

Resource allocation and fluid intelligence: Insights from pupillometry

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Abstract

Thinking is biological work and involves the allocation of cognitive resources. The aim of this study was to investigate the impact of fluid intelligence on the allocation of cognitive resources while one is processing low-level and high-level cognitive tasks. Individuals with high versus average fluid intelligence performed low-level choice reaction time tasks and high-level geometric analogy tasks. We combined behavioral measures to examine speed and accuracy of processing with pupillary measures that indicate resource allocation. Individuals with high fluid intelligence processed the low-level choice reaction time tasks faster than normal controls. The task-evoked pupillary responses did not differ between groups. Furthermore, individuals with high fluid intelligence processed the high-level geometric analogies faster, more accurately, and showed greater pupil dilations than normal controls. This was only true, however, for the most difficult analogy tasks. In addition, individuals with high fluid intelligence showed greater preexperimental pupil baseline diameters than normal controls. These results indicate that individuals with high fluid intelligence have more resources available and thus can solve *more demanding* tasks. Moreover, high fluid intelligence appears to be accompanied by more task-free exploration.

Descriptors: Fluid intelligence, Resource allocation, Geometric analogies, Pupillary response

It has long been argued that all human reasoning, including logical inference, is essentially analogical and that the essence of intelligent insights lies primarily in making fluid analogies (French, 2002; Halford, 1992; Hofstadter, 1995; Holyoak & Thagard, 1995; James, 1890/1950; Klix, 1993; Mitchell, 1993). Fluid reasoning is one of the core components of fluid intelligence. Importantly, there is a strong relationship between fluid intelligence and the central executive of working memory (Duncan, 2003; Engle, Tuholski, Laughlin, & Conway, 1999; Gray, Chabris, & Braver, 2003). There is evidence that analogical reasoning requires specific executive processes, namely, selecting relevant and inhibiting irrelevant features, building and mapping

relations, and providing interference resolution (Cho, Holyoak, & Cannon, 2007; Gentner, 1983; Holyoak & Thagard, 1995; van der Meer, 1996).

Across a broad range of cognitive tasks, individuals scoring high in fluid intelligence consistently perform better than individuals who score low. For example, individuals scoring high on the Raven Advanced Progressive Matrices (RAPM; Raven, 1958) show faster response times in reasoning tasks compared to individuals who score around the average (van der Meer, 1996; van der Meer & Klix, 1986). Furthermore, Neubauer (1997) has

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This research was supported by grants from the German Federal Ministry for Education and Research (NIL-I/II and Berlin NeuroImaging Center). I.W. is funded by the Stifterverband für die Deutsche Wissenschaft, Claussen-Simon-Stiftung. This work benefited from conversations with Herbert Hagendorf, Frank Krueger, and Steffen Landgraf. The authors acknowledge the assistance of Martin Brucks, Franziska Preusse, Roman Purkhart, Susanne Raisig, Torsten Schiemann, and Dorothea Ullwer.

¹RAPM are frequently used as a measure of fluid intelligence (e.g., Bates & Shieles, 2003; Haier, Sternberg, Lautrey, & Lubart, 2003; McCrory & Cooper, 2005; Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997; Prokosch, Yeo, & Miller, 2005; Tamez, Myerson, & Hale, 2008; Thoma et al., 2005). According to Carpenter, Just, and Shell (1990), the RAPM assesses analytical intelligence, which equals Cattell's concept of fluid intelligence as the "ability to reason and solve problems involving new information" (Carpenter et al., 1990, p. 404). Furthermore, Schweizer, Goldhammer, Rauch, and Moosbrugger (2007) have analyzed whether the RAPM measures fluid intelligence exclusively or also partially measures spatial ability. By means of structural equation modeling, they confirmed that RAPM "can be considered as a marker of fluid intelligence as well as of figural reasoning" (p. 2009). Various studies have shown that the RAPM has the highest loading on Spearman's gen-

observed a negative correlation (r=-.30) between psychometric intelligence and speed of information processing as indexed by the time required to perform elementary cognitive operations. Examples of these tasks are choice reaction time, reading rates, and coding of numbers or letters (e.g., Rindermann & Neubauer, 2001). This observation has led to the proposal that individuals who score high in fluid intelligence use a limited set of fundamental cognitive operations more efficiently (Jensen, 1998; Neubauer, Freudenthaler, & Pfurtscheller, 1995; Rypma et al., 2006; Vernon, 1983). These results, however, might also reflect the impact of other variables such as resource allocation.

Resource Allocation and Fluid Intelligence

Just, Carpenter, and Miyake (2003) have argued that cognition is biological work, which entails the consumption of resources. The concept of resources originally arose from Kahneman's (1973) capacity theory of attention and from the proposal by Just and Carpenter (1992) that defined resources as "the amount of activation available for information storage and processing" (p. 312) in the underlying cortical neural system. Importantly, the available pool of resources is assumed to be limited and to depend on (a) neurotransmitter functioning, (b) the various metabolic systems supporting the neural system, and (c) the structural connectivity of the neural system (Just et al., 2003). Variation within these systems is one source of individual differences in cognition. Similarly, Spearman (1904) suggested that fluid intelligence may correspond to the amount of "general mental energy" available to an individual. Another source of individual differences in cognition might be the allocation of resources—the amount of activation actually invested for information storage and processing. Just et al. verified three measures of activity as indices of resource allocation: functional brain imaging, event-related potentials, and pupil dilation.

One interesting question derived from this point of view refers to the relationship between the allocation of resources and fluid intelligence (cf. Ahern & Beatty, 1979). In the current work, we test resource allocation during the processing of cognitive tasks in individuals scoring high versus average in fluid intelligence.

Resource Allocation and Pupil Dilation

All cognitive efforts, like physical efforts and sensory stimuli, cause pupil dilation (Beatty & Kahneman, 1966; Hess & Polt, 1964; Kahneman & Beatty, 1967; Loewenfeld, 1993). Just et al. (2003) have demonstrated that the pupillary response reflects an overall aggregate of mental resource allocation that is not limited to a specific part of the cognitive system. According to this view, the pupil could thus be used to map the overall functional level of the cognitive system to the amount of activity in the underlying neural system. Beatty and Lucero-Wagoner (2000) argued that pupil dilation amplitude is a useful measure of task-evoked resource allocation. The more difficult a task, the more the pupil dilates (Nuthmann & van der Meer, 2005; Raisig, Welke, Hag-

eral factor of intelligence (Alderton & Larson, 1990; Bors & Stokes, 1998; Marshalek, Lohman, & Snow, 1983; Snow, Kyllonen, Marshalek, & Sternberg, 1984). Nevertheless, we do not assume that they are identical. We argue that fluid intelligence and (general factor of intelligence) are closely linked, but with respect to neuroscientific findings (Choi et al., 2008), they cannot be considered identical. By investigating neural correlates of intelligence at the structural and functional level, Choi et al. (2008) pointed out that different components of g, in particular fluid and crystallized components, are distinguishable in brain function and structure.

endorf, & van der Meer, 2007; Verney, Granholm, & Marshall, 2004). For example, in a visual search task where different levels of search difficulty were contrasted, only the pupillary responses, but not response times, differentiated between conditions (Porter, Troscianko, & Gilchrist, 2007).

Of course, the amount of resources that are allocated to a task does not depend only on the cognitive demands of the task, but also on the intensity with which an individual engages in it. This intensity of task engagement might also be reflected in pupil dynamics. It has long been known that pupil dilation increases with activation of the sympathetic nervous system (Loewenfeld, 1993). As the sympathetic nervous system regulates arousal, a higher pupillary dilation may indicate that an individual is applying his- or herself with more vigor to the task at hand (Ahern & Beatty, 1979). It has, however, been proposed by Yerkes and Dodson (1908) that performance increases with arousal only up to a point and declines if this point is exceeded. This effect is, in fact, even stronger with increasing task difficulty, as Broadhurst (1959) points out.

This idea is also incorporated in a more differentiated view of task-related arousal that has been recently proposed by Aston-Jones and Cohen (2005). They propose that the activation of the cortex is strongly influenced by the locus coeruleus (LC), a structure in the dorsorostral pons that sends norepinephric projections to vast portions of the brain. In monkeys, LC activity is highly correlated with pupil dilation (Rajkowski, Kubiak, & Aston-Jones, 1993). For humans, this connection is not yet well established; however, studies by Gilzenrat, Cohen, Rajkowski, and Aston-Jones (2003) tested predictions of Aston-Jones and Cohen's LC theory using pupillometry in humans and found the predictions to be surprisingly well confirmed.

It is therefore reasonable to interpret pupil dilation in the light of Aston-Jones and Cohen's (2005) theory of LC-mediated task engagement. In brief, the theory proposes two modes of activity: In the *tonic* mode, LC neurons exhibit a constantly high firing rate that renders the cognitive system sensitive to all kind of stimuli. This mode typically occurs when an individual is not bound to a particular task but rather "explores" his or her environment (low-task engagement). In the phasic mode, base-rate firing is reduced, and pronounced, punctual firings occur selectively in response to certain classes of stimuli. This mode typically occurs when the individual is engaged in a particular task and focuses on task-relevant stimuli while ignoring distracting environmental influences (high task engagement). Bearing these theories in mind, we can use the pupillary responses to examine differences in resource allocation between individuals with high and average fluid intelligence that are due to different degrees of task engagement.

Fluid Intelligence and Pupil Dilation

Pupil dilation also allows for discriminating between individuals who differ in fluid intelligence (for a review, see Beatty & Lucero-Wagoner, 2000). For example, Ahern and Beatty (1979) analyzed task-evoked pupil dilations in two groups of university students differing in intelligence (as indicated by their scores on the Scholastic Aptitude Test [SAT]) while they were solving mental multiplication problems across three levels of difficulty. Individuals with higher SAT scores showed higher accuracy and smaller task-evoked pupil dilation than individuals with lower SAT scores. As both groups did not differ in the magnitude of luminance-induced pupil dilations, the differences in the task-evoked pupillary responses were assumed to reflect differences in central brain

processes, indicating that more intelligent individuals invested fewer resources.

Moreover, Heitz, Schrock, Payne, and Engle (2008) investigated the effect of incentives on working memory capacity in high- and low-span individuals. Individuals were presented a reading span task (consisting of sentence reading, letter encoding, and recall). High-span individuals exhibited larger preexperimental and pretrial pupil diameter baselines than low-span individuals. The incentive, however, affected recall performance in the reading span task equally for high- and low-span groups. Furthermore, task-evoked pupillary responses in the most demanding recall phase indicated that low-span individuals consumed more resources than high-span individuals. Taking into account the strong relationship between working memory and fluid intelligence (Duncan, 2003; Engle et al., 1999; Gray et al., 2003; Salthouse & Pink, 2008), these data also point to a negative correlation between fluid intelligence and resource allocation. A finding by Heitz et al. (2008), however, remains of special interest: High-span individuals exhibit larger preexperimental and pretrial baselines across all types of tasks. Following classical interpretations of pupil size as an indicator of sympathetic activity, this may indicate a higher general arousal in high-span individuals (cf. Granholm & Steinhauer, 2004). Following Aston-Jones and Cohen's (2005) theory, however, the high-span individuals might be less engaged in the task, as it is less challenging to them (tonic mode of LC activity; cf. Aston-Jones & Cohen, 2005).

Fluid Intelligence, Resource Allocation, and Pupil Dilation

The goal of the present study was twofold. First, we intended to replicate findings concerning the differential impact of fluid intelligence on the processing of easy and difficult cognitive tasks. Second, we aimed to shed light on the relation between resource allocation and fluid intelligence using a pupil dilation measure. To test this relation we adopted an extreme-groups approach: We compared individuals with high fluid intelligence scores (h-IQ) and average fluid intelligence scores (a-IQ, i.e., normal controls). We investigated performance (response times and error rates) in a cognitively low-level choice reaction time task that required a limited set of fundamental, yet simple cognitive processes (Neubauer, 1997) as compared to a cognitively high-level geometric analogy task that additionally required executive processes (Cho et al., 2007). We assessed pupil dilation as an index of resource allocation during the two cognitive tasks and during a task-free preexperimental baseline condition.

There are three contrasting predictions about the effects of fluid intelligence and task difficulty on performance and pupil dilation (cf. Ahern & Beatty, 1979): First, if individuals with high fluid intelligence have more resources available and thus can solve more demanding tasks, they should only outperform normal controls in the most difficult analogy tasks (shorter or the same response times, lower or the same error rates, greater task-evoked pupil dilations; resource hypothesis). Second, if individuals with high fluid intelligence generally invest more resources, we expect shorter or the same response times, lower or the same error rates, and greater tasked-evoked pupil dilations across all types of tasks compared to normal controls (effort hypothesis). Third, if individuals with high fluid intelligence use resources more efficiently than normal controls, a negative interindividual correlation between resource allocation and task performance is expected. Consequently, we expect shorter or the same response times, lower or the same error rates, and smaller task-evoked pupil dilations across all types of tasks for individuals with high fluid intelligence compared to normal controls (efficiency hypothesis).

For the determination of resource allocation, the *preexperimental pupil baseline* is of interest, too. The preexperimental pupil baseline is assumed to index task-free exploration (Aston-Jones & Cohen, 2005). Furthermore, fluid intelligence is correlated with looking for new—that is, relevant or potentially interesting—information (Ackerman & Heggestad, 1997; Moutafi, Furnham, & Crump, 2003; Raine, Reynolds, Venables, & Mednick, 2002). Therefore, we predict for individuals with high fluid intelligence a higher preexperimental pupil baseline diameter compared to normal controls.

Method

Participants

Thirty-seven students took part in the experiment, 29 men and 8 women, with a mean age of 17 years (SD=0.6), and were paid for their participation. Their socioeconomic backgrounds were controlled. All participants attended the 11th grade of one of three Berlin schools specializing in mathematics and natural sciences. All students were right-handed as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision, had no history of neurological or psychiatric diseases, and did not take any medications. The students and their parents gave written consent prior to the investigation according to the Declaration of Helsinki (1964).

Three months prior to the experiment, all participants were screened for their fluid intelligence (F-IQ) through administration of the RAPM (Heller, Kratzmeier, & Lengfelder, 1998). Participants were divided into two groups based on their RAPM scores (whole sample: $M_{F-IQ} = 117.5$, SD = 16.9). Five female and 14 male participants were assigned to the average fluid intelligence group ($M_{F-IQ} = 102.6$, SD = 8.5), whereas 3 female and 15 male participants were assigned to the high fluid intelligence group ($M_{F-IQ} = 133.1$, SD = 4.7).

Tasks, Stimulus Material, and Procedure

The experiment took place in a quiet and moderately illuminated room (background luminance 500 lux). The three phases of experimentation—assessment of the preexperimental pupil baseline diameter, choice reaction time task, and geometric analogy task—were performed automatically under the control of a laboratory interface system (see "Apparatus"). At the beginning of the experiment, participants filled out a questionnaire that ascertained demographic data as well as factors that are known to affect pupil dilation (e.g., psychiatric and neurological dysfunction, drug consumption, medication; cf. Loewenfeld, 1993). Following this background luminance adaptation, participants were seated comfortably in front of a computer screen (size of the display: 19 in., display resolution: 1024×768) at a distance of approximately 100 cm.

Preexperimental pupil baseline diameter task. This task was explained as a calibration procedure prior to any task instructions to avoid task-related expectancy effects. Participants were asked to fixate on a cross presented 10 times with shuffled durations from 200 ms to 500 ms in steps of 50 ms resulting in a total fixation time of 3500 ms. The interval between fixations varied between 700 ms and 1000 ms. This procedure was repeated once after a self-paced blinking pause. The mean luminance of the stimuli was 49 cd/m². The individual average pupil diameter of

the 2450 ms of fixation was taken as a preexperimental pupil baseline not influenced by any instructional effects.

Choice reaction time task. In this low-level cognitive task, each trial started with a fixation cross presented in the middle of the screen for 1000 ms (pretrial baseline phase). Following the fixation cross, a vertical line was shown in the middle of the screen. After 500 ms, a dot appeared either to the left or right of the vertical line. The dots and the line were presented in black color on a light gray background, with a mean luminance of 48.5 cd/m². Participants had to decide as quickly and accurately as possible whether the dot was presented to the left or right of the vertical line. They were instructed to press the left button with the middle finger of the left hand if the dot appeared on the left and to press the right button with the index finger of the left hand if the dot appeared on the right. Immediately after pressing the button the next trial started. After every eight trials there was a self-paced blinking pause indicated by a smiley.

Prior to the choice reaction time task, participants received written instructions presented on the computer monitor and completed four practice trials with similar stimulus material to become familiar with the task as well as with the experimental procedure. During the practice session, feedback on the correctness of the participant's responses was given after each trial. The test block consisted of 20 trials. Overall, it took about 5 min to finish the choice reaction time task.

Geometric analogy task. In this high-level cognitive task, participants were presented with stimuli quadruplets. Each quadruplet consisted of a source pair (A:A') and a target pair (B:B') of geometric chessboard-like patterns. Each pattern consisted of an 8×8 grid of squares with each square colored either white or black (Chipman, 1977; Offenhaus, 1983; cf. Figure 1). The stimuli quadruplets were presented on a light gray background. Six different patterns were used, each in four possible alignments: "normal," vertically mirrored, horizontally mirrored, and diagonally mirrored. A pilot study had been conducted to select patterns of similar complexity. Three types of relation were applied: mirroring on the vertical, the horizontal, or the diagonal axis. These types of relation vary in difficulty (low [vertical] < medium [horizontal] < high [diagonal]; Offenhaus, 1983; Royer, 1981; van der Meer, 1996). Source pair and target pair had either the same type of relation (analogy items) or different types of relation (distractor items; Figure 1). The same patterns were used in analogy items and distractor items.

A trial consisted of four phases. It started with a fixation cross, which was presented for 1000 ms (pretrial baseline phase).

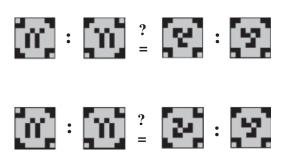


Figure 1. Geometric analogies. Examples of an analogy item (mirroring on the vertical axis) and a distractor item (mirroring on the vertical axis vs. mirroring on the diagonal axis).

Then, the item was presented (stimulus presentation phase). The mean luminance of the stimuli was 34.5 cd/m². Participants had to decide as quickly and accurately as possible whether there was the same type of relation in both the source and the target pairs. If there was, they were instructed to press the right button with the index finger of the left hand; if there was not, they were instructed to press the left button with the middle finger of the left hand. As soon as a response button was pressed by the participant, the item disappeared from the screen to prevent subsequent processing or rumination. The item was followed by a mask with the same luminance as the test items for 2000 ms (relaxation phase). The mask was used to ensure that the pupillary response was not disrupted or affected by changing light conditions. After the relaxation phase a smiley appeared on the screen, indicating that participants were now allowed to blink and could start the next trial by pressing one of the response buttons (blinking phase). During each trial, participants were asked not to move their heads and to restrict eyeblinks if possible to the blinking phase at the end of the trial.

Prior to the analogy task, participants received written instructions presented on the computer monitor and completed eight practice items with similar stimulus material to become familiar with the task as well as with the experimental procedure. During the practice session, feedback on the correctness of the participant's responses was given after each trial. The test block consisted of 60 items, 50% of which were targets equally distributed over the three conditions, vertical, horizontal, and diagonal mirroring. Overall, it took about 20 min to finish the geometric analogy task.

Dependent Variables

Choice reaction time task. Response times (RTs, measured as the time between the dot onset and a response), error rates, and pupillary responses were recorded as dependent variables.

Geometric analogy task

The following dependent variables were recorded: RTs (measured as the time between appearance of the item and the response), error rates, and pupillary responses. Note that only the data for correctly detected analogy items were further analyzed in detail, because we did not have specific hypotheses regarding the processing of distractor items.

Apparatus

Stimuli were presented using the experimental control software Presentation 9.01 (Neurobehavioral Systems Inc, Albany, CA) running on a Microsoft Windows XP operating system. The computer used for stimulus presentation collected the behavioral data (RTs and error rates) and was connected with another computer for registration and storage of the pupil data for offline analyses. The connection of these two computers allowed a transmission of trigger signals to mark the beginning of every trial in the experiments.

Pupillary responses were continuously recorded using an iView system (SensoMotoric Instruments GmbH, Teltow, Germany). The pupillometer (i.e., an infrared light source with $\lambda = 700$ –1049 nm and a video camera sensitive to infrared light) was mounted on a stand, which stabilized the participant's head. The light source and the camera were pointed at the participant's right eye. Pupil diameter was recorded at 240 Hz. The iView system measured pupil diameter in pixels. To relate this measure to absolute pupil size, however, we used the following calibration

procedure: At the beginning and the end of the experiment, a black dot (5 mm in diameter) was placed on the closed lid of the participant's right eye. This procedure made it possible to convert pupil diameter from pixels to millimeters for each participant by determining the size of this artificial pupil in pixels.

Data Analysis

Behavioral data (RTs and error rates) were analyzed using the Statistical Package for the Social Sciences 14 (SPSS Inc., Chicago, IL). Incorrect responses were excluded from data analyses. The distribution of RTs of all remaining items was determined per subject. Trials with RTs less or greater than two standard deviations from the individual's mean were excluded from the statistical analyses. For the choice reaction time task, 4.76% of the trials were eliminated, and for the geometric analogy task, 4.94%.

Pupillary responses were analyzed using Matlab 7.1 (The MathWorks, Inc., Natick, MA) and SPSS 14. Prior to statistical analyses, data were cleaned following standard procedures (Beatty & Lucero-Wagoner, 2000; Granholm, Asarnow, Sarkin, & Dykes, 1996; Verney, Granholm, & Dionisio, 2001). Artifacts due to excessive blinking were removed. Pupillary artifacts were not systematically distributed across experimental conditions. Very small blinks were replaced by linear interpolation. In the end (after discarding errors, outliers, and artifacts) an average of 87.1% of choice reaction time trials (h-IQ: 86.6%, a-IQ: 87.6%) and 56.4% of geometric analogy trials (h-IQ: 60.2%, a-IQ: 55.7%) remained for statistical analyses.

For each trial (choice reaction time task, geometric analogy task), the average pupil diameter of the 200 ms preceding the stimulus onset was subtracted from the task-evoked pupil diameter (pretrial baseline correction). We then computed stimulus-locked pupillary responses for each trial and averaged the responses for each condition and participant (cf. Beatty & Lucero-Wagoner, 2000). Data were smoothed using an unweighted 5-point moving average filter. For each participant and condition, peak dilation of the pupillary responses was defined as the maximal dilation obtained in the measurement interval of interest between 500 ms after stimulus onset and 1000 ms after response. This measure has the advantage of being independent of the number of data points occurring in the measurement interval (Beatty & Lucero-Wagoner, 2000). Data were expressed as millimeter deviation from the pretrial baseline (peak dilation).² This procedure was executed for the pupil dilation of each participant and each trial. Next, the data were averaged for each participant in each condition (cf. Granholm et al., 1996; Verney et al., 2004).

Repeated measure analyses of variance (ANOVAs) for RTs, error rates, and pupillary responses were conducted after testing for normal distributions (Kolmogorov–Smirnov test). Significant main effects were further analyzed by separate t-tests. A rejection criterion of p < .05 (two-tailed) was chosen for all analyses (corrected for multiple comparisons).

Results

Behavioral Results

Choice reaction time task. Individuals with high fluid intelligence (h-IQ) responded faster (RT: M = 317.70 ms, SD = 40.34) and with higher accuracy (error rate: M = 1.11%, SD = 2.14) than individuals with average fluid intelligence (RT: M = 356.37 ms, SD = 68.87; error rate: M = 1.58%, SD = 3.75). A one-way repeated measures ANOVA with group (h-IQ vs. a-IQ) as a between-subjects factor was performed. The analysis revealed a statistically significant main effect for group, F(1,35) = 4.28, MSE = 3,299, p = .05, $\eta^2 = .11$, indicating that RTs were shorter for the h-IQ group than for the a-IQ group. Error rates indicated that this result was not due to a speed/accuracy trade-off.

Geometric analogy task. Descriptive statistics are displayed in Table 1 including means and standard deviations of RTs and error rates for the geometric analogy task.

A 2 (group: h-IQ vs. a-IQ) \times 3 (task difficulty: low, medium, high) repeated measures ANOVA on RTs and error rates was performed. The RTanalysis revealed statistically significant main effects of task difficulty, F(2,34) = 44.81, MSE = 9,378,588, p < .001, $\eta^2 = .56$, and group, F(1,35) = 5.17, MSE = 30,343,166, p = .03, $\eta^2 = .13$, as well as for the interaction of Task Difficulty \times Group, F(2,35) = 4.79, MSE = 44,923,379, p = .035, $\eta^2 = .12$. RTs increased for more difficult analogy tasks, and the h-IQ group was faster than the a-IQ group (Figure 2).

Participants with high fluid intelligence, however, outperformed normal controls only for the more difficult tasks. That is, they did not solve the easiest tasks (i.e., mirroring on the vertical axis) significantly faster than normal controls, t(35) = 1.48, p = .15, $\eta^2 = .06$. Only the more difficult geometric analogy tasks were processed faster by participants with high fluid intelligence than by normal controls—mirroring on the horizontal axis: t(35) = 2.10, p = .04, $\eta^2 = .11$; mirroring on the diagonal axis: t(35) = 2.32, p = .03, $\eta^2 = .13$.

In general, our data concerning task difficulty replicate a number of recent studies (Bornstein & Krinsky, 1985; Ferguson, 2000; Offenhaus, 1983; Royer, 1981; Palmer & Hemenway, 1978; van der Meer, 1996), that is, mirroring on the diagonal axis appeared to be the most difficult type of relation, and mirroring on the vertical axis was the easiest type of relation.

The analysis of error rates revealed significant main effects of task difficulty, F(2,34) = 46.79, MSE = 191.37, p < .001, $\eta^2 = .57$, and group, F(1,35) = 7.12, MSE = 334.47, p = .01, $\eta^2 = .17$, as well as a significant interaction effect, F(2,35) = 7.90, MSE = 1,512.36, p = .008, $\eta^2 = .18$. In general, performance accuracy decreased with increasing task difficulty. The h-IQ group made fewer errors than the a-IQ group. However, the h-IQ group only made significantly fewer errors than the a-IQ group when processing more difficult tasks: mirroring on the horizontal axis: t(35) = 2.16, p = .038, $\eta^2 = .12$; mirroring on the diagonal axis: t(35) = 2.639, p = .01, $\eta^2 = .17$. For the easiest tasks, that is, mirroring on the vertical axis, error rates in participants with high fluid intelligence and normal controls did not differ, t(35) = 0.14, p = .889, $\eta^2 = .001$. These data confirm the RT results. Importantly, error rates indicated that there was no speed/accuracy trade-off in the data.

Pupillary Responses

Preexperimental pupil baseline diameter task. Individuals with high fluid intelligence exhibited a larger preexperimental

²The evidence indicates that the extent of the pupil dilation evoked by cognitive processing is independent of baseline pupillary diameter for baseline values smaller than 7 mm (Hoeks & Ellenbroek, 1993). Still, as a control analysis, the relative peak dilation was also calculated in our study. It yielded the same results compared to absolute peak dilation.

37.42

20.69

Table 1. Geometric Analogy Task

	Fluid intelligence								
	h-IQ ^a			a-IQ ^a					
Analogy items		Distractor items		Analogy items		Distractor items			
Response times									
$\hat{M}(\text{ms})$	8,003	6,804		10,382		8,745			
SD (ms)	2,104	1,474		3,935		2,852			
Error rates	ŕ		•	ŕ					
RF^{b} (%)	12.34	7.65		21.61		9.34			
SD (%)	10.16	5.40		10.93		5.98			
Task difficulty ^c	Low	Medium	High	Low	Medium	High			
Response times									
M (ms)	6,658	7,483	9,867	7,695	9,432	14,021			
SD (ms)	1,748	2,275	3,325	2,424	3,255	6,871			

19.75

20.01

10.49

10.41

Error rates

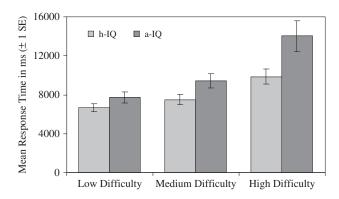
RF(%)

SD (%)

baseline pupil diameter (M = 4.96 mm, SD = 0.78) than individuals with average fluid intelligence (M = 4.51 mm, SD = 0.47). A one-way ANOVA revealed a significant effect of group, F(1,35) = 4.68, MSE = 0.41, p = .037, $\eta^2 = 0.12$, indi-

6.79

7.75



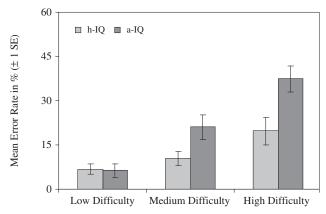


Figure 2. Geometric analogies. Effect of task difficulty (low: mirroring on the vertical axis, medium: mirroring on the horizontal axis, high: mirroring on the diagonal axis) on mean response times (RTs, in milliseconds) and error rates (in percent). SE: standard error; h-IQ= individuals with high fluid intelligence; a-IQ = individuals with average fluid intelligence.

cating that the h-IQ group has a greater preexperimental pupil baseline diameter than the a-IQ group. No sex differences within the two groups were found: a-IQ, F(1,17) = 1.01, MSE = 0.22, p = .33, $\eta^2 = 0.06$; h-IQ, F(1,16) = 0.05, MSE = 0.57, p = .82, $\eta^2 = 0.003$.

6.37

9.99

21.05

18.10

Choice reaction time task. Individuals with high fluid intelligence exhibited a larger pretrial baseline pupil diameter (M=4.83 mm, SD=0.71) and a larger pupil peak dilation (M=0.32 mm, SD=0.14) than individuals with average fluid intelligence: pretrial baseline pupil diameter, M=4.42 mm, SD=0.46 mm; pupil peak dilation, M=0.28 mm, SD=0.12. Figure 3 illustrates the pupillographic waveforms for the choice reaction time task.

A one-way ANOVA revealed a significant effect of group (h-IQ vs. a-IQ) for the mean pretrial baseline pupil diameter, F(1,35) = 4.53, MSE = 0.35, p = .04, $\eta^2 = .12$. The h-IQ group had a greater pretrial baseline pupil diameter than the a-IQ group. For the peak dilation, however, the ANOVA revealed no effect of group, F(1,35) = 0.65, MSE = 0.02, p = .43, $\eta^2 = .02$.

Geometric analogy task. Descriptive statistics are displayed in Table 2 and include means and standard deviations for pupil diameter (pretrial baseline, peak dilation) in this high-level cognitive task.

A one-way ANOVA revealed no significant effect of group on the mean pretrial baseline pupil diameter, F(1,35) = 0.80, MSE = 1.14, p = .37, $\eta^2 = .02$. That is, for the geometric analogy task, the h-IQ group and the a-IQ group did not differ in pretrial baseline diameters.

For pupil dilation in analogy items, a 2 (group: h-IQ vs. a-IQ) \times 3 (task difficulty: low, medium, high) repeated measures ANOVA was performed. There was a significant main effect of group, F(1,35)=8.45, MSE=0.06, $p\leq.01$, $\eta^2=.19$, that is, pupil peak dilation was greater in the h-IQ group than in the a-IQ group. There was no effect of task difficulty, F(2,34)=0.14, MSE=0.002, p=.874, $\eta^2=.004$, and no Group \times Task Difficulty interaction, F(2,35)=1.18, MSE=0.02, p=.31, $\eta^2=0.03$.

^ah-IQ = individuals with high fluid intelligence; a-IQ = Individuals with Average Fluid Intelligence.

^bRF = relative frequencies.

^cLow = mirroring on the vertical axis, medium = mirroring on the horizontal axis, high = mirroring on the diagonal axis.

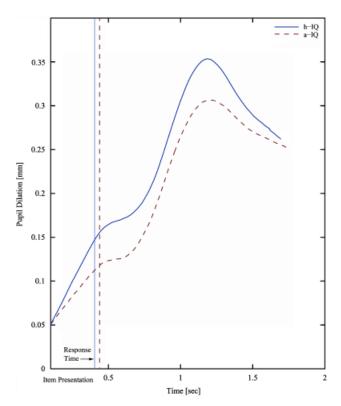


Figure 3. Choice reaction time. Effect of fluid intelligence on mean response times (vertical lines, in seconds) and mean pupillary responses (pupil dilation, in millimeters). h-IQ: individuals with high fluid intelligence; a-IQ: individuals with average fluid intelligence.

In line with our hypotheses, we examined the Group \times Task Difficulty interaction more closely. The resource hypothesis predicted that group differences would be most pronounced on the most difficult trials. We therefore analyzed the different levels of task difficulty separately, using one-way ANOVAs. The analysis yielded a significant effect, with higher peak dilation for the most difficult trials (mirroring on the diagonal axis) for the h-IQ group compared to the a-IQ group, F(1,35) = 11.70, MSE = 0.03, p < .01, $\eta^2 = .25$. For the easier trials—mirroring on the vertical and on the horizontal axes—the group differences did not reach significance: mirroring on the vertical axis, F(1,35) = 3.88, MSE = 0.02, p = .06, $\eta^2 = .10$; mirroring on the horizontal axis, F(1,35) = 3.785, MSE = 0.04, p = .06, $\eta^2 = .01$. Figure 4 illustrates these findings. Taken together, the pupil data show that the h-IQ group allocated more resources than the a-IQ group in solving the most difficult geometric analogies (mirroring on the diagonal axis): Higher processing load is reflected in higher peak dilation for the h-IQ group.

Furthermore, we assessed effects of sex as well as differences in the early periods of pupil dilation. First, no sex differences regarding task-evoked pupillary dilations within the two groups were found: h-IQ, F(1,16) = 0.15, MSE = 0.09, p = .70, $\eta^2 = .01$; a-IQ, F(1,17) = 1.07, MSE = 0.04, p = .32, $\eta^2 = .06$. Thus, our findings are independent of sex. Second, we ran a principal component analysis (PCA) to examine effects in the first 2 s of the geometric analogy task separately from the later period. For each level of task difficulty (low, medium, high), the analysis revealed five factors. A 2 (group: h-IQ vs. a-IQ) × 5 (factor) repeated measures ANOVA for each level of task difficulty was performed. The analysis yielded no significant effect

of factor or of group, and no significant interaction.³ Thus, the lack of group differences in the early periods of pupil dilation indicates that our findings reflect cognitive processing rather than spontaneous emotional responses to the stimuli (cf. Compton et al., 2003; Liddell et al., 2005; Ochsner & Feldman Barrett, 2001; Phelps, 2006; Prehn et al., 2008).

Changes in pupil baseline diameters. There is a decrease in pupil baseline diameter from the beginning to the end of the whole test session that differs between the h-IQ and the a-IQ groups. In the h-IQ group the mean geometric analogy pretrial baseline diameter is significantly smaller than the preexperimental baseline diameter, t(17) = 4.71, p < .001, and significantly smaller than the mean choice reaction time pretrial baseline diameter, t(17) = 4.33, p < .001. In the a-IQ group the geometric analogy pretrial baseline diameter is significantly smaller than the preexperimental baseline diameter, t(18) = 2.78, p = .01. Interestingly, the decrease in baseline diameter from the preexperimental condition to the geometric analogy task is significantly higher in the h-IQ group than in the a-IQ group, F(1,35) = 0.65, MSE = 0.15, p = .02, $\eta^2 = 0.14$ (note that there is no difference between groups in pretrial baseline pupil diameter in the geometric analogy task; see above).

Discussion

We used a choice reaction time task and a geometric analogy task to investigate the processing of low-level versus high-level cognitive tasks in individuals with high fluid intelligence compared to normal controls. We recorded RTs and error rates as well as phasic and tonic changes in pupil diameter (cf. Aston-Jones & Cohen, 2005; Granholm & Steinhauer, 2004).

The study yielded the following main findings: Individuals with high fluid intelligence processed the choice reaction time task faster than normal controls but task-evoked pupillary responses did not differ between the groups. In the geometric analogy task, only the more difficult task conditions were processed faster and more accurately, but with greater pupillary responses. Furthermore, individuals with high fluid intelligence showed greater preexperimental pupil baseline diameters than normal controls.

Impact of Fluid Intelligence on Processing Low-Level versus High-Level Cognitive Tasks

The shorter response times of the h-IQ group in the choice reaction time task are an expected replication of findings concerning the differential impact of fluid intelligence on processing a low-level cognitive task (inspection time; Neubauer, 1997) as compared to a high-level cognitive task (here: geometric analogies). This points to higher processing efficiency in individuals with high fluid intelligence. In a recent study, Salthouse and Pink (2008) asked for the critical factor in the relationship between fluid intelligence and working memory. Because strong influences were

³Low task difficulty: factor F(2,34) = 0.00, MSE = 1.02, p = 1.00, $η^2 = .00$, group F(1,35) = 3.15, MSE = 0.92, p = .06, $η^2 = .11$, Factor × Group interaction F(2,35) = 0.38, MS = 1.02, p = .82, $η^2 = .01$; medium task difficulty: factor F(2,34) = 0.001, MSE = 1.00, p = 1.00, $η^2 = .00$, group F(1,35) = 0.13, MSE = 1.03, p = .72, $η^2 = .13$, Factor × Group interaction F(2,35) = 0.84, MS = 1.00, p = .50, $η^2 = .02$; high task difficulty: factor F(2,34) = 0.00, MSE = 1.00, p = 1.00, $η^2 = .00$, group F(1,35) = 1.43, MSE = 0.99, p = .24, $η^2 = .04$, Factor × Group interaction F(2,35) = 0.94, MSE = 1.00, p = .44, $η^2 = .03$.

Table 2. Geometric Analogy Task

		Fluid intelligence								
	h-IQ ^a			a-IQ ^a						
	Analogy items	Distractor items		Analogy items		Distractor items				
Peak dilation										
M(mm)	0.54	0.48		0.40		0.37				
SD (mm)	0.17	0.13		0.12		0.19				
Pretrial baseline pupil	diameter									
M (mm)	4.45	4.47		4.27		4.26				
SD (mm)	0.73	0.74		0.48		0.50				
Task difficulty ^b	Low	Medium	High	Low	Medium	High				
Peak dilation										
M (mm)	0.53	0.53	0.58	0.43	0.40	0.39				
SD (mm)	0.17	0.20	0.21	0.14	0.20	0.11				
Pretrial baseline pupil	diameter									
M (mm)	4.43	4.44	4.48	4.22	4.28	4.30				
SD (mm)	0.71	0.76	0.74	0.53	0.45	0.47				

^ah-IQ = individuals with high fluid intelligence; a-IQ = individuals with average fluid intelligence.

apparent in the simplest versions and on the initial trials in their working memory tasks, the critical factor was not assumed to be related to how much storage and processing was required or to processes associated with successive trials in these tasks. Instead, the critical factor might be to quickly adapt to a new task and to perform effectively, "even in situations that have minimal demands for simultaneous storage and processing" (Salthouse & Pink, 2008, p. 370). Barrouillet, Lépine, and Camos (2008) extended this view in presenting empirical evidence that any elementary attention-demanding processing step is sensitive to variations in working memory capacity. The differences between individuals differing in working memory capacity observed on complex cognitive activities were exactly proportionate to those elicited by elementary activities. That is, the time to perform each processing step is assumed to "depend on a basic general capacity, conceived as the amount of available attention needed to activate relevant items of knowledge and procedures" (Barrouillet et al., 2008, p. 533). This conclusion corresponds with our findings in the choice reaction time task. This low-level cognitive task requires the participant to quickly detect the position of a critical stimulus. The effect of high fluid intelligence appears to make the accessing of items faster, that is, more efficient.

High fluid intelligence also leads to better performance in processing the high-level geometric analogy task for the more difficult analogy trials (mirroring on the diagonal axis) only. This finding suggests that individuals with high fluid intelligence do not necessarily clearly outperform normal controls in a cognitive problem, which is easily managed by individuals with average fluid intelligence, too. There are two explanations: First, as might be expected for the easiest trials (mirroring on the vertical axis; cf. Offenhaus, 1983; Royer, 1981; van der Meer, 1996), the groups do not differ in applying the global set of fundamental cognitive processes required in analogical reasoning (cf. Cho et al., 2007). This explanation, however, contradicts the findings of Salthouse and Pink (2008) and Barrouillet et al. (2008). Therefore, a second explanation should be taken into account. Considering the remarkable variances in RTs between participants, we assume that potential group differences in processing the easier trials may have been masked by different strategies that individuals use to perform the task (cf. van der Meer, 1996). For example, Vigneau, Caissie, and Bors (2006) explored strategic influences on performance in a fluid intelligence task in more detail. They presented individuals differing in fluid intelligence a selection of items from the RAPM. Latency and eye-movement data showed that individuals differed in terms of speed, but also in terms of strategies. Consequently, the impact of visual scanning strategies on performance in visually presented cognitive tasks should be considered in more detail in future research.

Modulation of Resource Allocation in Individuals with High versus Average Fluid Intelligence

The second goal of the present study was to investigate the modulation of resource allocation in individuals with high versus average fluid intelligence while they were performing cognitively low-level as compared to high-level geometric analogy tasks. Pupillometrics was used to shed light on resource allocation. Given the large group differences in fluid intelligence indicated by the RAPM scores, the pupillary response was expected to differentiate between the hypotheses outlined in the introduction, namely the *resource*, *effort*, and *efficiency hypotheses*. Measures of both *phasic* and *tonic* pupil dilation helped in contrasting these hypotheses.

Phasic pupillary response. The phasic pupillary responses indicated that individuals with high fluid intelligence allocated more resources than normal controls only for the most difficult geometric analogy task and not for the low-level choice reaction time task. Thus, the effort hypothesis was not supported. Because individuals with high fluid intelligence still had significantly shorter RTs during the choice reaction time task than normal controls, this finding points to a higher efficiency in h-IQ individuals compared to a-IQ individuals. Here, we argue that component processes of this task might be more automated in individuals with high fluid intelligence. For the cognitively high-level geometric analogy task, h-IQ individuals showed better performance corresponding with stronger task-evoked pupillary responses. That is, individuals with higher fluid intelligence allocate more resources compared to individuals of average fluid

^bLow = mirroring on the vertical axis, medium = mirroring on the horizontal axis, high = mirroring on the diagonal axis.

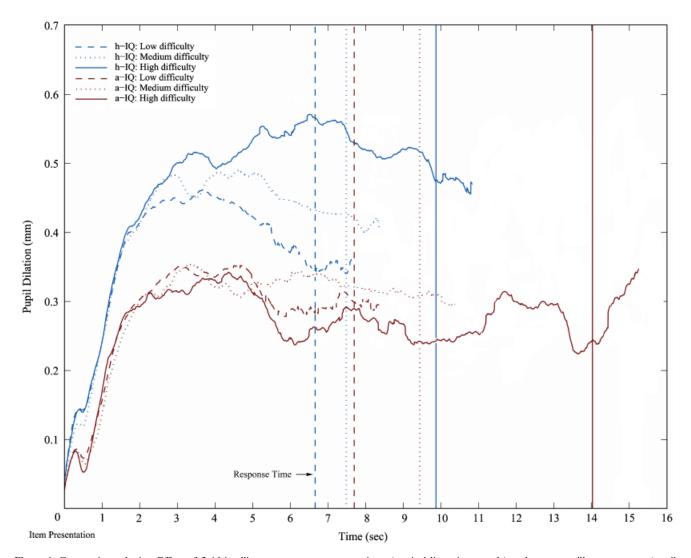


Figure 4. Geometric analogies. Effect of fluid intelligence on mean response times (vertical lines, in seconds) and mean pupillary responses (pupil dilation, in millimeters) depending on task difficulty (low: mirroring on the vertical axis, medium: mirroring on the horizontal axis, high: mirroring on the diagonal axis). h-IQ: individuals with high fluid intelligence; a-IQ: individuals with average fluid intelligence.

intelligence only when processing the most difficult geometric analogies. Consequently, our data clearly support the *resource hypothesis*. Individuals scoring high in fluid intelligence appear to have more resources available and thus perform better on more demanding tasks. These findings also correspond to the neuroimaging results found by Duncan (2003) and others (Gray et al., 2003; Lee et al., 2006; O'Boyle et al., 2005) who found a positive correlation between regional brain activation and intelligence (but see also Rypma et al., 2006, for a critical discussion).

Our results are, however, not consistent with findings by Ahern and Beatty (1979), who reported smaller pupillary responses in more intelligent individuals. These different patterns of results may occur for a number of reasons (cf. Rypma et al., 2006). First, Ahern and Beatty presented multiplication tasks of differing complexity. For students, these tasks are highly overlearned, that is, the component processes of arithmetic are assumed to be more automatic than the fluid processing required in the newly encountered analogical reasoning task. This is especially true for the most difficult geometric analogies, which appeared to best distinguish between individuals differing in fluid intelligence. Also note that the stimuli in the Ahern and Beatty

study were presented acoustically and sequentially whereas our stimuli were presented visually and simultaneously.

Second, the differences between experimental populations may have influenced the results. In contrast to our approach, Ahern and Beatty (1979) divided their participants based on SAT scores. The SAT is a standardized test for college admission in the United States that does not purely measure fluid intelligence, but rather measures proficiencies (e.g., in mathematics and writing). This supports our assumption that superior performance of the "high group" in the study of Ahern and Beatty was partly due to better trained skills (and thus more to automatic processes) rather than to fluid intelligence. Moreover, as SAT scores are influenced by training and preparation, the fluid intelligence of the "high group" may actually have been lower than that of the h-IQ group in our study that was selected by a fluid intelligence test (RAPM).

Altogether, we see sufficient evidence to argue that Ahern and Beatty (1979) favoring of the *efficiency hypothesis* is the result of a considerably different experimental design. We believe that during the process of learning there could be a larger increase in efficiency in intelligent/proficient subjects, whereas superior

performance on an unknown task (such as ours) is initially administered by additional allocation of resources. In line with this assumption, in a pre/posttraining design, Neubauer, Grabner, Freudenthaler, Beckmann, and Guthke (2004) reported a negative correlation between fluid intelligence and prefrontal brain activation during the posttest *only*. We deem the impact of learning on resource allocation to be an interesting area for future research

Another conclusion of our pupillary data refers to the interaction between fluid intelligence and subjective task difficulty as indicated by phasic pupillary responses. Granholm et al. (1996) used pupillometric recordings during a digit span recall task that differed in processing load. The authors found that pupillary responses increase systematically with increasing processing demands that are below resource limits, change little during active processing at or near the resource limits, and decline when processing demands exceed available resources. Similarly, in our study, the most difficult trials of the analogy task may have overstrained the resources of the individuals in the a-IQ group. This is suggested by both the dramatically increased error rate and a decrease in pupillary dilation as compared to the easier trials. Note that these findings add further support to the resource hypothesis. They are also of great value in explaining the differential findings of Ahern and Beatty (1979), as their tasks probably did not exceed the cognitive capacities of the individuals in their "low group."

Tonic pupillary response. Tonic pupil size also proved to be sensitive to fluid intelligence. This concerns the preexperimental pupil baseline, which was larger for individuals with high fluid intelligence. The contributions of the autonomic nervous system to pupil dilation have been known for some time (cf. Loewenfeld, 1993), and this suggests an interpretation in terms of general arousal: The dilation of the pupil is mediated by activation of the sympathetic dilator muscle as well as inhibition of the parasympathetic sphincter. Accordingly, a tonically dilated pupil is typically associated with wakefulness and activation. Related psychological concepts (e.g., stimulation seeking or the personality trait "openness to experience") have been shown to be positively correlated with fluid intelligence (Ackerman & Heggestad, 1997; Moutafi et al., 2003) and even to promote the development of cognitive abilities (cf. the longitudinal study by Raine et al., 2002). Following this line of reasoning, the larger baseline can be seen as an indicator of a more pronounced tendency toward taskfree exploring and scanning of the environment in the h-IQ group. This finding is comparable to the findings of Heitz et al. (2008), who report greater pupil baseline diameters for individuals with high working memory capacity as compared to individuals with low working memory capacity.

A related though more elaborate view on the interplay of arousal and performance has been proposed by Aston-Jones and Cohen (2005). Their theory allows for a differentiated dealing with overall activation and task performance, as it also accounts for individual differences in task engagement and elegantly

incorporates the Yerkes and Dodson (1908) relationship as discussed in more detail in the introduction section. Still, in the case of preexperimental baseline differences, this leads to a similar interpretation for the understanding of arousal in terms of activation in the autonomic nervous system: According to Aston-Jones and Cohen, a large tonic pupil diameter reflects *exploratory behavior*, that is, the individual is scanning the environment for possible sources of reward.

Interestingly, the pretrial pupil baselines (i.e., baseline measurements recorded before the beginning of each trial) show a striking difference between the high intelligence group and the normal controls, too. In the low-level choice reaction time task we found a significantly enlarged pretrial baseline for h-IQ individuals. However, we found a downward trend in pretrial pupillary data: In the geometric analogy task, tonic pupillary baselines were similar for both groups. Aston-Jones and Cohen's (2005) theory provides a satisfactory explanation for this result: It is only the difficult task that is demanding enough for the h-IQ group to display a comparably strong task engagement as the a-IQ individuals. Because the order of the tasks was not permutated in our study, we cannot exclude the possibility that the decrease in pupil baseline in the h-IQ group was due to a drop in autonomic arousal over the course of the experimental procedure irrespective of the administered tasks. Following this explanation, one would still have to explain why this drop was more pronounced in the h-IO group than in the a-IO group. Future studies should consider this in their experimental design.

Conclusion

Our study makes the crucial point that the combination of pupillometrics with traditional behavioral measures is promising as a way to assist our understanding of fluid intelligence and resource allocation in cognitive processing. Our results clearly favor the *resource hypothesis* over the *effort* and *efficiency hypotheses*, though we do see evidence that the latter can be correct in certain conditions (see the above discussion of Ahern & Beatty, 1979).

Thus, future studies will need to investigate the impact of task type and learning on the allocation of mental resources in more detail. In particular, learning-induced improvements and automatization of cognitive functions might be crucial for the relationship of task performance and resource allocation (cf. Neubauer et al., 2004; Poldrack, Desmond, Glover, & Gabrieli, 1998), as the coming into effect of such mechanisms could mark a transition from resource to efficiency explanations. Finally, individual processing strategies should be taken into account. In future fMRI studies, multiple cognitive tasks in individuals differing in fluid intelligence should be employed to further investigate the dynamic nature of resource allocation and the contribution of specific neural networks in the service of resource modulation and cognition (Critchley, Tang, Glaser, Butterworth, & Dolan, 2005; Grabner et al., 2007; Krueger et al., 2008; O'Boyle et al., 2005; Satterthwaite, Green, Myerson, Parker, Ramaratnam, & Buckner, 2007).

REFERENCES

Ackerman, P. L., & Heggestad, E. D. (1997). Intelligence, personality, and interests: Evidence for overlapping traits. *Psychological Bulletin*, *121*, 219–245.

Ahern, S., & Beatty, J. (1979). Pupillary responses during information processing vary with Scholastic Aptitude Test scores. Science, 205, 1289–1292. Alderton, D. A., & Larson, G. E. (1990). Dimensionality of Raven's Advanced Progressive Matrices items. Educational & Psychological Measurement, 50, 887–900.

Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. Annual Review of Neuroscience, 28, 403–450.

- Barrouillet, P., Lépine, R., & Camos, V. (2008). Is the influence of working memory capacity on high-level cognition mediated by complexity or resource-dependent elementary processes? *Psychonomic Bulletin & Review*, 15, 528–534.
- Bates, T. C., & Shieles, A. (2003). Crystallized intelligence as a product of speed and drive for experience: The relationship of inspection time and openness to g and Gc. *Intelligence*, 31, 275–287.
- Beatty, J., & Kahneman, D. (1966). Pupillary changes in two memory tasks. *Psychonomic Science*, 5, 371–372.
- Beatty, J., & Lucero-Wagoner, B. (2000). The pupillary system. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), *Handbook of psychophysiology* (2nd ed, pp. 142–162). New York: Cambridge University Press.
- Bornstein, M. H., & Krinsky, S. J. (1985). Perception of symmetry in infancy: The salience of vertical symmetry and the perception of pattern wholes. *Journal of Experimental Child Psychology*, 39, 1–19.
- Bors, D. A., & Stokes, T. L. (1998). Raven's Advanced Progressive Matrices: Norms for first-year university students and the development of a short form. *Educational and Psychological Measurement*, 58, 382–399.
- Broadhurst, P. L. (1959). The interaction of task difficulty and motivation: The Yerkes Dodson law revived. *Acta Psychologica*, *Amsterdam*, 16, 321–338.
- Carpenter, P. A., Just, M. A., & Shell, P. (1990). What one intelligence test measures: A theoretical account of the processing in the Raven Progressive Matrices Test. *Psychological Review*, 97, 404–431.
- Chipman, S. F. (1977). Complexity and structure in visual patterns. *Journal of Experimental Psychology: General*, 106, 269–301.
- Cho, S., Holyoak, K. J., & Cannon, T. D. (2007). Analogical reasoning in working memory: Resources shared among relational integration, interference resolution, and maintenance. *Memory & Cognition*, 35, 1445–1455.
- Choi, Y. Y., Shamosh, N. A., Cho, S. H., DeYoung, C. G., Lee, M. J., Lee, J.-M., et al. (2008). Multiple bases of human intelligence revealed by cortical thickness and neural activation. *Journal of Neuroscience*, 28, 10323–10329.
- Compton, R. J., Banich, M. T., Mohanty, A., Milham, M. P., Herrington, J., Miller, G. A., et al. (2003). Paying attention to emotion: An fMRI investigation of cognitive and emotional Stroop tasks. *Cognitive, Affective & Behavioral Neuroscience*, 3, 81–96.
- Critchley, H. D., Tang, J., Glaser, D., Butterworth, B., & Dolan, R. J. (2005). Anterior cingulate activity during error and autonomic response. *NeuroImage*, 27, 885–895.
- Duncan, J. (2003). Intelligence tests predict brain response to demanding task events. *Nature Neuroscience*, *6*, 207–208.
- Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. (1999).
 Working memory, short-term memory, and general fluid intelligence:
 A latent-variable approach. *Journal of Experimental Psychology: General*, 128, 309–331.
- Ferguson, R. W. (2000). Modeling orientation effects in symmetry detection: The role of visual structure. In *Proceedings of the 22nd Conference of the Cognitive Science Society*. Hillsdale, NJ: Erlbaum.
- French, R. M. (2002). The computational modeling of analogy-making. *Trends in Cognitive Sciences*, 6, 200–205.
- Gentner, D. (1983). Structure-mapping: A theoretical framework for analogy. Cognitive Science, 7, 155–170.
- Gilzenrat, M. S., Cohen, J. D., Rajkowski, J., & Aston-Jones, G. (2003).
 Pupil dynamics predict changes in task engagement mediated by locus coeruleus. Society of Neurosciences, Abstracts, Program No. 515.19.
- Grabner, R. H., Ansari, D., Reishofer, G., Stern, E., Ebner, F., & Neuper, C. (2007). Individual differences in mathematical competence predict parietal brain activation during mental calculation. *Neuro-Image*, 38, 346–356.
- Granholm, E., Asarnow, R. F., Sarkin, A. J., & Dykes, K. L. (1996).Pupillary responses index cognitive resource limitations. *Psychophysiology*, 33, 457–461.
- Granholm, E., & Steinhauer, S. R. (2004). Pupillometric measures of cognitive and emotional processes. *International Journal of Psycho*physiology, 52, 1–6.
- Gray, J. R., Chabris, C. F., & Braver, T. S. (2003). Neural mechanisms of general fluid intelligence. *Nature Neuroscience*, 6, 316–322.
- Haier, R. J., Sternberg, R. J., Lautrey, J., & Lubart, T. I. (2003). Brain imaging studies of intelligence: Individual differences and neurobiology. In R. J. Sternberg, J. Lautrey, & T I. Lubart (Eds.), Models of

- *intelligence for the new millennium* (pp. 185–193). Washington, DC: American Psychological Association.
- Halford, G. S. (1992). Analogical reasoning and conceptual complexity in cognitive development. *Human Development*, 35, 193–217.
- Heitz, R. P., Schrock, J. C., Payne, T. W., & Engle, R. W. (2008). Effects of incentive on working memory capacity: Behavioral and pupillometric data. *Psychophysiology*, 45, 119–129.
- Heller, K. A., Kratzmeier, H., & Lengfelder, A (1998). *Matrizen-Test-Manual (Band 2): Ein Handbuch mit deutschen Normen zu den Advanced Progressive Matrices von JC. Raven.* [Matrices-test-manual volume 2. A manual with German norms for the standard progressive matrices of J.C. Raven] Weinheim: Beltz-Test GmbH.
- Hess, E. H., & Polt, J. M. (1964). Pupil size in relation to mental activity during simple problem-solving. Science, 143, 1190–1192.
- Hoeks, B., & Ellenbroek, B. A. (1993). A neural basis for a quantitative pupillary model. *Journal of Psychophysiology*, 7, 315–324.
- Hofstadter, D. R. (1995). Fluid concepts and creative analogies: Computer models of the fundamental mechanisms of thought. New York: Basic Books.
- Holyoak, K. J., & Thagard, P. (1995). Mental leaps: Analogy in creative thought. Cambridge, MA: MIT Press.
- James, W. (1890/1950). The principles of psychology. New York: Dover. Jensen, A R. (1998). The g factor: The science of mental ability. Westport, CT: Praeger Publishers/Greenwood Publishing Group.
- Just, M. A., & Carpenter, P. A. (1992). A capacity theory of comprehension: Individual differences in working memory. *Psychological Review*, 99, 122–149.
- Just, M. A., Carpenter, P. A., & Miyake, A. (2003). Neuroindices of cognitive workload: Neuroimaging, pupillometric and event-related potential studies of brain work. *Theoretical Issues in Ergonomics Sci*ence, 4, 56–88.
- Kahneman, D. (1973). Attention and effort. Englewood Cliffs, NJ: Prentice-Hall.
- Kahneman, D., & Beatty, J. (1967). Pupillary responses in a pitch-discrimination task. *Perception & Psychophysics*, 2, 101–105.
- Klix, F (1993). Erwachendes Denken. [Awakening Thinking] Heidelberg: Spektrum.
- Krueger, F., Spampinato, M. V., Pardini, M., Pajevic, S., Wood, J. N., Weiss, G. H., et al. (2008). Integral calculus problem solving: An fMRI investigation. *Neuro Report*, 19, 1095–1099.
- Lee, K. H., Choi, Y. Y., Gray, J. R., Cho, S. H., Chae, J.-H., Lee, S., et al. (2006). Neural correlates of superior intelligence: Stronger recruitment of posterior parietal cortex. *NeuroImage*, 29, 578–586.
- Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., et al. (2005). A direct brainstem-amygdala-cortical 'alarm' system for subliminal signals of fear. *NeuroImage*, 24, 235–243.
- Loewenfeld, I. E. (1993). *The pupil*. Ames, IA: Iowa State University
- Marshalek, B., Lohman, D. F., & Snow, R. E. (1983). The complexity continuum in the radex and hierarchical models of intelligence. *Intelligence*, 7, 107–127.
- McCrory, C., & Cooper, C. (2005). The relationship between three auditory inspection time tasks and general intelligence. *Personality and Individual Differences*, 38, 1835–1845.
- Mitchell, M. (1993). Analogy-making as perception: a computer model. Cambridge, MA: MIT Press.
- Moutafi, J., Furnham, A., & Crump, J. (2003). Demographic and personality predictors of intelligence: A study using the Neo personality inventory and the Myers-Briggs type indicator. *European Journal of Personality*, 17, 79–94.
- Neubauer, A. C. (1997). The mental speed approach to the assessment of intelligence. In J. Kingma & W. Tomic (Eds.), Advances in cognition and educational practice: Reflections on the concept of intelligence (Vol. 4, pp. 149–173). New York: Elsevier Science/JAI Press.
- Neubauer, A. C., Grabner, R. H., Freudenthaler, H. H., Beckmann, J. F., & Guthke, J. (2004). Intelligence and individual differences in becoming neurally efficient. *Acta Psychologica (Amsterdam)*, 116, 55–74.
- Neubauer, A., Freudenthaler, H. H., & Pfurtscheller, G. (1995). Intelligence and spatiotemporal patterns of event-related desynchronization (ERD). *Intelligence*, 20, 249–266.
- Nuthmann, A., & van der Meer, E. (2005). Time's arrow and pupillary response. *Psychophysiology*, 42, 306–317.
- O'Boyle, M. W., Cunnington, R., Silk, T. J., Vaughan, D., Jackson, G., Syngeniotis, A., et al. (2005). Mathematically gifted male ado-

- lescents activate a unique brain network during mental rotation. Cognitive Brain Research, 25, 583-587.
- Ochsner, K. N., & Feldman Barrett, L. (2001). A multiprocess perspective on the neuroscience of emotion. In T. J. Mayne & G. A. Bonanno (Eds.), *Emotions: Current issues and future directions* (pp. 38–81). New York: Guilford Press.
- Offenhaus, B. (1983). *Analyse des analogen Schlussprozesses unter differentiellem Aspekt*. [Individual differences in analogical reasoning. Thesis] Dissertation. Berlin: Humboldt-Universität.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Palmer, S. E., & Hemenway, K. (1978). Orientation and symmetry: Effects of multiple, rotational, and near symmetries. *Journal of Experimental Psychology: Human Perception and Performance*, 4, 691–702.
- Phelps, E. A. (2006). Emotion and cognition: Insights from studies of the human amygdala. *Annual Review of Psychology*, *57*, 27–53.
- Poldrack, R. A., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998). The neural basis of visual skill learning: An fMRI study of mirror reading. *Cerebral Cortex*, 8, 1–10.
- Porter, G., Troscianko, T., & Gilchrist, I. D. (2007). Effort during visual search and counting: Insights from pupillometry. *The Quarterly Journal of Experimental Psychology*, 60, 211–229.
- Prabhakaran, V., Smith, J. A. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1997). Neural substrates of fluid reasoning:
 An fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test. Cognitive Psychology, 33, 43–63
- Prehn, K., Heekeren, H. R., Blasek, K., Lapschies, K., Mews, I., & van der Meer, E. (2008). Neuroticism influences pupillary responses during an emotional interference task. *International Journal of Psychophysiology*, 70, 40–49.
- Prokosch, M. D., Yeo, R. A., & Miller, G. F. (2005). Intelligence tests with higher g-loadings show higher correlations with body symmetry: Evidence for a general fitness factor mediated by developmental stability. *Intelligence*, *33*, 203–213.
- Raine, A., Reynolds, C., Venables, P. H., & Mednick, S. A. (2002). Stimulation seeking and intelligence: A prospective longitudinal study. *Journal of Personality and Social Psychology*, 82, 663–674.
- Raisig, S., Welke, T., Hagendorf, H., & van der Meer, E. (2007). Investigating dimensional organization in scripts using the pupillary response. *Psychophysiology*, 44, 864–873.
- Rajkowski, J., Kubiak, P., & Aston-Jones, G. (1993). Correlations between locus coeruleus (LC) neural activity, pupil diameter and behavior in monkey support a role of LC in attention. Society of Neurosciences, Abstracts, 19, 974.
- Raven, J. C. (1958). Advanced progressive matrices. London: Lewis.
- Rindermann, H., & Neubauer, A. C. (2001). The influence of personality on three aspects of cognitive performance: Processing speed, intelligence and school performance. *Personality and Individual Differences*, 30, 829–842.
- Royer, F. L. (1981). Detection of symmetry. Journal of Experimental Psychology: Human Perception and Performance, 7, 1186–1210.

- Rypma, B., Berger, J. S., Prabhakaran, V., Bly, B. M., Kimberg, D. Y., Biswal, B. B., et al. (2006). Neural correlates of cognitive efficiency. *NeuroImage*, 33, 969–979.
- Salthouse, T. A., & Pink, J. E. (2008). Why is working memory related to fluid intelligence? *Psychonomic Bulletin & Review*, *15*, 364–371.
- Satterthwaite, T. D., Green, L., Myerson, J., Parker, J., Ramaratnam, M., & Buckner, R. L. (2007). Dissociable but inter-related systems of cognitive control and reward during decision making: Evidence from pupillometry and event-related fMRI. *NeuroImage*, 37, 1017–1031.
- Schweizer, K., Goldhammer, F., Rauch, W., & Moosbrugger, H. (2007). On the validity of Raven's matrices test: Does spatial ability contribute to performance? *Personality and Individual Differences*, 43, 1998–2010.
- Snow, R. E., Kyllonen, C. P., Marshalek, B., & Sternberg, R. J. (1984). The topography of ability and learning correlations. In R. J. Sternberg (Ed.), *Advances in the psychology of human intelligence* (pp. 47–103). Hillsdale, NJ: Erlbaum.
- Spearman, C. (1904). General intelligence, objectively determined and measured. American Journal of Psychology, 15, 201–293.
- Tamez, E., Myerson, J., & Hale, S. (2008). Learning, working memory, and intelligence revisited: Proceedings of the Meeting of the Society for the Quantitative Analyses of Behavior (SQAB 2007), 2007, San Diego, CA, USA. *Behavioural Processes*, 78, 240–245.
- Thoma, R. J., Yeo, R. A., Gangestad, S. W., Halgren, E., Sanchez, N. M., & Lewine, J. D. (2005). Cortical volume and developmental instability are independent predictors of general intellectual ability. *Intelligence*, 33, 27–38.
- van der Meer, E. (1996). Memory and analogical reasoning. In D. Herrmann, C. McEvoy, C. Hertzog, P. Hertel, & M. K. Johnson (Eds.), *Basic and applied memory research: Practical applications* (pp. 139–151). Mahwah, NJ: Erlbaum.
- van der Meer, E., & Klix, F. (1986). Mathematical giftedness: Its nature and possible early identification. In A. J. Cropley, K. K. Urban, H. Wagner, & W. Wieczerkowski (Eds.), *Giftedness: A continuing worldwide challenge*. New York: Trillium Press.
- Verney, S. P., Granholm, E., & Dionisio, D. P. (2001). Pupillary responses and processing resources on the visual backward masking task. *Psychophysiology*, 38, 76–83.
- Verney, S. P., Granholm, E., & Marshall, S. P. (2004). Pupillary responses on the visual backward masking task reflect general cognitive ability. *International Journal of Psychophysiology*, 52, 23–36.
- Vernon, P. A. (1983). Speed of information processing and general intelligence. *Intelligence*, 7, 53–70.
- Vigneau, F., Caissie, A. F., & Bors, D. A. (2006). Eye-movement analysis demonstrates strategic influences on intelligence. *Intelligence*, 34, 261– 272
- Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit formation. *Journal of Comparative Neu*rology and Psychology, 18, 459–482.

(RECEIVED September 14, 2008; ACCEPTED March 20, 2009)