scholkmann, 2016). Third, when channels exhibited *task-evoked neural hemodynamic changes* in both tasks, MANOVAs were performed to check whether the hemodynamic responses differed significantly between the tasks. The MANOVAs were calculated separately for [O_2Hb] and [HHb], with each time-window of these channels included as dependent variable and task (WM experimental vs. control) included as a within-subjects factor. When a MANOVA revealed a significant effect, subsequent ANOVAs were performed separately per channel and time-window (Note that this criterion for the subsequent ANOVAs was applied to all further MANOVAs). Taken together, channels were only included in the age and MA group effect analyses if they (a) exhibited *task-evoked neural hemodynamic changes* only in the WM experimental task, but not in the control task or (b) exhibited *task-evoked neural hemodynamic responses* in both tasks, and if the activation was significantly stronger in the WM experimental task than in the control task.

The age and MA effects on WM-related neural hemodynamic changes were analyzed using MANOVAs separately for [O_2Hb] and [HHb]. Time-window (early, middle, and late) was included as a within-subjects factor, and age (younger vs. older) and MA (lower vs. higher) as between-subject factors. To obtain a complete picture, all time-windows, and also [HHb], were analyzed. In the case of an effect concerning the factor time-window with its three conditions, post-hoc tests (least-significant difference tests) based on the estimated marginal means were analyzed, using Benjamini-Hochberg *p*-value corrections. In the case of an interaction effect involving one channel, subsequent ANOVAs were performed. In the case of an interaction effect involving more than one channel, subsequent MANOVAs were performed.

For all statistical tests, we used an alpha level of 5 % (two-tailed). As estimates of effect size, Pearson's correlation coefficient r or the partial eta squared (η^2_p) are reported. A small, medium, and large effect is defined as $r = .10$, $r = .30$, and $r = .50$, or as $\eta^2_p = .01$, $\eta^2_p = .06$, and $\eta^2_p = .14$, respectively (Field, 2013; Richardson, 2011).

Results

Working Memory Task Performance—Behavioral Analyses

Descriptive statistics. Table 1 gives an overview of the age and IQ for the four groups. The results of the ANOVAs showed that older children were significantly older than the younger ones and children with higher MA had significantly higher IQ than children with lower MA (see Supplemental online Table S2 for more details). Further descriptive statistics of the behavioral data are presented in Table 2.

Age and mental ability effects on working memory performance. As hypothesized, the results of the letter-number-sequencing span task showed that (a) independent of MA, older children performed better than younger children, and (b) independent of age, children with higher MA performed better than children with lower MA (see Table 3). The age × MA interaction was not significant. These results were found for both the accuracy of performance and the relatively equal task difficulty variable.

We examined whether the age and MA group effects disappeared in the performance on the WM experimental task, when children were presented with a relatively equal task difficulty (Table 3). As this was the case, we can conclude that cortical activity triggered by the WM experimental task and the control task were independent of task difficulty.

Functional NIRS Data

Task-evoked neural hemodynamic changes. Seven channels showed significant *task-evoked neural hemodynamic changes* (see Figure 3). Results of the one-sample *t*-tests and descriptive statistics for these active channels are presented in Table D in Appendix D (see Supplemental online Table S3 for results across all channels). Figure 3 and Table D show that of the seven active channels, three were active during the WM experimental task as well as during the control task (channels 1 and 3 both located in BA 8; channel 8 located in BA 10), while the remaining four were specifically active during the WM experimental task (channels 9 and 14 located in BA 10; channels 11 and 16 located in BA 9 and 46, respectively).

Note that [O_2Hb] did not significantly differ between the two tasks in channels 1, 3, and 8. Surprisingly, [HHb] differed significantly between the two tasks in channels 1 and 8 (both in the early and middle time-window), but not in channel 3. In channels 1 and 8, these results possibly indicated a stronger activation in the WM experimental task compared to the control task (see Table E1 and E2 in Appendix E). However, channels 1, 3 and 8 were excluded from further analysis because in channels 1 and 8, the two tasks differed only in [HHb] but not in [O_2Hb], and in channel 3, the two tasks did not differ in any of the hemodynamic concentrations.

Taken together, only channels 9, 11, 14 and 16 exhibited *task-evoked neural hemodynamic changes* only in the WM experimental task but not in the control task, and were therefore included in the analysis reported below, investigating age and MA effects on cortical activity.

Age and mental ability effects on working memory task-evoked neural hemodynamic concentration changes. Results of the MANOVAs are presented in Table 4. The MANOVAs performed for [O_2Hb] revealed a significant main effect of time-window and a significant age x MA interaction effect. All other effects were non-significant. The MANOVAs performed for [HHb] revealed no significant effects.

Results of the subsequent ANOVAs are presented in Table 5. They revealed that in [O_2Hb], the main effect time-window was only significant for channel 11, but not for channel 9, 14 and 16. Post-hoc tests were performed for [O_2Hb] of channel 11. The results demonstrated significant differences between all time-windows, indicating that [O_2Hb] increased less strongly over time (see notes in Table 5). Furthermore, the subsequent ANOVAs revealed that in [O_2Hb], the age x MA interaction effect was significant for channels 11 and 16 (located in BA 9 and 46, both corresponding to the dorsolateral PFC), but not for channels 9 and 14 (both located in BA 10, which corresponds to the rostrolateral PFC; see Table 5 and Figure 4).

Four subsequent MANOVAs were performed with the [O_2Hb] of channels 11 and 16 as dependent variables (two MANOVAs performed separately for each age group, with MA included as between-subject factor; two MANOVAs performed separately for each MA group, with age included as between-subject factor). The results of these MANOVAs and the ensuing ANOVAs are presented in Table 6.

For channel 11 (Figure 4 and Table 6), the results revealed that (a) within the younger age group, children with higher MA had a significantly stronger [O_2Hb] increase compared to children with lower MA; while (b), in older children, the [O_2Hb] did not differ significantly between MA groups. Furthermore, (c) neither in children with lower MA nor (d) in children with higher MA could statistically significant age-differences be obtained.

For channel 16 (Figure 4 and Table 6), a similar pattern was observed: (a) within the younger age group, the results revealed a significant MA effect: children with higher MA showed a [O_2Hb] increase, while in contrast, children with lower MA demonstrated a decrease in [O_2Hb]; however, (b), in older children, the [O_2Hb] did not differ significantly between MA groups. Moreover, (c) within the lower MA group, the results revealed a significant age effect: older children displayed a [O_2Hb] increase, while in contrast, younger children showed a decrease in [O_2Hb]. (d) Also for the higher MA children, the results revealed a significant age effect, however, this effect was reversed: younger children revealed a [O_2Hb] increase, while in contrast, older children showed a decrease in the [O_2Hb].

Furthermore, the age x MA interaction for channels 11 and 16 showed that the following groups had the same changes in [O_2Hb]: (a) younger children with lower MA and older children with higher MA (channel 11: $t(53) = -0.70$, $p > .05$, $r = .10$; channel 16: $t(53) = -0.36$, $p > .05$, $r = .05$) , and (b) younger children with higher MA and older children with lower MA (channel 11: $t(52) = 0.66$, $p > .05$, $r = .09$; channel 16: $t(52) = -0.18$, $p > .05$, $r = .03$).

Discussion

The main question of the present study was how age and MA combine to affect verbal WM performance and WM-related brain activity in children. Behavioral data (assessed before the fNIRS data recording) revealed that independently of MA, older children performed more accurately than younger children, and independently of age, children with higher MA performed more accurately than children with lower MA. The fNIRS data showed an age × MA interaction for cortical responses of the left BA 9 and 46. In this discussion, we address some fNIRS methodological points and discuss our key findings in the context of prior studies.

Two fNIRS methodological points should be mentioned here: First, in four channels (9, 11, 14 and 16) we found significant *WM task-evoked hemodynamic changes*. Thus, fNIRS seems to be sensitive to verbal WM activity in children even after (a) controlling for the hemodynamic responses in the extra-cerebral space, (b) including an active control task, and (c) considering the relative time dynamics of [O_2Hb] and [HHb]. Despite these results, we cannot entirely rule out that [O_2Hb] and [HHb] changes were not confounded by systemic physiological effects (e.g., respiration). To control for such effects, in future studies systemic physiology needs to be synchronously measured with special devices (Scholkmann et al., 2014). Second, three channels (1, 3 and 8) were activated in the WM experimental task *and* in the control task. Both tasks were designed to be as identical as possible, except that (a) the control task should not involve the processing of information in WM and (b) the storage of information should be minimal. This implies that further task features, such as manipulation of language, attention or self-regulation processes (because the children had to sit still) may have activated the left PFC (Amso & Scerif, 2015; Gernsbacher & Kaschak, 2003; Zelazo, 2015). Consequently, it seems to be mandatory to include a control task to isolate cortical activity of a specific cognitive process such as the executive processing in WM.

As expected, the behavioral findings revealed that older children outperformed younger children, and children with higher MA outperformed children with lower MA. These findings are in line with several previous studies on individual differences in WM related to differences in age and MA (Best & Miller, 2010; Duan et al., 2009b; Gathercole, Pickering, Ambridge, & Wearing, 2004; Huizinga, Dolan, & van der Molen, 2006; Tourva et al., 2016). The absence of an age x MA interaction further indicates that both concepts affect WM ability independently of each other. Thus, it appears that younger children with higher MA may reach the same WM performance as children who are two years older but have a lower MA.

Across children, robust cortical activity specifically triggered by the WM experimental task was found in four channels located in the left BA 9 (channel 11), 10 (channels 9 and 14) and 46 (channel 16). These areas were also active in the few previous studies investigating verbal WM in children or adolescents (Ciesielski et al., 2006; Finn et al., 2010; Jog et al., 2016; Jolles et al., 2011; Thomason et al., 2009), and in many studies exploring higher cognitive tasks (Strand, Forssberg, Klingberg, & Norrelgen, 2008). BA 9 and 46 especially, belonging to the dorsolateral PFC, play a critical role in planning, holding information "online", and monitoring higher cognition (Bunge & Zelazo, 2006; Liakakis, Nickel, & Seitz, 2011; Nitschke, Köstering, Finkel, Weiller, & Kaller, 2017; Passingham & Wise, 2012). BA 10, belonging to the rostrolateral PFC, is associated with integration and coordination processes and holding the primary goal in mind while processing a secondary one (Bunge & Zelazo, 2006; Dumontheil, Burgess, & Blakemore, 2008; Passingham & Wise, 2012). Because the literature shows that these areas are associated with WM, we can interpret the brain activity in channels 9, 11, 14 and 16 as WM-related.

The finding that children's brain responses differed because of an age × MA interaction in the left PFC is consistent with the findings of Schmithorst and Holland (2006). They investigated brain activity with fMRI in a large sample of over 300 children and found an age x MA interaction in the left PFC. However, they used a non-executive verbal generation task. Thus, the present findings demonstrated that in a verbal executive WM task as well, brain responses differed due to an interaction of chronological age with mental age independently of task difficulty. At this point it should be mentioned that we assessed brain activity only from the left PFC and, owing to fNIRS constraints, only from the superior layers. Hence, all interpretations of the neural data are valid only for this specific cortical area. Investigation of further areas would allow for more sophisticated statements.

To our knowledge, this study is the first dissociating age and MA effects on WM-related brain activity. Therefore, we discuss our findings in the context of prior studies investigating children's or adolescents': (a) verbal WM activity considering age, (b) WM activity considering MA, and (c) brain activity triggered by the Tower of London task, which also requires the processing in WM, considering MA (Phillips, 1999). Most of the previous studies, together with our findings, indicate that age and MA influence WM-related cortical responses in the left frontal cortex (Ciesielski et al., 2006; Desco et al., 2011; Duan et al., 2009a; Jolles et al., 2011; Klingberg, Forssberg, & Westerberg, 2002; Thomason et al., 2009; Vogan et al., 2016). Some of these studies also found an effect of age in the left BA 9 and 46, as we did (Jolles et al., 2011; Klingberg et al., 2002; Vogan et al., 2016). The findings of our study go farther, by indicating that these areas are affected not only by age, but also by an interaction with MA.

Furthermore, the fact that we found no age or MA effect in children's left BA 10 is analogous to several previous findings (Ciesielski et al., 2006; Jolles et al., 2011; Klingberg et al., 2002; Thomason et al., 2009) and contradicts only two studies (Desco et al., 2011; Vogan et al., 2016). It is possible that the inconsistency is due to differences in the age groups or the investigated tasks. Hence, the results of the present work indicate that in 10- and 12-year-old children, BA 10 is involved independently of age and MA while solving a verbal executive WM task.

A closer look at the age x MA interaction revealed that for the left BA 9 and 46 (a) within the younger age group, children with higher MA displayed stronger activity compared to children with lower MA (Figure 4). However, (b) within the older age group, no such MA group differences were observed. The result for the younger age group is in line with the findings of Desco et al. (2011), who found that children with higher MA activated the PFC more strongly compared to children with lower MA. This result for the younger age group can be interpreted in terms of neural efficiency. Initially, the neural efficiency hypothesis of intelligence assumed that compared to individuals with lower MA, individuals with higher MA exhibit lower brain activity or activate fewer brain areas (more focal brain activation) while performing a cognitive task (Haier, Siegel, Tang, Abel, & Buchsbaum, 1992; Haier et al., 1988). However, testing this hypothesis produced heterogeneous results (Haier, 2017; Neubauer & Fink, 2009; Poldrack, 2015). A recent meta-analysis including fMRI studies reported that in brain regions showing a relation between MA and activity the relations were mostly positive (Basten, Hilger, & Fiebach, 2015). Moreover, it seems that individuals with higher MA invest more effort into brain regions associated with the task (Basten et al., 2015; Basten, Stelzel, & Fiebach, 2013). As BA 9 and 46 are regions associated with WM, it seems that already children with higher MA put more effort into these task relevant regions. However, this interpretation raises the question why within the older age group, no such MA group differences were observed. Hence, more research is needed to gain a better understanding of neural efficiency in children.

Furthermore, the age x MA interaction demonstrated that within the lower MA group, older children had a significant stronger [O_2Hb] increase in the left BA 46 compared to younger children. In contrast, within the higher MA group, younger children showed significantly stronger activation compared to older children. The result for the lower MA group is analogous to several previous studies, reporting that older individuals activated the PFC more strongly compared to younger individuals (Ciesielski et al., 2006; Crone et al., 2006; Jolles et al., 2011; Thomason et al., 2009; Vogan et al., 2016).

Moreover, the results of the age x MA interaction revealed that younger children with lower MA and older children with higher MA showed the same [O_2Hb] responses (BA 9 and 46). This result is surprising because these two groups differed most strongly from each other in terms of age, MA and objective WM task difficulty during the fNIRS. Hence, it is possible that both groups may have differed in activation of brain regions which were not investigated in the present study (Jolles et al., 2011; Thomason et al., 2009). Thus, future research may clarify this surprising result.

Moreover, the results of the age x MA interaction indicated that younger children with higher MA and older children with lower MA showed the same [O_2Hb] response in the left BA 46. In terms of WM ability, these two groups also solved the task equally well. In this age range the brain is undergoing rapid maturation (Bathelt, Gathercole, Johnson, & Astle, 2017). Hence, this result indicates that younger children with higher MA may have a more mature left PFC compared to their age-matched peers with lower MA, and already resemble two-year-older children with lower MA, at least in terms of WM ability, and probably also in their cortical response of this left prefrontal area.

Conclusion

Together with previous studies, the present work indicates that individual differences in verbal WM may be due to differences in brain responses in the PFC, which seem to be influenced by age and MA. To our knowledge, the present study is the first investigating age and MA simultaneously. The present findings contribute to the existing literature by suggesting that age and MA interact in their influences on the neural basis of WM, in the dorsolateral PFC. In other words, the dorsolateral PFC is associated with the neural development of verbal WM, however, neural development interacts with MA.

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Appendix A

Table A. Average of the Montreal Neurological Institute (MNI) Space Coordinates for each Axis and the corresponding Brain Area of each Channel (CH)

			X-Axis				Y-Axis				Z-Axis			
CH	Left Frontal Gyrus	Left BA	*M*	*SD*	Min	Max	*M*	*SD*	Min	Max	*M*	*SD*	Min	Max
1	Superior	8	-8.87	4.38	-18.83	1.33	48.52	5.04	32.33	62.83	47.20	4.69	30.00	60.17
2	Middle	8	-28.47	3.64	-37.33	-20.00	40.58	5.66	24.33	56.67	46.51	4.89	31.50	60.67
3	Middle	8	-42.95	3.38	-52.33	-36.00	24.66	6.50	8.00	40.33	46.68	4.15	36.50	57.33
4			3.15	5.46	-9.00	13.83	57.64	4.11	42.00	66.17	38.16	5.14	19.00	54.50
5	Middle	9	-39.56	3.29	-47.33	-29.17	41.17	5.36	25.33	54.50	36.15	4.82	22.83	53.17
6			3.45	5.36	-9.67	14.33	67.88	2.88	55.00	71.83	16.09	6.63	-1.83	43.00
7	Middle	10	-44.30	2.98	-50.00	-32.50	50.52	4.13	36.33	57.83	13.14	5.51	2.50	38.00
8	Medial	10	-11.13	4.56	-22.33	0.33	69.59	2.17	60.50	73.50	3.09	7.36	-10.83	35.83
9	Middle	10	-35.78	3.53	-42.67	-23.33	60.75	2.81	50.50	67.17	1.47	6.68	-8.83	32.50
10	Inferior	10	-50.84	2.07	-54.17	-43.00	42.17	4.56	29.33	51.67	0.80	5.63	-6.83	26.83
11	Superior	9	-10.21	4.42	-20.50	-0.33	56.34	4.40	40.50	67.17	37.30	5.12	20.00	53.83
12	Superior	9	-29.81	3.69	-39.00	-19.50	48.40	4.95	32.50	61.00	36.62	5.27	21.50	54.33
13	Middle	9	-45.59	3.11	-52.83	-37.50	30.57	5.81	15.33	44.33	36.08	4.40	26.33	52.00
14	Superior	10	-9.90	4.41	-20.67	0.83	66.58	3.00	53.50	71.17	15.24	6.62	-0.83	42.33
15	Superior	10	-34.55	3.27	-41.67	-22.83	57.74	3.68	43.50	64.33	13.61	5.89	1.17	39.17
16	Inferior	46	-50.33	2.81	-56.33	-40.83	39.91	4.64	26.33	47.33	13.08	5.22	6.00	36.83
17	Superior	8	-15.30	3.37	-23.33	-5.33	48.44	5.24	32.83	63.00	47.45	4.77	31.50	60.50
18	Superior	10	-19.17	3.87	-28.17	-6.83	70.38	1.97	60.83	72.50	3.26	7.34	-10.17	35.67
19	Superior	10	-31.64	3.91	-39.17	-17.50	65.17	2.41	55.17	69.83	2.01	6.96	-9.33	34.17
20	Inferior	45	-54.04	1.72	-56.50	-47.17	36.95	4.80	22.17	48.33	0.72	5.51	-8.00	26.00

Note. Gyri and Brondmann Area (BA) were defined based on the Talairach Client.

Appendix B

Formulas of the fNIRS Signal Processing

Formula B1. Transformation of the Log$_{10}$-based Optical Density Data to the Natural Logarithm Based Absorbance Data

The log$_{10}$-based optical density data were converted to natural logarithm based absorbance *A* and each time series (i.e., 20 channels x 3 wavelengths) was referenced to the mean of each complete time series (~12 min, per channel and wavelength) to obtain the change in absorbance $\Delta A(t, \lambda)$:

$$\Delta A(t,\lambda) = -ln\left[\frac{I(t,\lambda)}{\overline{I(\lambda)}}\right]$$

The term $\overline{I(\lambda)}$ represents the mean light intensity of a time series and $I(t, \lambda)$ the measured light intensity at a certain time *t* and wavelength λ.

Formula B2. Calculation of the Concentration Changes in Oxygenated Hemoglobin [O$_2$Hb] and Deoxygenated Hemoglobin [HHb]

The changes of [O$_2$Hb] and [HHb] were calculated by the modified Beer-Lambert law (Delpy et al., 1988):

$$\begin{bmatrix} \Delta[O_2Hb](t) \\ \Delta[HHb](t) \end{bmatrix} = (A^T A)^{-1} A^T \begin{bmatrix} \Delta A(t,\lambda_1)/DPF(\lambda_1) \\ \Delta A(t,\lambda_2)/DPF(\lambda_2) \\ \Delta A(t,\lambda_3)/DPF(\lambda_3) \end{bmatrix} \frac{1}{d}$$

Where *A* is the molar absorption matrix, λ the wavelength, *t* the time, and *d* the distance between the light emitter and light detector. The matrix ***A*** is natural logarithm based and defined as:

$$A = \begin{bmatrix} \alpha_{O2Hb,780nm} & \alpha_{HHb,780nm} \\ \alpha_{O2Hb,805nm} & \alpha_{HHb,805nm} \\ \alpha_{O2Hb,830nm} & \alpha_{HHb,830nm} \end{bmatrix} = \begin{bmatrix} 1.635 & 2.477 \\ 1.934 & 1.684 \\ 2.243 & 1.596 \end{bmatrix} cm^{-1}mM^{-1}$$

mM = milliMolar = 10^{-3} mol/liter. A time series for [O$_2$Hb] and [HHb] was obtained for every channel separately

Appendix C

Table C. Assignment Order of Long and Short Channels for the Short Channel Regression and Percentage of the Short Channel Regression Application

Long-Distance Channels	Corresponding Short Channel	% of applied SCHR	
		[O_2Hb]	[HHb]
1	17	92.66	99.08
2	17	80.73	91.74
3	(17, 20)	57.80	44.04
4	17	65.14	47.71
5	17	62.39	40.37
6	18	72.48	46.79
7	19	64.22	43.12
8	18	90.83	85.32
9	19	100	90.83
10	20	100	94.50
11	17	46.79	27.52
12	17	23.85	37.61
13	(17, 20)	50.46	41.28
14	18	44.04	37.61
15	19	30.28	42.20
16	20	49.54	33.03

Note. % of applied SCHR (short-channel regression) = how often the condition R2 > .01 was met, and the SCHR was applied in %; [O_2Hb] = oxygenated hemoglobin concentration, [HHb] = deoxygenated hemoglobin concentration; (17, 20) = the mean of channels 17 and 20 was used as short channel.

Appendix D

Table D. Descriptive Statistics and Results of One-Sample *t*-Tests Across all Children for the Working Memory Experimental Task and the Control Task of Channels 1, 3, 8, 9, 11, 14 and 16

			WM Experimental Task								Control Task							
CH	Time-Window	Hb	*M*	*SD*	Min	Max	*t* (108)	*p*	*p* -crit	*r*	*M*	*SD*	Min	Max	*t* (108)	*p*	*p* -crit	*r*
1	early	[O$_2$Hb]	**0.313**	0.733	-2.153	2.698	2.26	**0.0000**	0.0045	0.39	**0.380**	0.949	-0.943	5.017	2.76	**0.0001**	0.0051	0.37
		[HHb]	**-0.131**	0.353	-1.409	0.668	-1.34	**0.0002**	0.0095	0.35	-0.031	0.417	-1.456	0.752	-0.64	0.4425	0.0375	0.07
	middle	[O$_2$Hb]	0.134	0.922	-3.367	2.872	1.37	0.1325	0.0298	0.14	**0.296**	1.111	-1.946	5.325	2.43	**0.0064**	0.0188	0.26
		[HHb]	-0.101	0.439	-1.732	0.904	-0.78	**0.0180**	0.0217	0.23	0.070	0.546	-2.750	1.291	-0.05	0.1852	0.0313	0.13
	late	[O$_2$Hb]	0.110	1.170	-4.301	3.699	0.47	0.3273	0.0348	0.09	**0.354**	1.089	-1.935	4.864	2.37	**0.0010**	0.0140	0.31
		[HHb]	-0.073	0.470	-1.360	1.361	0.34	0.1096	0.0295	0.15	0.020	0.590	-2.548	1.269	-0.45	0.7245	0.0455	0.03
3	early	[O$_2$Hb]	**0.196**	0.555	-1.138	3.426	1.57	**0.0004**	0.0116	0.33	**0.156**	0.509	-1.084	2.566	2.75	**0.0019**	0.0161	0.29
		[HHb]	**-0.082**	0.251	-1.411	0.371	-2.26	**0.0009**	0.0137	0.31	**-0.041**	0.187	-0.556	0.951	-3.08	**0.0236**	0.0238	0.22
	middle	[O$_2$Hb]	**0.228**	0.815	-1.946	4.094	0.29	**0.0042**	0.0179	0.27	**0.203**	0.684	-1.774	3.130	2.45	**0.0025**	0.0167	0.29
		[HHb]	**-0.109**	0.364	-2.310	0.798	-1.56	**0.0023**	0.0164	0.29	**-0.052**	0.233	-0.808	0.966	-2.73	**0.0212**	0.0229	0.22
	late	[O$_2$Hb]	**0.174**	0.788	-2.485	3.843	-0.15	**0.0233**	0.0235	0.22	**0.282**	0.709	-1.448	2.854	3.67	**0.0001**	0.0063	0.37
		[HHb]	-0.078	0.367	-1.755	1.085	0.20	0.0285	0.0244	0.21	**-0.101**	0.285	-1.009	0.959	-2.33	**0.0003**	0.0113	0.34
8	early	[O$_2$Hb]	**0.267**	0.595	-1.896	1.809	3.68	**0.0000**	0.0039	0.41	0.232	0.744	-2.333	3.428	1.62	**0.0016**	0.0155	0.30
		[HHb]	-0.031	0.351	-1.402	1.319	-2.26	0.3570	0.0366	0.09	0.049	0.219	-0.639	0.854	0.63	**0.0202**	0.0223	0.22
	middle	[O$_2$Hb]	**0.271**	0.750	-2.506	2.613	3.07	**0.0003**	0.0104	0.34	**0.305**	0.964	-3.320	4.608	1.40	**0.0013**	0.0149	0.30
		[HHb]	-0.038	0.390	-0.925	1.684	-2.84	0.3164	0.0345	0.10	0.060	0.351	-1.561	1.526	1.04	0.0759	0.0274	0.17
	late	[O$_2$Hb]	**0.198**	0.826	-2.895	2.253	1.91	**0.0138**	0.0199	0.23	**0.341**	1.114	-3.953	5.591	1.46	**0.0018**	0.0158	0.29
		[HHb]	-0.012	0.498	-1.294	2.160	-2.14	0.8043	0.0473	0.02	0.028	0.437	-1.773	1.966	0.25	0.4971	0.0393	0.07
9	early	[O$_2$Hb]	**0.262**	0.706	-2.025	2.956	1.91	**0.0002**	0.0089	0.35	0.122	0.650	-1.795	2.859	1.42	0.0533	0.0265	0.18
		[HHb]	0.041	0.362	-1.406	0.996	0.13	0.2413	0.0336	0.11	0.151	0.353	-0.579	1.195	2.25	**0.0000**	0.0042	0.39
	middle	[O$_2$Hb]	**0.220**	0.842	-2.158	3.419	1.27	**0.0073**	0.0193	0.25	0.158	0.725	-1.644	3.185	0.42	0.0251	0.0241	0.21
		[HHb]	0.018	0.447	-1.282	1.356	0.30	0.6713	0.0435	0.04	0.236	0.420	-0.983	1.421	3.38	**0.0000**	0.0006	0.49
	late	[O$_2$Hb]	0.134	0.854	-2.309	4.197	0.32	0.1042	0.0292	0.16	0.281	0.812	-1.622	2.780	1.83	**0.0005**	0.0119	0.33
		[HHb]	0.030	0.479	-1.417	1.450	0.26	0.5143	0.0399	0.06	0.237	0.495	-0.822	1.586	2.57	**0.0000**	0.0030	0.43
11	early	[O$_2$Hb]	**0.047**	0.090	-0.375	0.370	1.27	**0.0000**	0.0018	0.47	0.029	0.074	-0.105	0.346	2.14	**0.0001**	0.0074	0.36
		[HHb]	-0.001	0.127	-0.381	0.450	1.00	0.9550	0.0494	0.01	0.037	0.117	-0.403	0.491	0.71	**0.0012**	0.0146	0.30
	middle	[O$_2$Hb]	**0.033**	0.087	-0.317	0.319	0.77	**0.0002**	0.0086	0.35	0.008	0.074	-0.181	0.262	1.39	0.2753	0.0342	0.10
		[HHb]	-0.010	0.143	-0.453	0.435	1.08	0.4729	0.0390	0.07	0.058	0.124	-0.280	0.386	2.24	**0.0000**	0.0033	0.42
	late	[O$_2$Hb]	**0.021**	0.093	-0.403	0.315	-0.60	**0.0189**	0.0220	0.22	0.017	0.072	-0.140	0.226	2.00	**0.0149**	0.0205	0.23
		[HHb]	-0.010	0.148	-0.545	0.368	0.87	0.4725	0.0387	0.07	0.051	0.129	-0.328	0.452	1.95	**0.0001**	0.0068	0.37
14	early	[O$_2$Hb]	**0.009**	0.023	-0.040	0.113	1.48	**0.0001**	0.0065	0.37	0.004	0.020	-0.065	0.060	2.07	0.0504	0.0262	0.19
		[HHb]	0.007	0.035	-0.102	0.135	1.19	0.0421	0.0259	0.19	0.014	0.026	-0.070	0.099	2.46	**0.0000**	0.0012	0.48
	middle	[O$_2$Hb]	**0.008**	0.020	-0.063	0.065	0.62	**0.0001**	0.0077	0.36	0.001	0.023	-0.087	0.089	1.34	0.5258	0.0405	0.06
		[HHb]	0.003	0.041	-0.177	0.169	0.73	0.4545	0.0381	0.07	0.020	0.036	-0.060	0.191	2.48	**0.0000**	0.0003	0.50
	late	[O$_2$Hb]	**0.006**	0.021	-0.053	0.075	0.18	**0.0036**	0.0176	0.28	0.005	0.023	-0.053	0.106	2.09	**0.0157**	0.0208	0.23
		[HHb]	0.003	0.044	-0.221	0.206	0.04	0.4991	0.0396	0.07	0.018	0.035	-0.102	0.170	1.79	**0.0000**	0.0024	0.46
16	early	[O$_2$Hb]	**0.010**	0.029	-0.063	0.107	0.08	**0.0006**	0.0125	0.32	0.001	0.031	-0.074	0.143	-0.06	0.6987	0.0446	0.04
		[HHb]	0.000	0.021	-0.084	0.052	-0.15	0.9646	0.0497	0.00	0.000	0.019	-0.071	0.040	-0.01	0.9830	0.0500	0.00
	middle	[O$_2$Hb]	0.005	0.033	-0.082	0.101	-1.15	0.0941	0.0286	0.16	-0.005	0.039	-0.085	0.147	-0.56	0.2132	0.0327	0.12
		[HHb]	0.002	0.027	-0.096	0.078	0.90	0.3312	0.0354	0.09	0.003	0.024	-0.116	0.093	0.45	0.1558	0.0304	0.14
	late	[O$_2$Hb]	0.005	0.039	-0.117	0.166	-1.83	0.1951	0.0315	0.12	0.002	0.038	-0.099	0.159	0.30	0.5722	0.0414	0.05
		[HHb]	0.002	0.027	-0.082	0.090	1.04	0.4076	0.0372	0.08	0.001	0.027	-0.105	0.097	-0.39	0.7797	0.0464	0.03

Note. Bold means (*M*) are ≠ 0 and interpretable as brain activity, bold *p* values = *p* < Benjamini-Hochberg critical *p* -value (*p* -crit) and thus significant > 0.

CH = channel; WM = working memory; Hb = hemoglobin, [O$_2$Hb] = oxygenated hemoglobin concentration (µM), [HHB] = deoxygenated hemoglobin concentration (µM).

Appendix E

Table E1. Multivariate Tests to Compare the Activation Between the Working Memory Experimental Task and the Control Task of Channels 1, 3, and 8

To compare the activation between the working memory (WM) experimental task and the control task, two multivariate analysis of variances (MANOVAs) were performed separately for oxygenated hemoglobin ([O_2Hb]) and deoxygenated hemoglobin concentration changes ([HHb]). As dependent variables, each time-window (i.e., early, middle and late) of channel 1, 3 and 8 was included.

Hb	Pillai's *V*	*F* (9, 100)	*p*	η^2_p
[O_2Hb]	0.09	1.05	*ns.*	.09
[HHb]	0.22	3.09	< .01	.22

Table E2. Subsequent Univariate Tests to Compare the Activation Between the Working Memory Experimental Task and the Control Task of Channels 1 and 8

As the MANOVA of [HHb] was significant, subsequent univariate analysis of variances were performed for each of the [HHb] variables.

CH	Time-Window	*F* (1, 108)	*p*	η^2_p	Direction of the Effect
1	early	6.20	< .05	.05	WM task < control task
	middle	10.26	< .01	.09	WM task < control task
	late	2.31	*ns.*	.02	
3	early	2.38	*ns.*	.02	
	middle	2.49	*ns.*	.02	
	late	0.34	*ns.*	.00	
8	early	5.00	< .05	.04	WM task < control task
	middle	4.00	< .05	.04	WM task < control task
	late	0.41	*ns.*	.00	

Note. CH = channel; WM = working memory.

Table 1

Descriptive Statistics of Age and IQ for Each Group

		Younger Age Group				Older Age Group			
Variable	MA Groups	*n* (girls%)	*M*	*SD*	Range	*n* (girls%)	*M*	*SD*	Range
Age (in months)									
	Lower MA	29 (62)	118.00	5.19	108-126	21 (57)	145.33	5.89	136-156
	Higher MA	33 (55)	117.67	5.73	106-126	26 (46)	145.62	5.89	136-156
IQ									
	Lower MA	29 (62)	89.14	5.14	76-95	21 (57)	89.14	6.74	72-96
	Higher MA	33 (55)	123.06	5.47	116-136	26 (46)	122.50	8.31	115-141

Note. MA = mental ability.

Table 2

Descriptive Statistics of Performance From all Variables of Each Group

		Younger Age Group			Older Age Group		
Variables	MA Groups	*M*	*SD*	Range	*M*	*SD*	Range
2nd Measurement Session							
LNS Span Task Accuracy							
	Lower MA	10.14	1.55	7-13	11.90	2.70	5-16
	Higher MA	11.61	1.95	8-16	13.92	2.46	9-19
Relatively Equal Task Difficulty							
	Lower MA	3.31	0.60	2-4	3.81	0.87	2-5
	Higher MA	3.70	0.73	2-5	4.31	0.74	3-6
3rd Measurement Session							
WM Experimental Task							
	Lower MA	90.77	8.63	67.50-100	88.83	8.61	68-98.08
	Higher MA	91.23	7.53	68.75-100	92.08	6.06	75-100
Control Task							
	Lower MA	99.49	1.31	95.27-100	99.39	1.06	95.95-100
	Higher MA	99.85	0.68	96.24-100	100	0.00	100-100

Note. MA = mentall abilitiy; LNS = letter-number-sequencing; WM = working memory.

Table 3

Results of the ANOVAs of Each Performance Variable With Age and MA as Factors

Dependent Variable	Factor	*F* (1,105)	*p*	η^2_p	Direction of the Effect
2nd Measurement Session					
LNS Span Task Accuracy					
	Age	23.84	< .001	.19	younger < older children
	MA	17.37	< .001	.14	lower < higher MA
	Age x MA	0.43	*ns.*	.00	
Relatively Equal Task Difficulty					
	Age	15.32	< .001	.13	younger < older children
	MA	9.74	< .01	.08	lower < higher MA
	Age x MA	0.15	*ns.*	.00	
3rd Measurement Session					
WM Experimental Task					
	Age	0.13	*ns.*	.00	
	MA	1.52	*ns.*	.01	
	Age x MA	0.86	*ns.*	.01	

Note. MA = mental ability; LNS = letter-number-sequencing; WM = working memory.
We did not perform ANOVAs for the control tasks, because there was no variance in this task.

Table 4

Results of MANOVAs Performed Separately for [O_2Hb] and [HHb] Over Channels 9, 11, 14 and 16 and With Time-Window, Age and MA Included as Factors

Factor	Hb	Pillai's *V*	*F* (df, df error)	*p*	η^2_p
Time-Window					
	[O_2Hb]	0.10	2.64 (8, 416)	< .05	.05
	[HHb]	0.05	1.22 (8, 416)	*ns.*	.02
Time-Window x Age					
	[O_2Hb]	0.04	1.01 (8, 416)	*ns.*	.02
	[HHb]	0.04	1.07 (8, 416)	*ns.*	.02
Time-Window x MA					
	[O_2Hb]	0.02	0.45 (8, 416)	*ns.*	.01
	[HHb]	0.02	0.56 (8, 416)	*ns.*	.01
Time-Window x Age x MA					
	[O_2Hb]	0.02	0.52 (8, 416)	*ns.*	.01
	[HHb]	0.05	1.32 (8, 416)	*ns.*	.02
Age					
	[O_2Hb]	0.00	0.05 (4, 102)	*ns.*	.00
	[HHb]	0.03	0.76 (4, 102)	*ns.*	.03
MA					
	[O_2Hb]	0.02	0.4 (4, 102)	*ns.*	.02
	[HHb]	0.03	0.73 (4, 102)	*ns.*	.03
Age x MA					
	[O_2Hb]	0.14	4.04 (4, 102)	< .001	.14
	[HHb]	0.03	0.78 (4, 102)	*ns.*	.03

Note. Results were sorted per effect and not per executed MANOVA. MA = mental ability; Hb = hemoglobin, [O_2Hb] = oxygenated hemoglobin concentration, [HHb] = deoxygenated hemoglobin concentration.

Table 5

Results of the Subsequent Univariate ANOVAs Performed for $[O_2Hb]$ With Time-Window, Age and MA as Factors

Factor	CH	*F* (df, df error)	*p*	η^2_p
Time-Window				
	9	2.87 (1.46, 153.57)	*ns.*	.03
	11	7.38 (1.55, 162.87)	<.01	.07
	14	1.4 (1.44, 151.55)	*ns.*	.01
	16	2.18 (1.62, 170.02)	*ns.*	.02
Age x MA				
	9	0.86 (1, 105)	*ns.*	.01
	11	4.19 (1, 105)	< .05	.04
	14	1.32 (1, 105)	*ns.*	.01
	16	12.61 (1, 105)	<.01	.11

Note. Results with the factor time-window show the Huynh-Feldt corrected values, because the assumption of sphericity had been violated. Post-hoc test time-window effect channel (CH) 11 $[O_2Hb]$: early time-window (*M* = 0.046, *SE* = 0.009) > middle time-window [*M* = 0.032, *SE* = 0.008; *p* = .02; Benjamini-Hochberg critical *p* -value (*p* -crit) = .03]; early time-window > late time-window (*M* = 0.022, *SE* = 0.009; *p* = .00, *p* -crit = .02); middle time-window > late time-window (*p* = .03 *p* -crit = .05).

MA = mental ability; Hb = hemoglobin, $[O_2Hb]$ = oxygenated hemoglobin concentration.

Table 6

Subsequen Tests Performed to Get a Better Understanding of the Age x MA Interaction Effects in Channels 11 and 16

	MANOVAs					ANOVAs			
Group	Factor	Pillai's *V*	*F* (df, df error)	*p*	η^2_p	CH	*F* (df, df error)	*p*	η^2_p
Younger Children									
	MA	0.17	5.99 (2, 59)	< .01	.17	11	4.41 (1, 60)	< .05	.07
						16	9.60 (1, 60)	< .01	.14
Older Children									
	MA	0.10	2.36 (2, 44)	*ns.*	.10				
Children with Lower MA									
	Age	0.17	4.65 (2, 47)	< .05	.17	11	1.72 (1, 48)	*ns.*	.03
						16	6.52 (1, 48)	< .05	.12
Children with Higher MA									
	Age	0.10	3.24 (2, 56)	< .05	.10	11	2.56 (1, 57)	*ns.*	.04
						16	5.97 (1, 57)	< .05	.09

Note. In each MANOVA oxygenated hemoglobin concentration changes of channels (CH) 11 and 16 were included as dependent variables. MA = mental ability.

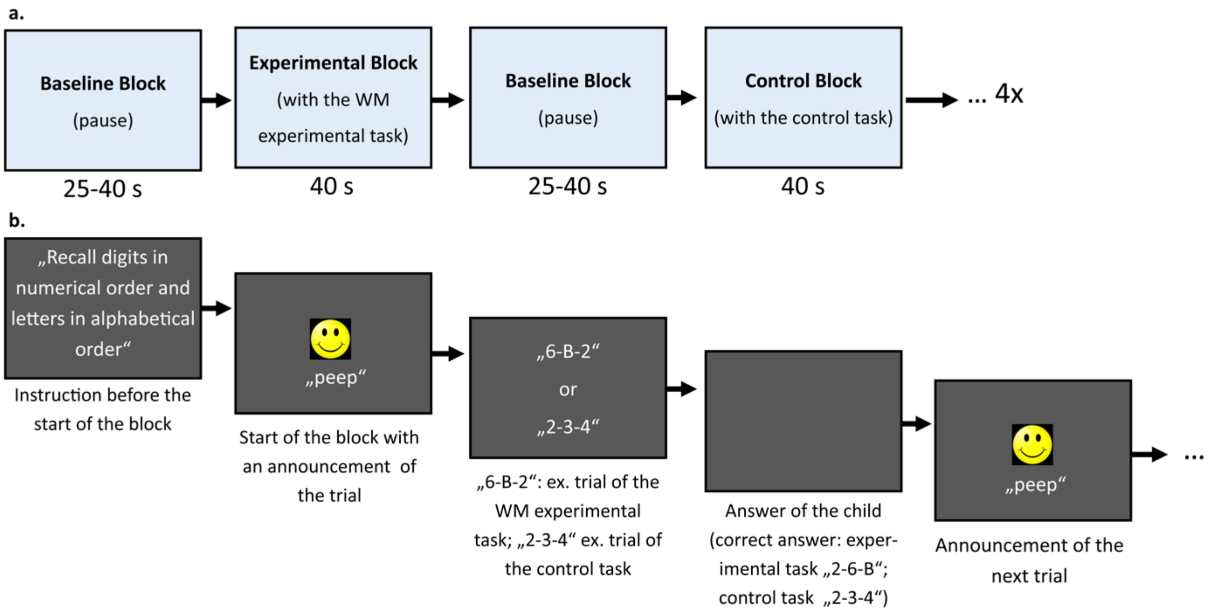

Figure 1. (a) Illustration of the block design, which contained 8 baseline blocks, 4 experimental blocks and 4 control blocks. Note that after the first baseline block, participants started either with the experimental block or with the control block. (b) Illustration of the procedure of the task blocks (experimental and control). Note that these task blocks lasted at least 40 s each. During this time, the child solved as many trials as possible (presented randomly). After the 40 s, the child finished the started trial.
WM = working memory.

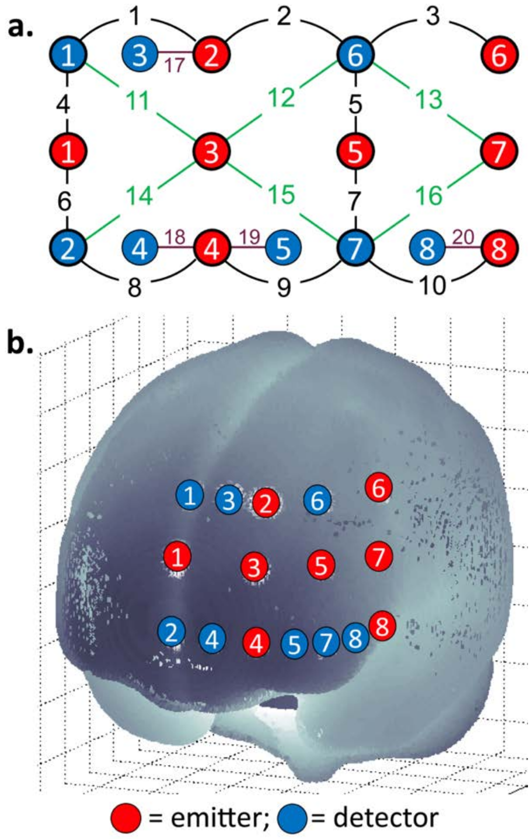

Figure 2. (a) Illustrates the channel configuration. Distances of emitter and detector are illustrated by different colored lines: Purple lines = ~15 mm; green lines = ~42 mm; black lines = ~30 mm. (b) Illustrates the locations of emitters and detectors on the left prefrontal cortex.

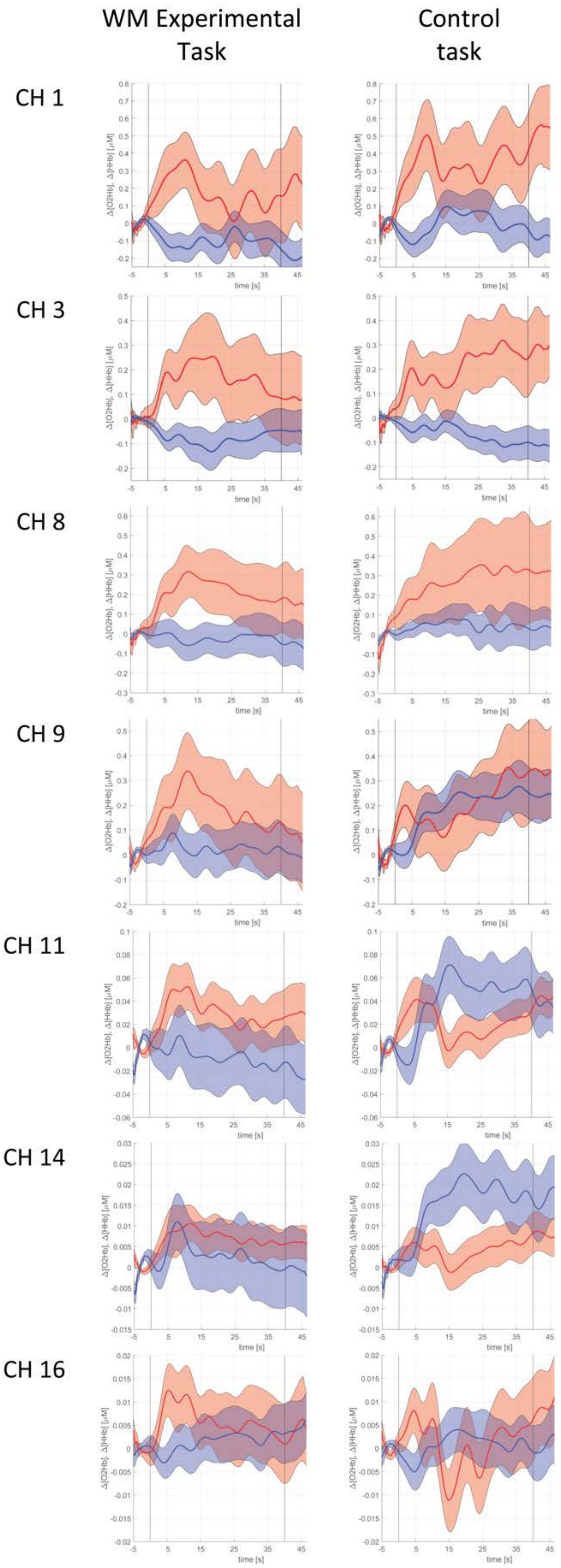

Figure 3. Grand averages and confidence intervals of evoked hemodynamic concentration changes across all subjects. Y-axis scales differ per channel (CH). Red line = oxygenated hemoglobin, blue line = deoxygenated hemoglobin, each with 95 % confidence interval.

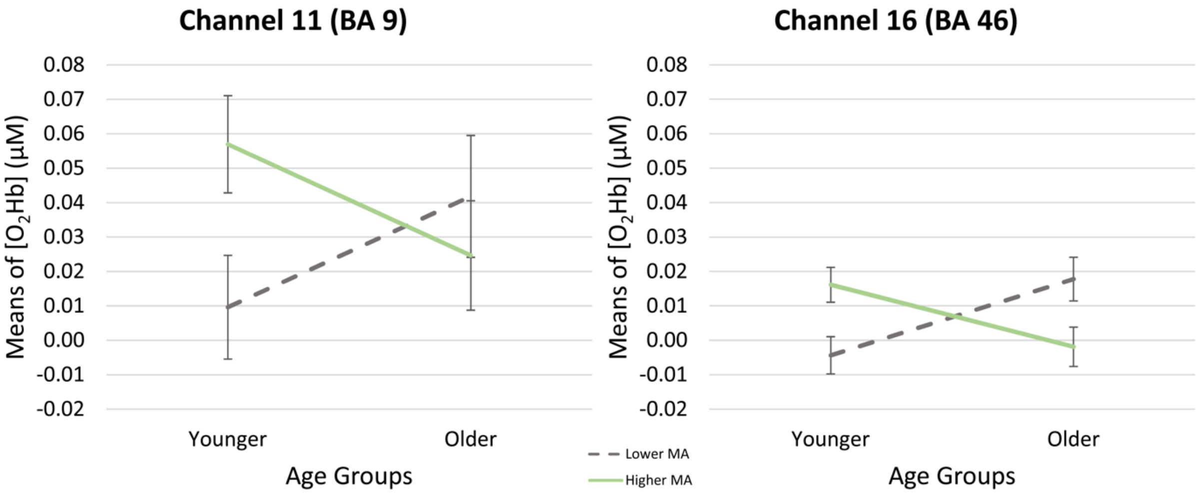

Figure 4. Illustration of the interaction effects found in channels 11 and 16. Error bars represent the standard error of the mean.
MA = mental ability; BA = Brodmann area.

Supplemental online Material 1

Supplemental Material Concerning the Headgear and Optode Placement

The optodes were secured by a customized headgear (Figure S1) placed on the participant’s head. The headgear was a modified version of the forehead fiber holder from Shimadzu (Shimadzu Corporation, 2010). After intensive piloting, we modified the holder for three reasons: (1) to avoid pressure sore due to the fibers on children`s forehead, (2) to have a headgear that fits the head size of children and adults and (3) to be able to add short channels (channel = measurement path between an emitter and detector). Beside ethical reasons, it is important to reduce pain because it activates frontal areas of the brain (Holper et al., 2014; Yücel et al., 2015).

Figure S1. Picture of the headgear

To realize reproducible measurement locations across subjects, the holder was attached for each subject in a procedure similar as described by Tsuzuki et al. (2007). Detector four was located at the F_{pz}, according to the international 10-20 EEG system (Klem, Lüders, Jasper, & Elger, 1999). The line from the forehead F_{pz} to the Inion (I_z) served as reference line. At the reference line, the border of the headgear was aligned. A 3D-digitizer

(FASTRAK, Pholemus) and the software “3D Position Measurement System” was used to localize the emitters and detectors in the Montreal Neurological Institute (MNI) space (Shimadzu Corporation, 2012). With the 3D-digitizer, the head landmarks (Nasion [N_z], Vertex [C_z], I_z, left preacular [A_1], right preacular [A_2]) and each emitter and detector position was recorded. In addition, we assessed the head size by aligning the measuring tap on the F_{pz} and the I_z ($M = 41.85$ cm; $SD = 22.38$ cm). Further, we measured the distance from the N_z to the I_z ($M = 33.60$; $SD = 1.47$), as well as from the A_1 to the A_2 across the C_z ($M = 35.65$; $SD = 1.35$). In the cases where the 3D-digitizer did not produce meaningful coordinates (24 %), coordinates of another child with the same head size and the same distances from N_z to I_z and from A_1 to A_2 were used.

To estimate with the emitter and detector positions the MNI averaged coordinates of each channel position (built over $n = 88$) the free-ware MATLAB toolbox NFRI was used (Functional Brain Science Laboratory, Jichi Medical University, Japan; http://www.jichi.ac.jp/brainlab/tools.html#GroupSp/; see also Singh, Okamoto, Dan, Jurcak, & Dan, 2005). These MNI coordinates and the corresponding brain regions are presented in Table A in Appendix A. The Talairach Client was used to define the gyri and Brodmann areas (BA; Lancaster et al., 1997; Lancaster et al., 2000).

To ensure a good light coupling between the emitters and detectors, hair was brushed away from the forehead and fixed (by a hairband or hair tie) before the headgear was fit. Moreover, before data collecting started, we removed the optodes from the headgear one by one, pushed hair away within the holes of the headgear and applied a clear ultrasound gel (Dispogel, Disposan, Switzerland) on the scalp in order to keep the hair away. Note that the ultrasound gel did not flow into the fibers. Then, we fixed the optodes again. Furthermore, the room was darkened in order to minimize background light. Bevor data recording was started, we checked the quality of the signal. If necessary, we repeated the procedure of removing the hair under the optodes.

References S1

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Supplemental online Material 2

Table S2. Results of the Analyses of Variance Performed to Prove that Age and Mental Ability Groups Were Built as Intended

To check whether the four groups differed in age and mental ability (MA) as intended, two two-way analyses of variance (ANOVAs) were performed. Each ANOVA was conducted with age (younger vs. older) and MA (lower vs. higher) as between-subjects factors. The first ANOVA was performed with age in months as dependent variable and the second one with the IQ as dependent variable.

Dependent Variable	Factor	F (1,105)	p	η^2_p	Direction of the Effect
Age (in months)					
	Age	631.88	< .001	.86	younger < older children
	MA	0.00	*ns.*	.00	
	Age x MA	0.08	*ns.*	.00	
IQ					
	Age	0.05	*ns.*	.00	
	MA	726.84	< .001	.87	lower < higher MA
	Age x MA	0.05	*ns.*	.00	

Note. MA = mental ability

Supplemental online Material 3

Table S3. Descriptive Statistics and Results of the One-Sample t-Test Across all Children for the Working Memory Experimental Task and the Control Task

			WM Experimental Task								Control Task							
CH	Time-Window	Hb	M	SD	Min	Max	t(108)	p	p-crit	r	M	SD	Min	Max	t(108)	p	p-crit	r
1	early	$[O_2Hb]$	**0.313**	0.733	-2.153	2.698	2.26	**0.0000**	0.0045	0.39	**0.380**	0.949	-0.943	5.017	2.76	**0.0001**	0.0051	0.37
		[HHb]	**-0.131**	0.353	-1.409	0.668	-1.34	**0.0002**	0.0095	0.35	-0.031	0.417	-1.456	0.752	-0.64	0.4425	0.0375	0.07
	middle	$[O_2Hb]$	0.134	0.922	-3.367	2.872	1.37	0.1325	0.0298	0.14	**0.296**	1.111	-1.946	5.325	2.43	**0.0064**	0.0188	0.26
		[HHb]	-0.101	0.439	-1.732	0.904	-0.78	**0.0180**	0.0217	0.23	0.070	0.546	-2.750	1.291	-0.05	0.1852	0.0313	0.13
	late	$[O_2Hb]$	0.110	1.170	-4.301	3.699	0.47	0.3273	0.0348	0.09	**0.354**	1.089	-1.935	4.864	2.37	**0.0010**	0.0140	0.31
		[HHb]	-0.073	0.470	-1.360	1.361	0.34	0.1096	0.0295	0.15	0.020	0.590	-2.548	1.269	-0.45	0.7245	0.0455	0.03
2	early	$[O_2Hb]$	0.080	1.288	-3.476	4.468	0.99	0.5163	0.0402	0.06	0.286	1.439	-3.338	8.457	1.67	0.0403	0.0253	0.20
		[HHb]	0.046	0.527	-1.837	1.568	0.89	0.3637	0.0369	0.09	0.063	0.536	-1.346	1.850	0.70	0.2199	0.0330	0.12
	middle	$[O_2Hb]$	-0.012	1.809	-5.579	5.080	0.38	0.9454	0.0488	0.01	0.278	2.072	-4.858	11.308	0.66	0.1636	0.0310	0.13
		[HHb]	0.030	0.690	-2.140	2.330	0.32	0.6473	0.0432	0.04	0.178	0.766	-1.826	2.964	2.36	**0.0168**	0.0214	0.23
	late	$[O_2Hb]$	-0.109	1.996	-7.450	7.243	-0.99	0.5702	0.0411	0.05	0.459	2.264	-4.431	10.846	0.69	0.0366	0.0250	0.20
		[HHb]	0.098	0.800	-1.834	2.732	0.56	0.2022	0.0318	0.12	0.160	0.868	-2.039	3.701	2.12	0.0562	0.0271	0.18
3	early	$[O_2Hb]$	**0.196**	0.555	-1.138	3.426	1.57	**0.0004**	0.0116	0.33	**0.156**	0.509	-1.084	2.566	2.75	**0.0019**	0.0161	0.29
		[HHb]	**-0.082**	0.251	-1.411	0.371	-2.26	**0.0009**	0.0137	0.31	**-0.041**	0.187	-0.556	0.951	-3.08	**0.0236**	0.0238	0.22
	middle	$[O_2Hb]$	**0.228**	0.815	-1.946	4.094	0.29	**0.0042**	0.0179	0.27	**0.203**	0.684	-1.774	3.130	2.45	**0.0025**	0.0167	0.29
		[HHb]	**-0.109**	0.364	-2.310	0.798	-1.56	**0.0023**	0.0164	0.29	**-0.052**	0.233	-0.808	0.966	-2.73	**0.0212**	0.0229	0.22
	late	$[O_2Hb]$	**0.174**	0.788	-2.485	3.843	-0.15	**0.0233**	0.0235	0.22	**0.282**	0.709	-1.448	2.854	3.67	**0.0001**	0.0063	0.37
		[HHb]	-0.078	0.367	-1.755	1.085	0.20	0.0285	0.0244	0.21	**-0.101**	0.285	-1.009	0.959	-2.33	**0.0003**	0.0113	0.34
5	early	$[O_2Hb]$	0.031	0.347	-1.189	1.588	-0.42	0.3496	0.0363	0.09	0.011	0.312	-1.261	1.152	1.15	0.7093	0.0452	0.04
		[HHb]	0.038	0.170	-0.490	0.598	1.63	**0.0224**	0.0232	0.22	0.076	0.202	-0.519	0.804	2.26	**0.0001**	0.0080	0.35
	middle	$[O_2Hb]$	0.011	0.428	-1.486	1.806	-0.94	0.7964	0.0470	0.02	-0.020	0.400	-1.784	1.374	0.45	0.6007	0.0426	0.05
		[HHb]	0.056	0.240	-0.704	1.436	0.90	**0.0160**	0.0211	0.23	0.089	0.248	-0.765	0.886	2.40	**0.0003**	0.0107	0.34
	late	$[O_2Hb]$	-0.014	0.543	-2.498	2.141	-1.26	0.7845	0.0467	0.03	0.048	0.397	-1.427	1.597	0.90	0.2107	0.0324	0.12
		[HHb]	0.081	0.292	-0.728	1.923	1.22	**0.0046**	0.0182	0.27	0.063	0.280	-1.070	1.228	2.18	**0.0203**	0.0226	0.22
7	early	$[O_2Hb]$	0.075	0.445	-1.133	1.536	-0.42	0.0810	0.0283	0.17	-0.022	0.434	-1.212	1.457	-0.32	0.5976	0.0423	0.05
		[HHb]	0.349	0.644	-1.024	2.290	2.35	**0.0000**	0.0009	0.48	0.219	0.548	-1.615	1.729	1.67	**0.0001**	0.0054	0.37
	middle	$[O_2Hb]$	-0.004	0.467	-1.470	1.516	-1.76	0.9349	0.0482	0.01	-0.095	0.452	-1.024	1.042	-0.80	0.0308	0.0247	0.21
		[HHb]	0.414	0.832	-1.759	2.825	3.12	**0.0000**	0.0027	0.45	0.285	0.724	-1.716	2.510	2.19	**0.0001**	0.0071	0.37
	late	$[O_2Hb]$	-0.017	0.491	-1.338	1.737	-2.37	0.7249	0.0458	0.03	0.007	0.476	-1.181	1.180	0.51	0.8762	0.0476	0.02
		[HHb]	0.395	0.853	-2.277	3.838	2.45	**0.0000**	0.0036	0.42	0.317	0.795	-1.861	2.720	2.44	**0.0001**	0.0057	0.37
8	early	$[O_2Hb]$	**0.267**	0.595	-1.896	1.809	3.68	**0.0000**	0.0039	0.41	0.232	0.744	-2.333	3.428	1.62	**0.0016**	0.0155	0.30
		[HHb]	-0.031	0.351	-1.402	1.319	-2.26	0.3570	0.0366	0.09	0.049	0.219	-0.639	0.854	0.63	**0.0202**	0.0223	0.22
	middle	$[O_2Hb]$	**0.271**	0.750	-2.506	2.613	3.07	**0.0003**	0.0104	0.34	**0.305**	0.964	-3.320	4.608	1.40	**0.0013**	0.0149	0.30
		[HHb]	-0.038	0.390	-0.925	1.684	-2.84	0.3164	0.0345	0.10	0.060	0.351	-1.561	1.526	1.04	0.0759	0.0274	0.17
	late	$[O_2Hb]$	**0.198**	0.826	-2.895	2.253	1.91	**0.0138**	0.0199	0.23	**0.341**	1.114	-3.953	5.591	1.46	**0.0018**	0.0158	0.29
		[HHb]	-0.012	0.498	-1.294	2.160	-2.14	0.8043	0.0473	0.02	0.028	0.437	-1.773	1.966	0.25	0.4971	0.0393	0.07
9	early	$[O_2Hb]$	**0.262**	0.706	-2.025	2.956	1.91	**0.0002**	0.0089	0.35	0.122	0.650	-1.795	2.859	1.42	0.0533	0.0265	0.18
		[HHb]	0.041	0.362	-1.406	0.996	0.13	0.2413	0.0336	0.11	0.151	0.353	-0.579	1.195	2.25	**0.0000**	0.0042	0.39
	middle	$[O_2Hb]$	**0.220**	0.842	-2.158	3.419	1.27	**0.0073**	0.0193	0.25	0.158	0.725	-1.644	3.185	0.42	0.0251	0.0241	0.21
		[HHb]	0.018	0.447	-1.282	1.356	0.30	0.6713	0.0435	0.04	0.236	0.420	-0.983	1.421	3.38	**0.0000**	0.0006	0.49
	late	$[O_2Hb]$	0.134	0.854	-2.309	4.197	0.32	0.1042	0.0292	0.16	0.281	0.812	-1.622	2.780	1.83	**0.0005**	0.0119	0.33
		[HHb]	0.030	0.479	-1.417	1.450	0.26	0.5143	0.0399	0.06	0.237	0.495	-0.822	1.586	2.57	**0.0000**	0.0030	0.43
10	early	$[O_2Hb]$	0.016	0.317	-0.926	0.779	0.29	0.5941	0.0420	0.05	-0.118	0.348	-1.224	0.679	-2.37	**0.0006**	0.0128	0.32
		[HHb]	0.085	0.537	-1.636	1.511	2.03	0.1006	0.0289	0.16	0.159	0.557	-1.348	1.894	2.80	**0.0035**	0.0173	0.28
	middle	$[O_2Hb]$	-0.047	0.346	-1.015	1.030	-1.10	0.1595	0.0307	0.14	-0.178	0.418	-1.559	0.734	-2.95	**0.0000**	0.0048	0.39
		[HHb]	0.127	0.642	-2.207	1.905	1.77	0.0416	0.0256	0.19	0.198	0.601	-1.407	1.804	3.25	**0.0009**	0.0134	0.31
	late	$[O_2Hb]$	-0.066	0.384	-1.026	1.305	-1.23	0.0763	0.0277	0.17	-0.104	0.393	-1.046	0.743	-0.81	**0.0067**	0.0190	0.26
		[HHb]	0.179	0.700	-2.680	1.850	1.40	**0.0086**	0.0196	0.25	0.229	0.665	-1.749	2.340	3.78	**0.0005**	0.0122	0.33
11	early	$[O_2Hb]$	**0.047**	0.090	-0.375	0.370	1.27	**0.0000**	0.0018	0.47	0.029	0.074	-0.105	0.346	2.14	**0.0001**	0.0074	0.36
		[HHb]	-0.001	0.127	-0.381	0.450	1.00	0.9550	0.0494	0.01	0.037	0.117	-0.403	0.491	0.71	**0.0012**	0.0146	0.30
	middle	$[O_2Hb]$	**0.033**	0.087	-0.317	0.319	0.77	**0.0002**	0.0086	0.35	0.008	0.074	-0.181	0.262	1.39	0.2753	0.0342	0.10
		[HHb]	-0.010	0.143	-0.453	0.435	1.08	0.4729	0.0390	0.07	0.058	0.124	-0.280	0.386	2.24	**0.0000**	0.0033	0.42
	late	$[O_2Hb]$	**0.021**	0.093	-0.403	0.315	-0.60	**0.0189**	0.0220	0.22	0.017	0.072	-0.140	0.226	2.00	**0.0149**	0.0205	0.23
		[HHb]	-0.010	0.148	-0.545	0.368	0.87	0.4725	0.0387	0.07	0.051	0.129	-0.328	0.452	1.95	**0.0001**	0.0068	0.37
12	early	$[O_2Hb]$	0.002	0.014	-0.026	0.098	-0.66	0.0777	0.0280	0.17	0.001	0.015	-0.061	0.084	0.22	0.6983	0.0443	0.04
		[HHb]	0.003	0.010	-0.027	0.039	2.41	**0.0010**	0.0143	0.31	0.004	0.012	-0.017	0.064	2.11	**0.0002**	0.0092	0.35
	middle	$[O_2Hb]$	0.000	0.012	-0.035	0.067	-1.64	0.9487	0.0491	0.01	-0.002	0.018	-0.092	0.100	-0.90	0.1507	0.0301	0.14
		[HHb]	0.004	0.015	-0.043	0.081	1.45	**0.0054**	0.0185	0.26	0.006	0.016	-0.057	0.087	2.90	**0.0001**	0.0083	0.35
	late	$[O_2Hb]$	-0.001	0.014	-0.036	0.074	-1.96	0.3296	0.0351	0.09	-0.001	0.016	-0.066	0.084	-0.60	0.6893	0.0440	0.04
		[HHb]	0.006	0.018	-0.044	0.092	1.34	**0.0014**	0.0152	0.30	0.005	0.016	-0.068	0.078	2.96	**0.0007**	0.0131	0.32
13	early	$[O_2Hb]$	0.015	0.164	-0.720	0.868	-0.83	0.3429	0.0360	0.09	0.008	0.175	-0.615	0.785	1.14	0.6154	0.0429	0.05
		[HHb]	0.001	0.072	-0.139	0.317	-0.02	0.9109	0.0479	0.01	0.009	0.078	-0.300	0.357	-0.41	0.2291	0.0333	0.12
	middle	$[O_2Hb]$	0.010	0.241	-1.012	1.042	-1.77	0.6724	0.0438	0.04	0.016	0.236	-0.899	1.057	0.54	0.4671	0.0384	0.07
		[HHb]	0.009	0.100	-0.231	0.418	0.75	0.3355	0.0357	0.09	0.013	0.106	-0.455	0.497	-0.19	0.2040	0.0321	0.12
	late	$[O_2Hb]$	0.002	0.258	-1.022	1.071	-1.45	0.9447	0.0485	0.01	0.050	0.267	-1.191	1.464	1.58	0.0546	0.0268	0.18
		[HHb]	0.011	0.100	-0.325	0.339	0.95	0.2605	0.0339	0.11	-0.009	0.119	-0.578	0.406	-1.52	0.4491	0.0378	0.07
14	early	$[O_2Hb]$	**0.009**	0.023	-0.040	0.113	1.48	**0.0001**	0.0065	0.37	0.004	0.020	-0.065	0.060	2.07	0.0504	0.0262	0.19
		[HHb]	0.007	0.035	-0.102	0.135	1.19	0.0421	0.0259	0.19	0.014	0.026	-0.070	0.099	2.46	**0.0000**	0.0012	0.48
	middle	$[O_2Hb]$	**0.008**	0.020	-0.063	0.065	0.62	**0.0001**	0.0077	0.36	0.001	0.023	-0.087	0.089	1.34	0.5258	0.0405	0.06
		[HHb]	0.003	0.041	-0.177	0.169	0.73	0.4545	0.0381	0.07	0.020	0.036	-0.060	0.191	2.48	**0.0000**	0.0003	0.50
	late	$[O_2Hb]$	**0.006**	0.021	-0.053	0.075	0.18	**0.0036**	0.0176	0.28	0.005	0.023	-0.053	0.106	2.09	**0.0157**	0.0208	0.23
		[HHb]	0.003	0.044	-0.221	0.206	0.04	0.4991	0.0396	0.07	0.018	0.035	-0.102	0.170	1.79	**0.0000**	0.0024	0.46
15	early	$[O_2Hb]$	0.012	0.049	-0.141	0.177	0.01	**0.0140**	0.0202	0.23	0.002	0.049	-0.187	0.148	-0.01	0.7041	0.0449	0.04
		[HHb]	0.023	0.063	-0.156	0.207	1.61	**0.0003**	0.0110	0.34	0.024	0.059	-0.130	0.177	2.03	**0.0001**	0.0060	0.37
	middle	$[O_2Hb]$	0.002	0.047	-0.146	0.141	-1.54	0.7358	0.0461	0.03	-0.014	0.048	-0.187	0.092	-1.60	**0.0031**	0.0170	0.28
		[HHb]	0.029	0.079	-0.127	0.311	2.17	**0.0002**	0.0098	0.35	0.042	0.079	-0.163	0.428	3.42	**0.0000**	0.0015	0.47
	late	$[O_2Hb]$	-0.003	0.048	-0.181	0.151	-2.46	0.5772	0.0417	0.05	-0.002	0.045	-0.155	0.105	-0.34	0.5640	0.0408	0.06
		[HHb]	0.030	0.083	-0.164	0.339	2.42	**0.0003**	0.0101	0.34	0.045	0.085	-0.154	0.384	3.05	**0.0000**	0.0021	0.47
16	early	$[O_2Hb]$	**0.010**	0.029	-0.063	0.107	0.08	**0.0006**	0.0125	0.32	0.001	0.031	-0.074	0.143	-0.06	0.6987	0.0446	0.04
		[HHb]	0.000	0.021	-0.084	0.052	-0.15	0.9646	0.0497	0.00	0.000	0.019	-0.071	0.040	-0.01	0.9830	0.0500	0.00
	middle	$[O_2Hb]$	0.005	0.033	-0.082	0.101	-1.15	0.0941	0.0286	0.16	-0.005	0.039	-0.085	0.147	-0.56	0.2132	0.0327	0.12
		[HHb]	0.002	0.027	-0.096	0.078	0.90	0.3312	0.0354	0.09	0.003	0.024	-0.116	0.093	0.45	0.1558	0.0304	0.14
	late	$[O_2Hb]$	0.005	0.039	-0.117	0.166	-1.83	0.1951	0.0315	0.12	0.002	0.038	-0.099	0.159	0.30	0.5722	0.0414	0.05
		[HHb]	0.002	0.027	-0.082	0.090	1.04	0.4076	0.0372	0.08	0.001	0.027	-0.105	0.097	-0.39	0.7797	0.0464	0.03

Note. Bold means (M) are ≠ 0 and interpretable as brain activity, bold p values = p < Benjamini-Hochberg critical p-value (p-crit) and thus significant > 0.

CH = channel; Hb = hemoglobin, $[O_2Hb]$ = oxygenated hemoglobin concentration (μM), [HHB] = deoxygenated hemoglobin concentration (μM).