High fluid intelligence is characterized by flexible allocation of attentional resources:

Evidence from EEG

Runhao Lu ^{a, b} Jie Xi ^{a, b} Xingli Zhang ^{a, b*} Jiannong Shi ^{a, b*}

^a CAS Key Laboratory of Behavioral Science, Institute of Psychology, Chinese Academy of

Sciences, Beijing, 100101, China

^b Department of Psychology, University of Chinese Academy of Sciences, Beijing, 100049, China

Author Note

This work was supported by the Pioneer Initiative of the Chinese Academy of Sciences, Feature Institutes Program, TSS-2015-06.

Correspondence concerning this article should be addressed to Xingli Zhang and Jiannong Shi, Institute of Psychology, Chinese Academy of Sciences, 16 Lincui Road, Chaoyang District, Beijing, 100101, P.R. China. Tel: +86 010 64877971, Email: zhangxl@psych.ac.cn; shijn@psych.ac.cn

Abstract

Recently, the *integrated control hypothesis* (Lu et al., 2020) was proposed to explain the relationship between fluid intelligence (Gf) and attentional resource allocation. This hypothesis suggested that individuals with higher Gf tend to flexibly and adaptively allocate their limited resources according to the task type and task difficulty rather than simply exert more or fewer resources in any conditions. To examine this hypothesis, the present study used electroencephalogram (EEG) indicators (i.e., frontal theta-ERS and parietal-occipital alpha-ERD) as the measurement of participants' resource allocation during the exploration task and exploitation task with different difficulties. The results found that higher Gf individuals tend to allocate fewer resources in all difficulty levels in the exploitation task compared to average Gf participants. In contrast, in the exploration task, higher Gf participants would allocate more resources in the medium- and high-difficulty levels than average Gf participants, but this phenomenon was only found in males. These findings provided supportive evidence for the integrated control hypothesis that flexible and adaptive attentional control ability are important characteristics of human intelligence.

Key words: fluid intelligence, attentional resource allocation, integrated control hypothesis, alpha-ERD, theta-ERS

Introduction

To explore how people with different fluid intelligence (Gf) allocate their limited attentional resources (or referred to as mental effort) is crucial to understand the nature of intelligence. Previous studies have provided many valuable theories and empirical findings on this question (e.g., Haier et al., 1988; Neubauer & Fink, 2009), but it still remains inconsistent as many moderating factors such as task type (Capotosto et al., 2009; Lee, Ojha, Kang, & Lee, 2015) and task difficulty (Bornemann et al., 2010; Doppelmayr et al. 2005; Lipp et al., 2012; van der Meer et al., 2010) make this relationship complicated.

In empirical studies, pupillometry and electroencephalogram (EEG) are two typical methods adopted by researchers to record attentional resource allocation. Task-evoked pupillary response (TEPR) is a sensitive index reflecting domain-general attentional resource allocation: The more resources required to perform a cognitive task, the greater the pupil dilation evoked by the task (Alnaes et al., 2014; Klingner, Tversky, & Hanrahan, 2011). As for EEG indicators, previous studies have suggested that parietal-occipital EEG alpha activity (power in 8–12 Hz) is associated with cortical inhibition (Händel, Haarmeier, & Jensen, 2011; van Dijk et al., 2008; Wostmann, Alavash, & Obleser, 2019) and default mode brain activity (Jann et al., 2009; Laufs et al., 2003). In contrast, frontal EEG theta activity (power in 5–8 Hz) is related to workload associated processes (Brouwer, Hogervorst, Holewijn, & van Erp, 2014; Dong, Reder, Yao, Liu, & Chen, 2015; Jensen & Tesche, 2002). Therefore, cortical activity accompanying cognitive tasks is typically related to the percentage

increase of frontal theta power (i.e., theta event-related synchronization, ERS) and with a percentage decrease of parietal-occipital alpha power (i.e., alpha event-related desynchronization, ERD) (Capotosto et al., 2009; Pfurtscheller & Lopes da Silva, 1999). In this regard, parietal alpha-ERD and frontal theta-ERS are suggested to be indicators reflecting attentional resource allocation or mental effort (Dong et al., 2015; Gevins, Smith, McEvoy, & Yu, 1997; Klimesch, 1997; Klimesch, 1999; Krause et al., 2000; Pesonen, Hamalainen, & Krause, 2007; Raghavachari et al., 2001; Stipacek, Grabner, Neuper, Fink, & Neubauer, 2003).

Many pupillometry and EEG studies supported the idea of the *neural efficiency hypothesis* (Haier et al., 1988) that higher Gf people could solve cognitive problems with fewer resource allocation (Ahern & Beaty, 1979; Jaušovec, 1996; Neubauer & Fink, 2003; Neubauer, Fink, & Schrausser, 2002). However, there were also existing literature indicating the opposite results to this hypothesis (Gray et al., 2003; Klimesch, Doppelmayr, & Hanslmayr, 2006; Klimesch, Doppelmayr, Pachinger, & Ripper, 1997). To clarify this contradiction, a number of studies indicated that task difficulty plays a crucial moderating role in the relationship between Gf and resource allocation (Doppelmayr et al., 2005; van der Meer et al., 2010). To be specific, higher Gf individuals would allocate fewer or equivalent resources when the task difficulty is relatively low. In contrast, when task difficulty getting higher, higher Gf individuals would exert more attentional resources to solve them. This account concerning the moderating role of task difficulty is referred to as *the resource hypothesis* (van der Meer et al., 2010) and has been supported by both pupillometry and EEG studies

(Bornemann et al., 2010; Doppelmayr et al. 2005; van der Meer et al., 2010).

In addition to the task difficulty, task type also seems to play a significant role in the relationship between Gf and attentional resource allocation because the resource hypothesis could not explain early results that neural efficiency existed in all the difficulty levels (e.g., Ahern & Beatty, 1979). For instance, Capotosto et al. (2009) found that higher Gf people showed stronger theta-ERS in the memory encoding period but showed lower alpha-ERD in the memory retrieval period. Similarly, Doppelmayr and colleagues (2005) indicated that the neural efficiency hypothesis holds true when participants could use efficient strategies either in easy tasks or under specific instructions in tasks with any difficulty levels. From the perspective of brain activation, it is suggested that when tasks become familiar and automatic, the brain activity across the frontal cortex will decrease (Duncan & Owen, 2000). Moreover, Hayes and Petrov (2016) proposed a *control hypothesis* that task demands (exploration vs. exploitation) will influence people's resource allocation policy. They conducted a pupillometry study using concurrent think-aloud verbal protocols in Raven's Advanced Progressive Matrices (RAPM) to support their hypothesis. They found that higher Gf people tend to use fewer resources in the exploitation period (requiring the utilization of limited knowledge about what is already known to solve problems) while allocating more resources in the exploration period (requiring to explore potential problem space to forage potential ways for problem-solving). From the point of view of the control hypothesis, all accounts from Capotosto et al. (2009), Doppelmayr et al. (2005), and Duncan et al. (2000) make sense because using strategy,

memory retrieval, or automatic processing based on familiarity is more like exploitation state while not using strategy, memory encoding, or controlled processing based on novelty is closer to exploration state.

The control hypothesis still had some directions to be further studied. Firstly, this study distinguished exploration and exploitation states in a single task (i.e., RAPM), which was also used as the scale measuring participants' Gf. Whether participants' resource allocation in two independent tasks that mainly involve exploration or exploitation should be verified. Moreover, the control hypothesis did not pay much attention to the role of task difficulty. As mentioned above, both task type and task difficulty play important roles in the relationship between Gf and attentional resource allocation, thus it is sensible to take both factors together.

To take both effects of task type and task difficulty into account, Lu et al. (2020) proposed an *integrated controlled hypothesis* combining both factors into the theoretical model (Figure 1). According to this hypothesis, in exploitation tasks, task difficulty will not influence the relationship between Gf and resource allocation, as higher Gf people use fewer resources to solve tasks in all difficulty levels as the neural efficiency hypothesis proposed. In contrast, in tasks mainly involving exploration, task difficulty will influence the relationship between Gf and resource allocation as the resource hypothesis proposed. Lu et al. (2020) have conducted a pupillometry study to preliminarily supported this new proposal. To further examine this account, it is necessary to provide converging evidence for it from another perspective such as cortical activation measured by EEG. In addition, Lu et al. (2020)

found the integrated control hypothesis for the exploration task was only supported in male participants, which reminds us that gender is another influential factor that should be concerned as suggested by previous studies (Dunst et al., 2014; Grabner et al., 2004; Neubauer & Fink, 2003; Neubauer, Fink, & Schrausser, 2002). Since the pupillometry is an indirect indicator of an individual's arousal state (Alnaes et al., 2014), using EEG method to examine this hypothesis will be possible to check whether the role of gender is sensitive to measurement or is a generally existing phenomenon.

The integrated control hypothesis emphasizes that higher Gf people have a better ability of attention control that could flexibly and adaptively allocate their limited resources according to specific task demands rather than simply allocating fewer or more resources. The idea of the integrated control hypothesis echoes another suggestion about human intelligence that high Gf people have better attentional control (also referred to as *cognitive control* and *executive control*) ability that could help them flexibly and smoothly solve cognitive tasks (Burgoyne & Engle, 2020; Rueda, 2018). Similarly, the multiple-demand (MD) theory of human intelligence (Duncan, 2010; Duncan, Assem, & Shashidhara, 2020) suggested that a wide-spread brain network that could adaptively and flexibly encode task-relevant information according to the task demands is the neural basis of Gf. These ideas suggested that high Gf people do not necessarily exert fewer resources when they come across cognitive tasks but are able to flexibly allocate their limited resources according to the actual condition.

To sum up, the present study aims to examine the integrated control hypothesis by using EEG method with frontal theta-ERS and parietal-occipital alpha-ERD as indicators of resource allocation. According to the integrated control hypothesis, we hypothesized that higher Gf participants tend to have more flexible and adaptive attentional control abilities compared with average Gf participants. Specifically, we hypothesized that: (1) In the exploration task, compared with average Gf participants, higher Gf participants would allocate more resources in high-difficulty trials but allocate fewer or equivalent resources in low- or medium-difficulty trials; (2) In the exploitation task, higher Gf participants would allocate fewer resources than average Gf individuals in all difficulty levels, but this phenomenon may be more evident in males.

Figure 1 Integrated control hypothesis.

Methods

Participants

We recruited 45 participants (23 men and 22 women) with a mean age of 22.47 years ($SD = 2.69$) from local universities for the present study. All participants are right-handed and have normal or corrected-to-normal vision without astigmatism. All participants had no psychiatric or neurological disorders. All participants received basic subsidies for their participation and additional bonus if they complete the whole experiments seriously. The study was approved by the Ethical Review Committee of Institute of Psychology, Chinese Academy of Sciences, and informed consent was obtained from each participant.

Measurements and tasks

Measurement of fluid intelligence

RAPM (Raven, 1958) in the paper-and-pencil form was used to evaluate participants' Gf. All participants were required to complete this 36-item test in 40 minutes, and the final Gf score was calculated as the number of correct items as each item was assigned one point. The obtained RAPM scores showed adequate split-half reliability (0.83), indicating good reliability in this sample.

All participants were divided into two groups according to the mean Gf score (26.71). Individuals scoring over 26.71 were assigned to the high Gf group ($N = 24$, $M_{Gf} = 30.08$, $SD = 2.10$), and individuals scoring below 26.71 were assigned to the average Gf group ($N = 21$, $M_{Gf} = 22.86$, $SD = 4.34$). The Gf scores significantly differed between the two groups [$t(63) = 7.25$, $p < 0.001$].

Exploration task

The mental paper folding task (Shepard & Feng, 1972) was used as the exploration task (Figure 2). In this task, the stimuli consist of six squares joined together representing an unfolded cube, with a black dot presented in one of the squares as the base of the cube and two arrows pointing to one of the sides of particular squares. The participants were needed to mentally fold this two-dimensional pattern into a three-dimensional cube taking the surface with the black spots as the base and then judge whether the two edges indicated by the two arrows could overlap after folding. In this study, half of the stimuli were ‘match’ trials, and the other half were ‘mismatch’ trials. Previous studies have suggested that participants have to perform psychological operations step-by-step each time without applying any rules because the mental folding task can force subjects to fold one surface at a time (Sun & Feng, 2016). This characteristic made this task a good example of the exploration task. In addition, we also interviewed all the participants about their thoughts when they performed this task using two questions (Q1: You tend to use some rules that you already know to answer these questions; Q2: You cannot be sure of its rules, and you have to keep exploring in order to answer it), and required them to evaluate how correct the two expressions are from 0 (completely disagree) to 100 (completely agree). The results showed that the mean scores of these two questions are 29.15 and 77.78, indicating this task is a typical task involving more exploration. In addition, from the interview we also noticed that the low-difficulty trails in the exploration task may show fewer exploratory features because they were

relatively easy, while medium- and high-difficulty trials exactly showed exploratory features.

The difficulty level of this task was classified by the total number of squares involved in the match-mismatch decision according to previous studies (Milivojevic, Johnson, Hamm, & Corballis, 2003; Shepard & Feng, 1972). As shown in Figure 2, the low-, medium-, and high-difficulty problems involved folding two, four and six squares, respectively. Before the formal experiment started, the participants would complete six practice trials to be familiar with the procedure and would be provided feedback regarding the correctness of their answers after each trial. The formal experiment consisted of 120 trials (40 trials per difficulty level) divided into 5 blocks, and each block included 24 trials presented in a Latin square order.

Each trial included five phases (Figure 3) beginning with a fixation cross presented for 2000 ms, and the EEG signal in the last 1000 ms was calculated as the baseline EEG power (fixation phase). Then, the stimuli were presented on the screen (stimulus presentation phase), and the subjects were required to press the space key to progress to the answering phase (the maximum duration was 30 s) once they had their answers. The EEG signal from 1250 ms to 250 ms before the response was calculated as the active EEG power. After the answer (yes/no) was entered, a mask with the same luminance as the test items was presented for 1000 ms to allow the EEG signal to return to its baseline state (mask phase), followed by a smiley face on the screen indicating that the subjects were allowed to start the next trial by pressing the space key (relaxation phase). During each trial, the participants were required to not move

their head or body.

Figure 2 Examples of the stimuli of the mental paper folding tasks with different difficulty levels (from left to right: low-, medium-, and high-difficulty trials).

Figure 3 Illustrations of the five phases in each trial in the exploration task.

Exploitation task

The matrix completion tasks with limited rules generated by a software program (Matzen, Benz, Dixon, Posey, Kroger, & Speed, 2010) were adopted as the exploitation task. Although this task involved a reasoning process, we only chose questions with limited attributes in this task. Moreover, we completely taught these limited attributes to the participants during the practice session to allow them to directly use these rules to solve the tasks, meeting the requirements of exploitation tasks. In addition, after the whole study, we also interviewed all the participants towards their thoughts when they performed this task using two questions (Q1: You tend to use some rules that you already know to answer the questions; Q2: You cannot

be sure of its rules, and you have to keep exploring in order to answer it), and asked them to evaluate how correct the two expressions are from 0 (completely disagree) to 100 (completely agree). The results showed that the mean scores of these two questions are 85.4 and 32.82, indicating that this task is a good example of the exploitation task. Further interview results indicated that all three difficulty levels showed exploitative features. Notably, although this task is similar to RAPM in form, the two tasks have different natures because participants have been familiar with all the rules during the practice period in the present task. We also asked participants to answer the two same questions towards RAPM, and the results of the two scores are 50.69 and 48.46, indicating that RAPM is a more balanced task involving both exploration and exploitation.

The difficulty level of this task was classified by the number of attributes required to be considered in each trial. As shown in Figure 4, the stimuli were divided into three difficulty levels with the low-, medium-, and high-difficulty trials involving one, two, and three attributes to be considered, respectively. Prior to the formal experiment, the participants would complete eight practice items to become fully familiar with the procedure and the limited rules of the task and would be provided feedback regarding the correctness of their answers after each trial. The formal experiment consisted of 120 trials (40 trials per difficulty level) divided into 5 blocks, and each block included 24 trials presented in a Latin square order. The experimental phases of each trial and the time interval during which the participants' EEG were recorded were the same as those in the exploration task (Figure 3), except that the

stimuli were changed in the exploitation tasks.

Figure 4 Examples of the stimuli of the matrix completion tasks with different difficulty levels (from left to right: low-, medium-, and high-difficulty trials).

EEG recording and data analysis

Continuous EEG data was recorded using a 64-channel Ag-AgCl electrode cap (NeuroScan Inc., Herndon, VA, USA; amplified by a SynAmps 2 system; bandwidth: 0.1-100 Hz, DC; sample rate: 1000 Hz) based on 10-20 system of electrode locations. Vertical and horizontal electrooculograms were recorded bipolarly with the electrodes placed above and below the left eye and the outer canthi of each eye using the nose as a reference. During the data recording, electrode impedance was maintained below 5 k Ω .

The preprocessing of EEG data was processed using EEGLAB (Delorme & Makeig, 2004) and custom scripts running in the MATLAB environment (The MathWorks Inc., Natick, Massachusetts) after excluding participants who did not complete the whole task (5 participants in the exploitation task and 2 participants in the exploration task) and invalid trials (e.g., incorrect trials and those trials with

response time below 1250 ms). Valid trials in each condition in average for each person are 39.13 (97.83%), 34.36 (85.89%), and 28.04 (70.11%) in the exploitation task and are 28.64 (71.61%), 36.31 (90.78%), and 33.31 (83.28%) in the exploration task. Continuous EEG data were re-referenced to a common average reference and were band-pass filtered between 1 - 30 Hz. The baseline epochs were extracted with the signal 1000 ms prior to the stimulus onset and the active epochs were extracted with the signal from 1250 ms to 250 ms prior to the response (Figure 3). We chose the time window of around one second prior to the response because previous studies showed that participants had relatively large and evident resource allocation in that time window (e.g., Klingner, Tversky, & Hanrahan, 2011; Lu, Bao, Zhang, & Shi, 2020). Subsequently, trials contaminated by eye blinks and movements were corrected using an independent component analysis (ICA) algorithm. In all datasets, these independent components had a large EOG channel contribution and a frontal scalp distribution.

In the concept of this study, theta (5-8 Hz) and alpha (8-12 Hz) band power were computed by the application of Fourier Transform to each epoched window. To calculate the ERD (or ERS), we used the ERD-formula: $ERD = ((power\ baseline - power\ active) / power\ baseline) \times 100$ (Doppelmayr et al., 2005; Pfurtscheller & Aranibar, 1977). In this case, positive values indicate a power decrease (ERD) and negative values indicate a power increase (ERS). Frontal (Fz, F3, F4) and parietal-occipital (POz, PO3, PO4) electrode subsets were selected for the analyses of frontal theta power and posterior alpha power, respectively, according to the typical

topological distribution of these two oscillations (Brouwer, Hogervorst, Holewijn, & van Erp, 2014; Dong, Reder, Yao, Liu, & Chen, 2015). Finally, processed data were submitted to statistical analyses (e.g., correlation analysis and ANOVA) by using JASP (v.0.11.1.0; JASP Team, 2019).

Procedures

The participants were tested individually in the same windowless room after completing an informed consent form. First, two sessions of the EEG experiment were conducted, with half of the participants starting with the exploration task and the other half beginning with the exploitation task. The EEG experiment was taking up to a total of around 2.5 hours (including preparation of EEG recording, data acquisition, and voluntary breaks). After the EEG experiment and a five-minute break, the participants completed RAPM in 40 minutes. After the entire experiment was completed, the participants were paid for participating in this research.

Results

Behavioural results

After calculating the mean and standard deviation of the behavioural results (Table 1), we performed 2 (Gf group: high vs. average) $\times$ 2 (task type: exploration task vs. exploitation task) $\times$ 3 (task difficulty: low vs. medium vs. high) repeated-measures ANOVAs to examine the differences in task performances.

The results of behavioural accuracy did not find a three-way interaction effect among task type, Gf group and task difficulty [$F(2,74) = 0.86, p = 0.43, \eta_p^2 = 0.02$]. However, a significant interaction effect was detected between Gf group and task

difficulty [$F(2,74) = 7.73, p < 0.001, \eta_p^2 = 0.17$]. Further simple effect analysis results indicated that the accuracy of high Gf individuals was significantly higher than the average Gf individuals' accuracy when the task difficulty was medium [$F(1,74) = 10.52, p = 0.003$] or high [$F(1,74) = 11.38, p = 0.002$], but this difference was not significant in the low-difficulty trials [$F(1,74) = 1.80, p = 0.19$]. Moreover, the results revealed a significant interaction effect between task type and task difficulty [$F(2,74) = 50.79, p < 0.001, \eta_p^2 = 0.58$]. The participants' accuracy was significantly higher in the exploration task when the task difficulty was medium [$F(1,74) = 16.16, p < 0.001$] or high [$F(1,74) = 54.23, p < 0.001$].

With regards to the behavioural reaction time (RT), the results did not detect a significant three-way interaction effect among task type, Gf group and task difficulty [$F(2,74) = 0.57, p = 0.57, \eta_p^2 = 0.02$], while there was a significant interaction effect between Gf group and task difficulty [$F(2,74) = 3.63, p = 0.03, \eta_p^2 = 0.08$]. Further simple effect analysis showed that high Gf participants' RT were faster than those of the average Gf individuals in the low-difficulty trials [$F(1,74) = 2.53, p = 0.12$] rather than in the medium- [$F(1,74) = 0.01, p = 0.95$] or high-difficulty trials [$F(1,74) = 0.23, p = 0.63$], although all these difference in RT did not reach a statistically significant level. In addition, there is a significant interaction effect between task type and task difficulty [$F(2,74) = 4.32, p = 0.02, \eta_p^2 = 0.10$] and the RT in the exploitation task are significantly longer than those in the exploration task in all three difficulty levels [$Fs > 127.00, ps < 0.001$].

Table 1 Means and standard deviations (in brackets) of behavioural results in the exploitation and exploration tasks with different difficulty levels

Task type	Difficulty	RT (s)		Accuracy (%)	
		H-Gf	A-Gf	H-Gf	A-Gf
Exploitation ($N_{H-Gf} = 22, N_{A-Gf} = 18$)	Low-difficulty	5.87	6.94	98.45	97.78
		(1.28)	(1.94)	(2.30)	(2.96)
	Medium-difficulty	9.40	10.17	90.36	84.86
		(1.94)	(1.76)	(5.32)	(6.15)
	High-difficulty	13.21	13.27	77.26	68.33
		(1.81)	(1.34)	(8.14)	(10.11)
Exploration ($N_{H-Gf} = 23, N_{A-Gf} = 20$)	Low-difficulty	2.41	2.52	98.69	95.83
		(1.18)	(0.85)	(2.03)	(9.89)
	Medium-difficulty	5.65	4.93	94.76	89.72
		(2.50)	(1.23)	(3.25)	(9.15)
	High-difficulty	8.53	7.88	88.45	80.28
		(3.39)	(2.19)	(7.56)	(11.31)

Note: RT, reaction time; H-Gf, high fluid intelligence participants; A-Gf, average fluid intelligence participants

EEG results

Firstly, we performed descriptive statistics of both frontal theta-ERS and parietal-occipital alpha-ERD in each condition (Table 2). Subsequently, we conducted a 2 (Gf group: high vs. average) $\times$ 3 (task difficulty: low vs. medium vs. high) repeated-measures ANOVA taking theta-ERS and alpha-ERD as dependent variables in both exploitation and exploration tasks to examine the roles of Gf and task difficulty in them.

Exploitation task

In the exploitation task, ANOVA results found that there were significant or marginally significant main effects of Gf group [$F(1,38) = 5.15, p = 0.03, \eta_p^2 = 0.12$] and task difficulty [$F(2,76) = 2.55, p = 0.08, \eta_p^2 = 0.06$] on theta-ERS (Figure 5). To be specific, participants with average Gf showed larger theta-ERS in all three difficulty conditions. In addition, as the task became more difficult, participants tended to show larger theta-ERS. We further conducted Pearson's correlation analyses to examine the correlation between Gf and theta-ERS in three difficulty levels and the results showed that Gf was significantly negatively correlated with theta-ERS in all difficulty levels ($r = -0.52, p < 0.001$; $r = -0.36, p = 0.02$; $r = -0.39, p = 0.01$, respectively; Figure 6).

Moreover, we conducted a data-driven analysis to calculate the correlation between Gf and theta-ERS across all the electrodes to explore the topological distribution of theta-ERS associated with Gf. As shown in Figure 7, the results found that in all difficulty levels, participants' Gf negatively correlated with theta-ERS around frontal regions (F1, F2, Fz, F4, F6, F8, FC5, FC4, FC6, FT7, FT8, C5, C6, TP7; all $r_s < -0.33, p_s < 0.04$). In addition, the correlation between Gf and theta-ERS also reached significance around frontal regions specifically in the low- (AF3, F3, F7, FC1, FC2, FC3, C4, P5, T7, T8, CP5, CP6, TP8; all $r_s < -0.31, p_s < 0.05$), medium- (F7, FC2, CP3, T7, C4, CP5, P5; all $r_s < -0.32, p_s < 0.05$), and high-difficulty level (AF3, AF4, F3; all $r_s < -0.33, p_s < 0.04$), respectively.

As for the results of alpha-ERD, surprisingly, we found neither significant main effects of task difficulty [$F(2,76) = 0.15, p = 0.85, \eta_p^2 < 0.001$] nor Gf group [$F(1,38)$]

$= 0.001, p = 0.98, \eta_p^2 < 0.001$] on alpha-ERD. Also, the interaction effect between Gf group and task difficulty did not reach a significant level [$F(2,76) = 0.51, p = 0.60, \eta_p^2 = 0.01$]. Further correlation analyses did not find significant correlations between Gf and alpha-ERD ($p_s > 0.16$). The data-driven correlation analyses between Gf and alpha-ERD across all the electrodes only found results just reaching significance in few individual and separated electrodes (e.g., FT8, C6, F8) that could not be taken as robust results.

Figure 5 EEG theta event-related synchronization (theta-ERS) of participants with high and average fluid intelligence (Gf) in (A) exploitation and (B) exploration tasks with different difficulty levels. * $p < 0.05$.

Figure 6 Correlations between fluid intelligence (Gf) and theta event-related synchronization (theta-ERS) in the (A) low-difficult, (B) medium-difficult, and (C) high difficult exploitation task.

Figure 7 Correlations between fluid intelligence (Gf) and theta event-related synchronization (theta-ERS) across all the electrodes in the (A) low-difficult, (B) medium-difficult, and (C) high-difficult exploitation task. The red line in left figures represent the Pearson's r value when $p = 0.05$. In all difficulty levels, participants' Gf negatively correlated with theta-ERS around frontal regions.

Table 2 Means and standard deviations (in brackets) of EEG results in the exploitation and exploration tasks with different difficulty levels

Task type	Difficulty	theta-ERS (%)		alpha-ERD (%)	
		H-Gf	A-Gf	H-Gf	A-Gf
Exploitation ($N_{H-Gf} = 22, N_{A-Gf} = 18$)	Low-difficulty	-1.99	27.20	44.92	47.35
		(38.69)	(39.37)	(34.26)	(34.06)
	Medium-difficulty	1.45	30.09	47.75	45.40
		(41.31)	(42.37)	(35.94)	(39.98)
	High-difficulty	7.16	39.15	47.12	47.74
		(52.88)	(53.17)	(36.62)	(32.38)
Exploration ($N_{H-Gf} = 23, N_{A-Gf} = 20$)	Low-difficulty	16.91	14.64	46.55	36.77
		(50.96)	(19.90)	(29.79)	(27.29)
	Medium-difficulty	24.72	23.19	42.51	28.26

	(65.81)	(43.28)	(50.68)	(34.57)
High-difficulty	9.97	31.48	45.10	30.76
	(46.14)	(46.95)	(39.03)	(39.06)

Note: RT, reaction time; H-Gf, high fluid intelligence participants; A-Gf, average fluid intelligence participants

Subsequently, to check whether gender plays an important role in the relationship among Gf, task difficulty, and EEG results, we performed another two 2 (Gf group: high vs. average) $\times$ 2 (Gender: males vs. females) $\times$ 3 (task difficulty: low vs. medium vs. high) repeated-measures ANOVA taking theta-ERS and alpha-ERD as dependent variables in the exploitation tasks. However, the results of both ANOVAs (on theta-ERS and alpha-ERD) showed that neither interaction effects nor main effects regarding gender reached a significant level.

Exploration task

In the exploration task, the interaction effect of task difficulty $\times$ Gf group on theta-ERS was marginally significant [$F(2,82) = 2.78, p = 0.07, \eta_p^2 = 0.06$], but simple effect analysis did not find any significant differences between high- and average-Gf participants in any difficulty levels. In addition, the results did not find significant main effects of Gf group [$F(1,41) = 0.20, p = 0.66, \eta_p^2 = 0.01$] and task difficulty [$F(2,82) = 1.03, p = 0.36, \eta_p^2 = 0.03$] on theta-ERS. Corresponding Pearson's correlation analyses also did not find any significant correlations between Gf and theta-ERS in any difficulty levels (all $ps > 0.44$).

As for the results of alpha-ERD, we found neither significant main effects of task difficulty [$F(2,82) = 1.31, p = 0.28, \eta_p^2 = 0.03$] nor Gf group [$F(1,41) = 1.45, p = 0.24, \eta_p^2 = 0.03$] on alpha-ERD. Also, the interaction effect between Gf group and

task difficulty did not reach a significant level [$F(2,82) = 0.22, p = 0.80, \eta_p^2 = 0.01$].

Due to a previous study (Lu, Bao, Zhang, & Shi, 2020) have found that gender plays a crucially moderating role in the relationship between Gf and attentional resource allocation in the exploration task, we further performed another two 2 (Gf group: high vs. average) $\times$ 2 (Gender: males vs. females) $\times$ 3 (task difficulty: low vs. medium vs. high) repeated-measures ANOVAs taking theta-ERS and alpha-ERD as dependent variables in the exploration tasks. The results found that neither the main effect of gender nor any interaction effects regarding gender reached a significant level when taking theta-ERS as the dependent variable. However, as shown in Figure 8, when taking alpha-ERD as the dependent variable, we found a marginally significant effect of the three-way interaction effect among Gf group, gender, and task difficulty [$F(2,78) = 2.95, p = 0.06, \eta_p^2 = 0.07$]. Subsequently simple effect analysis indicated that high Gf males showed significantly larger alpha-ERD in medium- [$F(1,78) = 10.66, p = 0.004$] and high-difficulty [$F(1,78) = 7.04, p = 0.02$] exploration task compared with average Gf males. This phenomenon did not exist in the low-difficulty level [$F(1,78) = 2.83, p = 0.11$] or in females (all p s > 0.38). Subsequently, we performed Pearson's correlation analyses (Figure 9) and found that male's Gf had a significantly or marginally significantly positive correlation with their alpha-ERD in medium- and high-difficulty conditions ($r = 0.45, p = 0.04$; $r = 0.42, p = 0.06$, respectively) while this correlation was not significant in low-difficulty level ($r = 0.33, p = 0.14$). Also, the correlation between Gf and alpha-ERD was not significant in females in all three difficulty levels ($r = 0.07, r = -0.01, r = -0.03$,

respectively; $ps > 0.77$).

Moreover, we conducted a data-driven correlation analysis between Gf and alpha-ERD across all the electrodes to explore the topological distribution of alpha-ERD associated with Gf. As shown in Figure 10, there were no significant correlations between Gf and alpha-ERD in the exploitation task and the exploration task for females. In contrast, in the exploration task, males' Gf was positively correlated with alpha-ERD in parietal and occipital regions mainly in medium- (P7, P8, PO7, PO5, PO3, O1, O2, Oz; $rs > 0.46$, $ps < 0.04$) and high-difficulty (P8, O1, O2, Oz, FP1; $rs > 0.44$, $ps < 0.05$) condition. Also, there were positive correlations between Gf and alpha-ERD in low-difficulty condition in a few electrodes (P7, O1, Oz, FP1, FP2; $rs > 0.43$, $ps < 0.05$).

Figure 8 (A) Male and (B) female participants' EEG alpha event-related desynchronization (alpha-ERD) in the exploration task with different difficulty levels. ** $p < 0.01$; * $p < 0.05$.

Figure 9 Male's and female's correlations between fluid intelligence (Gf) and EEG alpha event-related desynchronization (alpha-ERD) in the (A) low-difficult, (B) medium-difficult, and (C) high difficult exploration task. Male's fluid intelligence positively correlated with alpha-ERD in medium- and high-difficulty conditions while this correlation was not significant in low-difficulty condition or in females.

Figure 10 Correlations between fluid intelligence (Gf) and alpha event-related desynchronization (alpha-ERD) across all the electrodes in the (A) low-difficult, (B) medium-difficult, and (C) high difficult exploitation task and (D) low-difficult, (E) medium-difficult, and (F) high difficult exploration task. In the exploration task, males' Gf was positively correlated with alpha-ERD in parietal and occipital regions mainly in medium- and high-difficulty conditions. There were no significant correlations between Gf and alpha-ERD in the exploitation task and the exploration task for females.

Discussion

The present study examined the relationship between Gf and attentional resource allocation by using EEG method. Behavioural results showed that people with higher Gf performed better than people with average Gf in both accuracy and RT, which is in line with the previous study using the same tasks (Lu et al., 2020). With regards to the EEG results, interestingly, the results of frontal theta-ERS and parietal-occipital alpha-ERD supported one part of the assumption of the integrated control hypothesis.

To be specific, we found that higher Gf individuals showed significantly smaller theta-ERS than average Gf participants in the exploitation task no matter what difficulty was. As suggested by previous studies, theta oscillation and its increment (i.e., theta-ERS) positively reflect ongoing cognitive processes associated with mental effort or resource allocation in a wide range of cognitive tasks (Jensen & Tesche, 2002; Mussel, Ulrich, Allen, Osinsky, & Hewig, 2016; Missonnier et al., 2006; Raghavachari et al., 2001; Zakrzewska & Brzezicka, 2014). The significant main effect of task difficulty found in this study supported this account as with the task difficulty rose, theta-ERS increased. In this case, our results indicated that higher Gf people tended to allocate fewer resources in the exploitation task compared with their counterparts. This result is consistent with previous studies supporting the neural efficiency hypothesis (Ahern & Beatty, 1979; Gray et al., 2003; Haier et al., 1988; Klimesch, Doppelmayr, & Hanslmayr, 2006) and the integrated control hypothesis (Lu et al., 2020) positing that more intelligent people could solve problems more efficiently especially when tasks require more exploitation.

The results of parietal-occipital alpha-ERD suggested that the interaction among task difficulty, Gf group, and gender significantly influences alpha-ERD in the exploration task. Specifically, higher Gf male participants tend to show stronger alpha-ERD in medium- and high-difficulty trials, instead of low-difficulty trials, in the exploration task. As suggested by previous findings, parietal-occipital alpha activity reflects idling, task disengagement or cortical inhibition (Depue et al., 2013; Händel, Haarmeier, & Jensen, 2011; Sadaghiani & Kleinschmidt, 2016) and correspondingly the ERD of alpha reflects task engagement and cortical activation, which could be seen as a positive indicator of resource allocation. In this case, higher Gf males exerted more resources than average Gf males in medium- and high-difficulty exploration tasks, supporting the account of the integrated control hypothesis. This result also replicates previous studies supporting the resource hypothesis that task difficulty moderates the relationship between Gf and resource allocation (Bornemann et al., 2010; Doppelmayr et al., 2005; van der Meer et al., 2010). Notably, the moderating role of gender in this relationship is also in line with the previous study using pupillometry (Lu et al., 2020). Both higher Gf and average Gf females tended to allocate equivalent resources as higher Gf males but average Gf males exerted significantly fewer resources than higher Gf males. We suppose it may result from some reasons regarding sex differences. Firstly, the exploration task used in this study is visuospatial and similar to mental rotation, which required participants to actively operate their mental images. Previous studies suggested that gender differences are existed in the visuospatial domain (Halpern, 2013; McGowan & Duka, 2000) and

males tend to perform better in such tasks than females (Boone & Hegarty, 2017; Gill & O'Boyle, 1997). Therefore, one reasonable explanation is that females with both higher or average Gf require more resources while solving these tasks due to their relative weakness in visuospatial tasks. Secondly, the personality differences between males and females could be another reason. Females tend to be more cautious when performing cognitive tasks like mental rotation (Kerkman, Wise, & Harwood, 2001) and are more prone to be influenced by the expectation effect from experimenters, which made them make more effort in doing cognitive tasks (Halpern, 2013).

Taken together, these results support the integrated control hypothesis that higher intelligent people have better attentional control ability and could flexibly and adaptively allocate their limited attentional resource according to the exact task type and task difficulty. Importantly, as the suggestions by recent researchers (Ramchandran, Zeien, & Andreasen, 2019), the efficiency of highly intelligent people may not be simply characterised as using fewer or more resources in any conditions but be featured as adaptively choosing the optimal resource allocation policy according to particular task demands (Dunst et al., 2014). This idea also echoes recent intelligence theories such as the MD theory (Duncan, 2010; Duncan, Assem, & Shashidhara, 2020) and the attentional control account of intelligence (Burgoyne & Engle, 2020; Engle, 2018). Researchers proposed that attentional control plays a core role in higher-order cognition, which allows us to focus on goals despite distractions and irrelevant thoughts (Burgoyne & Engle, 2020). Tsukahara et al. (2020) found that attentional control fully mediated the relationship between Gf and sensory

discrimination ability, suggesting that attentional control may lay the foundation for higher-order cognition such as Gf. In addition, from the perspective of the cognitive neuroscience of Gf, the MD theory suggested that the MD network, which is always found activated in multiple cognitive tasks, is the neural basis of human general intelligence. The core characteristic of the MD network is to adaptively and flexibly code task-relevant information according to specific task demands (Duncan, 2013; Woolgar, Jackson, & Duncan, 2016). Therefore, according to these theoretical views and empirical results, we supposed that adaptive and flexible attentional control may be the key to human intelligence.

This study adopted both frontal theta and alpha oscillation as the indicator of attentional resource allocation, but they were only significantly influenced in one of the tasks. In other words, theta and alpha activity tend to be task-specific although both indicators could reflect mental effort or resource allocation to some extent, which suggests that the essential meaning of both oscillations are relatively different (Doppelmayr et al., 2005). From the perspective of the source of both neural oscillations, theta oscillation may rely on functional connectivity between the frontal and medial temporal cortex including the hippocampus (Capotosto et al., 2009; Klimesch, 1999), which is important for the memory process (Itthipuripat, Wessel, & Aron, 2013; Jensen & Tesche, 2002). In contrast, alpha oscillation is suggested to show the functional modes of thalamo-cortical and cortico-cortical loops for visual attention and facilitating or inhibiting the process of both sensorimotor and cognitive information (Capotosto et al., 2009; Clayton, Yeung, & Cohen Kadosh, 2018;

Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller, Neuper, & Mohl, 1994). In the present study, the exploitation task requires participants to use known rules learned in the practice period to solve problems, this process mainly involving memory retrieval and relating more closely with theta activity. Similarly, the previous study found that the neural efficiency hypothesis is true during the memory retrieval period but not the memory encoding period (Capotosto et al., 2009; Grabner et al., 2004). In contrast, the exploration task requires participants to explore relatively new question environment to solve problems, in which process the requirement of memory is relatively low but the process of sensory information associated with the alpha activity is more needed. Compared with the previous study taking pupillometry (TEPR) as the indicator of resource allocation (Lu et al., 2020), it is likely that pupillary response may represent a domain-general indicator of resource allocation or mental effort while EEG alpha or theta indicators may show task-specific characteristics in the context of resource allocation.

Some limitations should be noted regarding the present study. Firstly, both tasks used in the present study are examples of typical exploration and exploitation tasks. They are not univocal and have some differences in physical properties. Future studies could try to find a single task having two separated conditions (one for exploration and the other for exploitation) to further verify this hypothesis. In addition, both tasks are in the visuospatial form that benefits male participants, which may cause gender differences in the exploration task. Future studies could also try to use verbal exploration and exploitation tasks favourable to females to explore whether the

task domain or inherent gender differences lead to the moderating effect of gender between the Gf group and resource allocation in the exploration tasks.

In conclusion, the present study used both alpha-ERD and theta-ERS as the indicators of attentional resource allocation to examine the integrated control hypothesis. We found that, in the exploitation task, higher Gf individuals tend to allocate fewer resources in all difficulty levels compared to average Gf participants. In the exploration task, high Gf male participants would allocate more resources in the medium- and high-difficulty levels than average Gf male participants. The findings supported the integrated control hypothesis that both task type and task difficulty play important roles in the relationship between Gf and resource allocation, suggesting the flexible and adaptive attentional control ability may lay the foundation of human intelligence.

Compliance with Ethical Standards

Funding This work was funded by the Pioneer Initiative of the Chinese Academy of Sciences, Feature Institutes Program, TSS-2015-06.

Conflict of interest Authors have no conflict of interest to declare.

Ethics statement This study has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and later amendments. Ethical approval had been obtained from the ethics committee of the Institute of Psychology, Chinese Academy of Sciences.

Informed consent Informed consent was obtained from all individual participants included in the study.

References

- Ahern, S. K., & Beatty, J. (1979). Pupillary responses during information processing vary with scholastic aptitude test scores. *Science*, 205(4412), 1289-1292. <https://doi.org/10.1126/science.472746>
- Alnaes, D., Sneve, M. H., Espeseth, T., Endestad, T., van de Pavert, S. H., & Laeng, B. (2014). Pupil size signals mental effort deployed during multiple object tracking and predicts brain activity in the dorsal attention network and the locus coeruleus. *Journal of Vision*, 14(4). <https://doi.org/10.1167/14.4.1>
- Assem, M., Glasser, M. F., Van Essen, D. C., & Duncan, J. (2020). A domain-general cognitive core defined in multimodally parcellated human cortex. *Cerebral Cortex*, 30(8), 4361-4380. <https://doi.org/10.1093/cercor/bhaa023>
- Boone, A. P., & Hegarty, M. (2017). Sex differences in mental rotation tasks: Not just in the mental rotation process! *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 43(7), 1005–1019.
- Bornemann, Boris, Foth, Manja, Horn, Judith, Ries, Jan, Warmuth, Elke, Wartenburger, Isabell, & Meer, Elke. (2010). Mathematical cognition: individual differences in resource allocation. *Zdm*, 42(6), 555-567. <https://doi.org/10.1007/s11858-010-0253-x>
- Brouwer, A. M., Hogervorst, M. A., Holewijn, M., & van Erp, J. B. (2014). Evidence for effects of task difficulty but not learning on neurophysiological variables associated with effort. *International Journal of Psychophysiology*, 93(2), 242-252. <https://doi.org/10.1016/j.ijpsycho.2014.05.004>
- Burgoyne, A. P., & Engle, R. W. (2020). Attention control: A cornerstone of higher-order cognition. *Current Directions in Psychological Science*, 29(6), 624-630. <https://doi.org/10.1177/0963721420969371>
- Capotosto, P., Perrucci, M. G., Brunetti, M., Del Gratta, C., Doppelmayr, M., Grabner,

- R. H., . . . Pfurtscheller, G. (2009). Is there “neural efficiency” during the processing of visuo-spatial information in male humans? An EEG study. *Behavioural Brain Research*, 205(2), 468-474. <https://doi.org/10.1016/j.bbr.2009.07.032>
- Clayton, M. S., Yeung, N., & Cohen Kadosh, R. (2018). The many characters of visual alpha oscillations. *European Journal of Neuroscience*, 48(7), 2498-2508. <https://doi.org/10.1111/ejn.13747>
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Depue, B. E., Ketz, N., Mollison, M. V., Nyhus, E., Banich, M. T., & Curran, T. (2013). ERPs and neural oscillations during volitional suppression of memory retrieval. *Journal of Cognitive Neuroscience*, 25(10), 1624-1633. https://doi.org/10.1162/jocn_a_00418
- Dong, S., Reder, L. M., Yao, Y., Liu, Y., & Chen, F. (2015). Individual differences in working memory capacity are reflected in different ERP and EEG patterns to task difficulty. *Brain Research*, 1616, 146-156. <https://doi.org/10.1016/j.brainres.2015.05.003>
- Doppelmayr, M., Klimesch, W., Sauseng, P., Hodlmoser, K., Stadler, W., & Hanslmayr, S. (2005). Intelligence related differences in EEG-bandpower. *Neuroscience Letters*, 381(3), 309-313. <https://doi.org/10.1016/j.neulet.2005.02.037>
- Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, 14(4), 172-179. <https://doi.org/10.1016/j.tics.2010.01.004>
- Duncan, J. (2013). The structure of cognition: attentional episodes in mind and brain. *Neuron*, 80(1), 35-50. <https://doi.org/10.1016/j.neuron.2013.09.015>
- Duncan, J., Assem, M., & Shashidhara, S. (2020). Integrated intelligence from distributed brain activity. *Trends in Cognitive Sciences*.

<https://doi.org/10.1016/j.tics.2020.06.012>

- Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences*, 23(10), 475-483.
- Dunst, B., Benedek, M., Jauk, E., Bergner, S., Koschutnig, K., Sommer, M., . . . Neubauer, A. C. (2014). Neural efficiency as a function of task demands. *Intelligence*, 42(100), 22-30. <https://doi.org/10.1016/j.intell.2013.09.005>
- Engle, R. W. (2018). Working memory and executive attention: A revisit. *Perspectives on Psychological Science*, 13(2), 190-193. <https://doi.org/10.1177/1745691617720478>
- Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, 7(4), 374-385. <https://doi.org/10.1093/cercor/7.4.374>
- Gill, H. S., & O'Boyle, M. W. (1997). Sex differences in matching circles and arcs: A preliminary EEG investigation. *Laterality: Asymmetries of Body, Brain and Cognition*, 2(1), 33-48.
- Grabner, R. H., Fink, A., Stipacek, A., Neuper, C., & Neubauer, A. C. (2004). Intelligence and working memory systems: Evidence of neural efficiency in alpha band ERD. *Brain Research: Cognitive Brain Research*, 20(2), 212-225. <https://doi.org/10.1016/j.cogbrainres.2004.02.010>
- Gray, J. R., Chabris, C. F., & Braver, T. S. (2003). Neural mechanisms of general fluid intelligence. *Nature Neuroscience*, 6(3), 316-322. <https://doi.org/10.1038/nn1014>
- Haier, R. J., Siegel Jr, B. V., Nuechterlein, K. H., Hazlett, E., Wu, J. C., Paek, J., ... & Buchsbaum, M. S. (1988). Cortical glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography. *Intelligence*, 12(2), 199-217. [https://doi.org/10.1016/0160-2896\(88\)90016-5](https://doi.org/10.1016/0160-2896(88)90016-5)
- Händel, B. F., Haarmeier, T., & Jensen, O. (2011). Alpha oscillations correlate with

- the successful inhibition of unattended stimuli. *Journal of Cognitive Neuroscience*, 23(9), 2494-2502. <https://doi.org/10.1162/jocn.2010.21557>
- Halpern, D. F. (2013). *Sex differences in cognitive abilities*. Psychology press.
- Hayes, T. R., & Petrov, A. A. (2016). Pupil diameter tracks the exploration-exploitation trade-off during analogical reasoning and explains individual differences in fluid intelligence. *Journal of Cognitive Neuroscience*, 28(2), 308-318. https://doi.org/10.1162/jocn_a_00895
- Itthipuripat, S., Wessel, J. R., & Aron, A. R. (2013). Frontal theta is a signature of successful working memory manipulation. *Experimental Brain Research*, 224(2), 255-262. <https://doi.org/10.1007/s00221-012-3305-3>
- Jann, K., Dierks, T., Boesch, C., Kottlow, M., Strik, W., & Koenig, T. (2009). BOLD correlates of EEG alpha phase-locking and the fMRI default mode network. *Neuroimage*, 45(3), 903-916. <https://doi.org/10.1016/j.neuroimage.2009.01.001>
- JASP Team (2019). *JASP (Version 0.11.1) [Computer software]*.
- Jaušovec, N. (1996). Differences in EEG alpha activity related to giftedness. *Intelligence*, 23(3), 159-173. [https://doi.org/10.1016/S0160-2896\(96\)90001-X](https://doi.org/10.1016/S0160-2896(96)90001-X)
- Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience*, 15(8), 1395-1399. <https://doi.org/10.1046/j.1460-9568.2002.01975.x>
- Kerkman, D. D., Wise, J. C., & Harwood, E. A. (2000). Impossible “mental rotation” problems: A mismeasure of women's spatial abilities? *Learning and Individual Differences*, 12(3), 253-269.
- Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*, 26(1-3), 319-340. [https://doi.org/10.1016/S0167-8760\(97\)00773-3](https://doi.org/10.1016/S0167-8760(97)00773-3)
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, 29(2-3), 169-195. [https://doi.org/10.1016/S0165-0173\(98\)00056-3](https://doi.org/10.1016/S0165-0173(98)00056-3)
- Klimesch, W., Doppelmayr, M., & Hanslmayr, S. (2006). Upper alpha ERD and

- absolute power: their meaning for memory performance. *Progress in Brain Research*, 159, 151-165. [https://doi.org/10.1016/S0079-6123\(06\)59010-7](https://doi.org/10.1016/S0079-6123(06)59010-7)
- Klimesch, W., Doppelmayr, M., Pachinger, T., & Ripper, B. (1997). Brain oscillations and human memory: EEG correlates in the upper alpha and theta band. *Neuroscience Letters*, 238(1-2), 9-12. [https://doi.org/10.1016/S0304-3940\(97\)00771-4](https://doi.org/10.1016/S0304-3940(97)00771-4)
- Klingner, J., Tversky, B., & Hanrahan, P. (2011). Effects of visual and verbal presentation on cognitive load in vigilance, memory, and arithmetic tasks. *Psychophysiology*, 48(3), 323-332.
- Krause, C. M., Sillanmäki, L., Koivisto, M., Saarela, C., Häggqvist, A., Laine, M., & Hämäläinen, H. (2000). The effects of memory load on event-related EEG desynchronization and synchronization. *Clinical Neurophysiology*, 111(11), 2071-2078. [https://doi.org/10.1016/S1388-2457\(00\)00429-6](https://doi.org/10.1016/S1388-2457(00)00429-6)
- Laufs, H., Krakow, K., Sterzer, P., Eger, E., Beyerle, A., Salek-Haddadi, A., & Kleinschmidt, A. (2003). Electroencephalographic signatures of attentional and cognitive default modes in spontaneous brain activity fluctuations at rest. *Proceedings of the National Academy of Sciences*, 100(19), 11053-11058. <https://doi.org/10.1073/pnas.1831638100>
- Lee, Giyoung, Ojha, Amitash, Kang, Jun-Su, & Lee, Minho. (2015). Modulation of resource allocation by intelligent individuals in linguistic, mathematical and visuo-spatial tasks. *International Journal of Psychophysiology*, 97(1), 14-22. <https://doi.org/10.1016/j.ijpsycho.2015.04.013>
- Lipp, I., Benedek, M., Fink, A., Koschutnig, K., Reishofer, G., Bergner, S., . . . Neubauer, A. (2012). Investigating neural efficiency in the visuo-spatial domain: an FMRI study. *PloS One*, 7(12), e51316. <https://doi.org/10.1371/journal.pone.0051316>
- Lu, R., Bao, N., Zhang, X., Shi, J. (2020). Attention resource allocation among individuals with different fluid intelligence in exploration and exploitation tasks: The integrated control hypothesis and its evidence. *PsyArXiv*. <https://doi.org/10.31234/osf.io/wfkan>

- Matzen, L. E., Benz, Z. O., Dixon, K. R., Posey, J., Kroger, J. K., & Speed, A. E. (2010). Recreating Raven's: software for systematically generating large numbers of Raven-like matrix problems with normed properties. *Behavior Research Methods*, 42(2), 525-541. <https://doi.org/10.3758/BRM.42.2.525>
- McGowan, J. F., & Duka, T. (2000). Hemispheric lateralisation in a manual-verbal task combination: the role of modality and gender. *Neuropsychologia*, 38, 1018-1027. [https://doi.org/10.1016/S0028-3932\(99\)00155-4](https://doi.org/10.1016/S0028-3932(99)00155-4)
- Milivojevic, B., Johnson, B. W., Hamm, J. P., & Corballis, M. C. (2003). Non-identical neural mechanisms for two types of mental transformation: event-related potentials during mental rotation and mental paper folding. *Neuropsychologia*, 41(10), 1345-1356. [https://doi.org/10.1016/s0028-3932\(03\)00060-5](https://doi.org/10.1016/s0028-3932(03)00060-5)
- Missonnier, P., Deiber, M. P., Gold, G., Millet, P., Gex-Fabry Pun, M., Fazio-Costa, L., . . . Ibanez, V. (2006). Frontal theta event-related synchronization: comparison of directed attention and working memory load effects. *Journal of Neural Transmission*, 113(10), 1477-1486. <https://doi.org/10.1007/s00702-005-0443-9>
- Mussel, P., Ulrich, N., Allen, J. J., Osinsky, R., & Hewig, J. (2016). Patterns of theta oscillation reflect the neural basis of individual differences in epistemic motivation. *Scientific Reports*, 6, 29245. <https://doi.org/10.1038/srep29245>
- Neubauer, A. C., & Fink, A. (2003). Fluid intelligence and neural efficiency: effects of task complexity and sex. *Personality and Individual Differences*, 35(4), 811-827. [https://doi.org/10.1016/S0956-053X\(03\)00103-X](https://doi.org/10.1016/S0956-053X(03)00103-X)
- Neubauer, A. C., & Fink, A. (2009). Intelligence and neural efficiency. *Neuroscience and Biobehavioral Reviews*, 33(7), 1004-1023. <https://doi.org/10.1016/j.neubiorev.2009.04.001>
- Neubauer, A. C., Fink, A., & Schrausser, D. G. (2002). Intelligence and neural efficiency: The influence of task content and sex on the brain-IQ relationship. *Intelligence*, 30(6), 515-536. [https://doi.org/10.1016/S0160-2896\(02\)00091-0](https://doi.org/10.1016/S0160-2896(02)00091-0)

- Pesonen, M., Hamalainen, H., & Krause, C. M. (2007). Brain oscillatory 4-30 Hz responses during a visual n-back memory task with varying memory load. *Brain Research, 1138*, 171-177. <https://doi.org/10.1016/j.brainres.2006.12.076>
- Pfurtscheller, G., & Aranibar, A. (1977). Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalography and clinical neurophysiology, 42*(6), 817-826.
- Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology, 110* (11), 1842–1857. [https://doi.org/10.1016/S1388-2457\(99\)00141-8](https://doi.org/10.1016/S1388-2457(99)00141-8)
- Pfurtscheller, G., Neuper, C., & Mohl, W. (1994). Event-related desynchronization (ERD) during visual processing. *International Journal of Psychophysiology, 16*(2-3), 147-153.
- Raghavachari, S., Kahana, M. J., Rizzuto, D. S., Caplan, J. B., Kirschen, M. P., Bourgeois, B., . . . Lisman, J. E. (2001). Gating of human theta oscillations by a working memory task. *Journal of Neuroscience, 21*(9), 3175-3183. <https://doi.org/10.0000/PMID11312302>
- Ramchandran, K., Zeien, E., & Andreasen, N. C. (2019). Distributed neural efficiency: Intelligence and age modulate adaptive allocation of resources in the brain. *Trends in Neuroscience and Education, 15*, 48-61. <https://doi.org/10.1016/j.tine.2019.02.006>
- Raven, J. C. (1958). *Advanced progressive matrices*. London, UK: Lewis.
- Rueda, M. R. (2018). Attention in the heart of intelligence. *Trends in Neuroscience and Education, 13*, 26-33. doi:10.1016/j.tine.2018.11.003
- Sadaghiani, S., & Kleinschmidt, A. (2016). Brain Networks and alpha-Oscillations: Structural and Functional Foundations of Cognitive Control. *Trends in Cognitive Sciences, 20*(11), 805-817. <https://doi.org/10.1016/j.tics.2016.09.004>
- Shepard, R. N., & Feng, C. (1972). A chronometric study of mental paper folding. *Cognitive Psychology, 3*(2), 228-243.
- Stipacek, A., Grabner, R. H., Neuper, C., Fink, A., & Neubauer, A. C. (2003).

- Sensitivity of human EEG alpha band desynchronization to different working memory components and increasing levels of memory load. *Neuroscience Letters*, 353(3), 193-196. <https://doi.org/10.1016/j.neulet.2003.09.044>
- Sun, W., & Feng, C. (2016). How to develop a new index to measure the difficulty degree of mental paper-folding. *Advances in Psychology*, 6(3), 281-289. <https://doi.org/10.12677/ap.2016.63037>
- Tsukahara, J. S., Harrison, T. L., Draheim, C., Martin, J. D., & Engle, R. W. (2020). Attention control: The missing link between sensory discrimination and intelligence. *Attention, Perception, & Psychophysics*, 82, 3445–3478. <https://doi.org/10.3758/s13414-020-02044-9>
- van der Meer, E., Beyer, R., Horn, J., Foth, M., Bornemann, B., Ries, J., . . . Wartenburger, I. (2010). Resource allocation and fluid intelligence: insights from pupillometry. *Psychophysiology*, 47(1), 158-169. <https://doi.org/10.1111/j.1469-8986.2009.00884.x>
- van Dijk, H., Schoffelen, J. M., Oostenveld, R., & Jensen, O. (2008). Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *Journal of Neuroscience*, 28(8), 1816-1823. <https://doi.org/10.1523/JNEUROSCI.1853-07.2008>
- Woolgar, A., Jackson, J., & Duncan, J. (2016). Coding of visual, auditory, rule, and response information in the brain: 10 years of multivoxel pattern analysis. *Journal of Cognitive Neuroscience*, 28(10), 1433-1454. https://doi.org/10.1162/jocn_a_00981
- Wostmann, M., Alavash, M., & Obleser, J. (2019). Alpha Oscillations in the Human Brain Implement Distractor Suppression Independent of Target Selection. *Journal of Neuroscience*, 39(49), 9797-9805. <https://doi.org/10.1523/JNEUROSCI.1954-19.2019>
- Zakrzewska, M. Z., & Brzezicka, A. (2014). Working memory capacity as a moderator of load-related frontal midline theta variability in Sternberg task. *Frontiers in Human Neuroscience*, 8, 399. <https://doi.org/10.3389/fnhum.2014.00399>