

Evaluation of a "Mental Effort" Hypothesis for Correlations Between Cortical Metabolism and Intelligence

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Previous research indicates that low scores on the Raven's Advanced Progressive Matrices (RAPM) test are associated with increased cortical glucose utilization during problem solving. We hypothesized that previous results may reflect the neurophysiological consequences of patterns of effort requirements; that is, high-effort expenditure from lower aptitude participants (for whom the problems are hard) and low-effort expenditure from higher aptitude participants (for whom the problems are easy). In this experiment, positron emission tomography (PET) data were gathered on participants ($N = 28$) who solved easy and hard problems that were tailored to the participants' own ability levels, thereby eliminating aptitude group differences in effort requirements. Contrary to previous results, high aptitude was associated with high cortical glucose use. Average aptitude participants showed diminished glucose use in the hard condition. A significant Group \times Condition \times Hemisphere Effect was also noted, with greater right hemisphere activation in the hard condition for the high-aptitude group. These results demonstrate that the relation of cerebral glucose use and cognitive ability is sensitive to participant and task selection.

BACKGROUND

One of neuropsychology's most promising research thrusts is the analysis of cognitive functioning in the brain via imaging techniques, such as positron emission tomography (PET). In PET, a small dose of positron-labeled material is

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injected into the bloodstream. Detectors are used to determine the rate of uptake of the positron-emitting agent in the brain during psychological task performance, providing a snapshot of regional brain function during a discreet time period. This allows researchers to study functional localization by varying task demands and observing subsequent shifts in primary sites of brain activity (Pheps & Mazziotta, 1985). For example, Corbetta, Miezin, Dobmeyer, Shulman, and Petersen (1991) used PET to measure changes in regional cerebral activity of normal participants who were discriminating different attributes (shape, color, and velocity) of the same set of visual stimuli. Their main result was that different, identifiable regions of extrastriate visual cortex were activated when attending to different attributes of a visual display. Similarly, Posner, Petersen, Fox, and Raichle (1988) reported that PET can be used to differentiate between the neural activity patterns underlying the visual, phonological, articulatory, and semantic analysis of words.

Partly because of these successes in studying simple cognitive processes, interest has grown in studying the neural substrates of complex, higher order (or "executive") processes, including skills and processes critical to individual differences in human intelligence. Initial PET studies of intelligence, however, have produced somewhat counterintuitive evidence concerning localization and direction of relationships. With regard to localization, one would expect that the likely brain sites for problem solving (based on existing neuropsychological data) would also be the likely sites for intelligence–metabolism correlations. For example, research indicates that certain frontal and prefrontal brain areas are involved in directing attention, planning, holding stimuli in memory, and performing complex stimulus transformations (e.g., Goldman-Rakic, 1987; Owen, Downes, Sahakian, Polkey, & Robbins, 1990; Posner & Peterson, 1990; Roland & Friberg, 1985)—processes required to solve items on many common intelligence tests. Yet, despite the "logical" tie-in between certain specific brain regions and intelligence, PET results to date suggest diffuse or "whole-brain" relationships.

Haier et al. (1988), for example, attempted to delineate the brain sites of abstract reasoning as measured by the Raven's Advanced Progressive Matrices (RAPM) test of general intelligence. They measured cortical metabolic rates in participants solving RAPM items ($n = 8$), as well as in separate groups of participants performing visual vigilance ($n = 13$) and target observation ($n = 9$) control tasks. Analyses were carried out on glucose metabolic rate within various brain sectors, as well as on relative glucose metabolic rate (i.e., sector metabolic rate is divided by whole-slice glucose metabolic rate). Several significant differences were found. For example, compared to both the vigilance and target observation groups, the RAPM participants had greater relative glucose metabolic rates in the left occipital lobe at the midventricular slice, and in the right occipital lobe and the right middle temporal lobe (midventricular level). However, no significant

correlations between relative metabolic rates and intelligence (RAPM) scores were found. The only metabolic correlates of RAPM scores were for absolute metabolic rates, and these correlations were not region specific (i.e., they were scattered across brain regions and hemispheres). Similar findings of regionally diffuse metabolism–performance correlations have been reported by Parks et al. (1988) and Boivin et al. (1992), who found that verbal fluency scores were significantly correlated with brain metabolic activity in many cortical areas. This evidence suggests that correlations between problem-solving aptitudes and cortical activity are diffuse rather than localized.

Along with whole-brain (vs. localized) correlations between intelligence and cortical activity, the second major finding from the Haier et al. (1988) study was that the correlations were uniformly negative, indicating that higher metabolic rates were associated with lower intelligence scores. Again, a similar finding was reported by Parks et al. (1988) and Boivin et al. (1992), who found that verbal fluency scores were negatively correlated with brain metabolism, although Boivin et al. also reported some positive correlations. Similarly, Charlot, Tzourio, Zilbovicius, Mazoyer, and Denis (1992)—who measured blood flow rather than glucose utilization—reported that participants with low mental imagery ability tended to show an overall elevation of cortical activity during imagery tasks, whereas participants with good imagery abilities tended to show regional activity decreases. Thus, for most brain regions in the Charlot et al. study, lower imagery performance was associated with elevated cortical activity, a finding in accord with other studies cited. Although positive correlations between cortical activity and task performance have also been found (e.g., Gur et al., 1988), the negative correlations are more prevalent and have now also been shown in studies with retardates (Haier et al., 1995). This finding appears counterintuitive because glucose utilization reflects task engagement and, all things being equal, one would expect participants who are more engaged to perform better.

To summarize, aptitude for complex problem solving seems associated with the whole brain rather than theoretically "appropriate" brain structures, and aptitude level is negatively correlated with brain glucose utilization. One remaining question is: To what extent do these findings depend on the use of standardized cognitive tests in previous experiments? We argue that test format has important implications for the interpretation of brain imaging results.

Mental Effort Implications of Standardized Tests

On standardized intelligence tests, such as RAPM, all participants receive the same items in the same order. Typically, some low-aptitude participants will experience difficulty with most of the test items, whereas many high-aptitude participants will excel. From this, it is quite logical to assume that low-aptitude participants may be required to expend more effort. Ahern and Beatty (1979), for example, found that low-aptitude participants showed greater task-evoked pupill-

ary dilations during problem solving compared to high-aptitude participants. This is in line with the preceding arguments because pupil dilation can be interpreted as a measure of effort or resource expenditure. Note that individual difference in "motivation" are not the issue under consideration. Rather, we are concerned with the effort required of a low-aptitude participant and a high-aptitude participant to successfully perform a complex cognitive task.

In most studies, one can dismiss as irrelevant the fact that task-evoked effort covaries with ability. In PET studies, however, effort (or task difficulty) variations may in and of themselves elicit potentially misleading cortical activity. Elicitation of cortical activity by increased task difficulty has been shown in several studies, including Risberg and Prohovnik (1983) and Posner, Peterson, Fox, and Raichle (1988). At issue is whether individual differences in effort underlie much of the cortical activity measured in PET studies of cognition. An effort hypothesis was proposed by Parks et al. (1988) following their study of cortical metabolism and verbal fluency.

It is conceivable that subjects who found the verbal fluency task to be difficult exerted a greater degree of effort so that they evidenced the greatest amount of activation. Similarly, it is possible that those with greater verbal fluency used more efficient strategies in their cognitive operations so that little effort needed to be expended. (p. 572)

Similar logic can be applied to the results from the study by Haier et al. (1988). For example, suppose that solutions to RAPM problems were inaccessible to low-aptitude participants who attempted to compensate by exerting greater effort. Under these conditions, the metabolic differences revealed by PET could reflect the secondary effort differences rather than the primary "mechanics" of problem solving. If this were the case, then the whole-brain, negative correlations between metabolism and intellectual performance could simply reflect general arousal induced by relatively greater effort expenditure (or task difficulty) for low-aptitude participants. Moreover, if previous metabolism-intelligence correlations were largely due to individual differences in mental effort, then intelligence may have the same indirect link with whole-brain metabolism as it has with other effort measures, such as pupil dilation (or heart rate or skin conductance), and the value of some PET results as grist for intelligence theories would be considerably diminished. To clarify this, consider again the study by Ahern and Beatty (1979), who found that high-aptitude participants showed smaller task-evoked pupillary dilations during problem solving than did low-aptitude participants. Despite this finding, it is unreasonable to think that pupil dilations have a causal role in intelligence. Likewise, if the effort hypothesis for correlations between brain metabolism and intelligence is valid, then it is unparsimonious to use PET findings as a building block for intelligence theories; they would simply be a surrogate for the test score.

This study is designed to answer the following question: What intelligence–metabolism correlations emerge when all participants are working at an equal level of effort/task difficulty? If the brains of high-intelligence participants still showed reduced activation in either whole-brain or regional analyses, then it is possible that “intelligent brains” are simply more efficient, where efficiency is defined as the amount of neural activity required to sustain a given level of cognitive activity. Such results would support “neural efficiency” theories of intelligence (e.g., Haier et al., 1988) in which individual differences depend on constructs, such as neural circuit selection or circuit density. However, if previous metabolism–intelligence correlations were largely due to individual differences in mental effort, then a reinterpretation of previous findings is in order.

METHOD

Overview

One way to determine whether previous metabolism–intelligence correlations were confounded by mental effort is to have participants of high and average intelligence perform individually tailored cognitive tasks where the within-subjects difficulty level is the same for all participants. In other words, a high-aptitude participant and an average-aptitude participant would each solve problems on which they achieve, for example, 75% accuracy. Under the assumption that equal task difficulty evokes equal effort, the continued emergence of PET differences would be evidence that brain activity during problem solving reflects systemic IQ-related differences rather than global differences in mental effort.

In this study, right-handed, male participants were pretested on RAPM in order to select high- and average-RAPM groups. The final sample consisted of 14 high-RAPM participants with scores greater than or equal to 28 (M RAPM score = 30.4, SD = 1.9, range = 28–33) and 14 average-RAPM participants with scores less than or equal to 22 (M RAPM = 18.9, SD = 2.7, range = 14–22). The approximate IQ equivalents are an IQ range of 119 to 131 (M = 123) for the high-RAPM group and 97 to 107 (M = 104) for the average RAPM group. Each group was matched for age (M = 21.6, SD = 2.3 vs. 22.1 and 2.8, respectively: *ns*).

Each of these 28 participants returned for two separate PET sessions. During one session, PET measures were taken from participants following a 32-min tracer uptake period in which they solved “easy” backwards digit-span items; that is, items for which the participant could achieve 90% accuracy. During the second session, PET measures were taken from participants following a 32-min tracer uptake period in which they solved “hard” backwards digit-span items; that is, items for which the participant could achieve 75% accuracy. Session order was counterbalanced. Digits were presented every second on a computer display; a visual prompt signified the end of the string. Participants then responded verbally by repeating the string backwards. A research assistant recorded each

response directly into the computer. Accuracy level was maintained through software that adaptively adjusted item difficulty, after every 10 trials, to participants' performance in order to maintain either 75% or 90% accuracy.

Backwards Digit Span

There are several reasons why backwards digit span was chosen as the experimental task. First, a large number of items can be generated at any difficulty level simply by randomizing single digits (1–9). The latter feature is important because the experimental design required us to customize item sets according to participants' ability levels. Second, backwards digit span involves enough cognitive activity to activate and engage important brain mechanisms and thereby yield activity for PET scanning. Finally, because backwards digit span correlates approximately .50 with IQ (Banken, 1985; Jensen & Figueroa, 1975), participants are performing a task relevant to individual differences in intelligence and theories of intelligence.

PET Scan Procedures

A standard procedure was followed as described in Haier, Siegel, Tang, Abel, and Buchsbaum (1992). Task stimuli began about 30 s before the participant was injected with 18 fluoro-2-deoxyglucose (FDG), a glucose analog tracer used to determine regional brain glucose metabolic rate (GMR) during task performance. Participants then performed backwards digit span items for 32 min while the FDG was taken up by the brain. Following the uptake period, the injected FDG remains metabolically fixed for several hours, with the highest concentrations occurring in the brain areas that were the most metabolically active during task performance. Scanning was done following the FDG uptake and labeling with a NeuroECAT scanner (FWHM resolution about 7.6 mm in plane and 10.9 mm in the Z dimension). Ten axial slices parallel to the canthomeatal (CM) line were obtained at 10 mm intervals. Each participant wore an individually molded thermoplastic mask to locate the CM line and hold the head still during the scanning. This results in head placement errors between the two scans of less than 2 mm, well within the spatial resolution of the scanner. GMR was calculated following Sokolov et al. (1977) and is reported in micromoles glucose per 100 g of brain tissue per minute. Relative GMR is calculated by dividing GMR within a specific brain region by whole-slice GMR. This shows regional GMR relative to each individual's overall brain metabolic rate. Relative GMR corrects for the wide individual differences in whole-brain GMR normally found.

Following a procedure described elsewhere (Haier, Siegel, Maclachlan, 1992), measurements of cortical GMR and relative cortical GMR were obtained in the areas illustrated in Figure 1. Briefly, a computer algorithm identifies the outer 2 cm cortical strip of each of the 10 axial slices. Each strip contains about

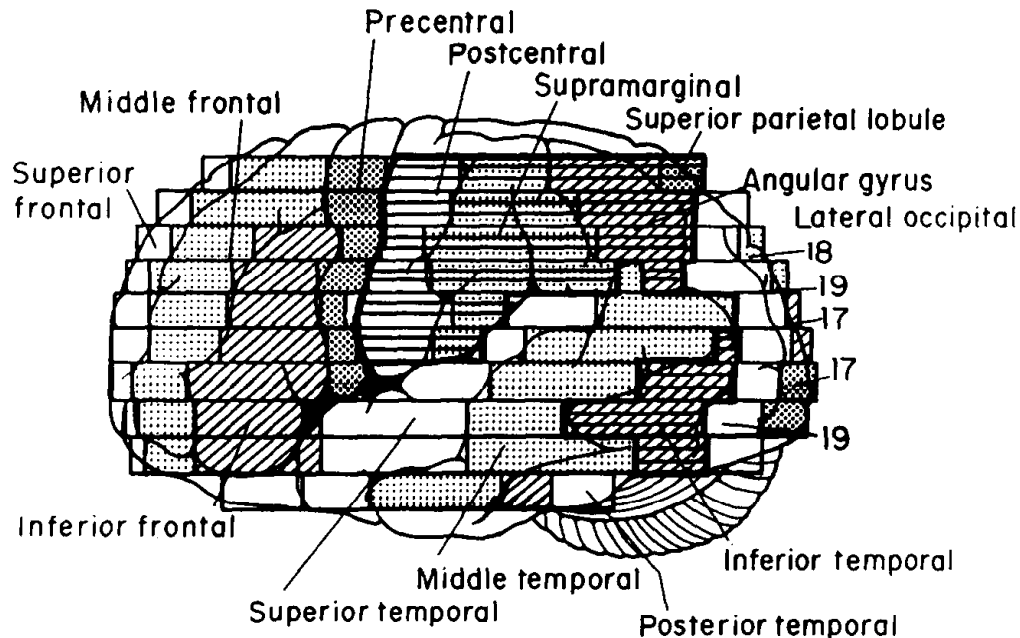


Figure 1. Ten PET slices superimposed on a lateral reconstruction of Matsui and Hirano's (1978) brain-slice atlas. Blocks in each slice indicate region contributing to the combined mean of GMR for that area.

70 to 98 pixel values for GMR in each hemisphere. Based on a digitized brain atlas (Matsui & Hirano, 1978), anatomically defined segments of the cortex are proportionally marked on each PET slice of each participant as a percentage of circumference of the hemisphere. For example, the Number 3 slice has 34 pixels in the atlas from frontal midline to the posterior margin of the frontal lobe. There are another 36 pixels in the parietal lobe and 19 pixels in the occipital lobe for a total of 89 pixels in this slice for one hemisphere. The frontal lobe, therefore, extends from 1 to 38% of the perimeter (34 out of 89). This proportion of PET Slice 3, therefore, is measured as frontal lobe GMR. Four segments of each lobe are defined in this way and shown in Figure 1. Metabolic rates for cortical segments falling across more than one slice are calculated as the weighted average of the number of pixels contributing from each slice.

It should be noted that this method of cortical peel segmentation is a substantial improvement over that used in the original Haier et al. (1988) study because it sums areas across slices and produces lobe segments that are anatomically accurate. The 1988 data, which defined four equal area segments within each lobe using only three independent slices, were reanalyzed using this improved method; again, significant inverse correlations were found between RAPM score and GMR (Haier, 1993). Although inverse correlations were again found throughout the cortex, most of the strongest correlations were in the superior, mid-, and inferior segments of the temporal lobes (bilaterally).

RESULTS

In the average RAPM group, the mean digit spans for the easy (90% correct) and hard (75% correct) conditions were 4.5 ($SD = 0.86$) and 6.1 ($SD = 0.92$), respectively (dependent t test: $p < .00001$). For the high RAPM group, the digit span means were 5.2 ($SD = 1.03$) and 7.0 ($SD 0.89$), respectively ($p < .00001$). Group comparison tests indicated that mean digit lengths for the high-RAPM group exceeded those for the average RAPM group in both the easy, $t(26) = -1.93$, $p < .05$, and hard, $t(26) = -2.63$, $p < .05$, digit-span conditions.

The major comparisons of GMR between groups (high vs. average RAPM) and conditions (easy vs. hard) were made with a factorial analysis of variance (ANOVA) design: Group \times Condition \times Hemisphere \times Lobe \times Segment (structure procedure excluded noninterpretable segment terms). Table 1 shows the significant comparisons. Several results are noteworthy. First, contrary to previous findings, no significant main effect of group on metabolic rates was evident, although participants with higher intelligence (RAPM) scores tended to exhibit higher cortical metabolic rates than participants in the lower intelligence (RAPM) group, $F(1, 26) = 3.56$, $p = .07$. There was not a significant main

TABLE 1
Cortical Metabolic Rates in Each Lobe and Hemisphere for High- and Average-RAPM
Participants Performing Easy and Hard Backwards Digit-Span Tasks

	Average RAPM				High RAPM			
	Easy		Hard		Easy		Hard	
	Left	Right	Left	Right	Left	Right	Left	Right
Whole cortex ^a	32.0	33.2	29.9	30.8	32.9	34.2	34.9	36.3
<i>SD</i>	5.5	5.5	5.0	5.0	7.9	7.9	6.6	6.7
Lobe								
Frontal	34.9	35.4	32.4	32.7	36.1	36.8	38.1	39.0
<i>SD</i>	4.6	4.9	4.3	4.6	7.8	7.8	6.0	6.6
Parietal	32.9	34.2	31.7	32.2	35.3	36.5	36.7	38.1
<i>SD</i>	4.6	4.7	4.9	5.1	8.2	8.6	5.2	5.5
Temporal	27.6	29.2	25.6	26.8	27.6	29.4	29.6	31.7
<i>SD</i>	5.0	5.2	4.0	4.2	5.6	6.2	6.0	6.2
Occipital	32.6	34.1	30.0	31.6	32.8	34.0	34.9	36.5
<i>SD</i>	5.1	5.0	4.0	4.0	7.2	6.5	5.9	6.0

Note. RAPM = Raven's Advanced Progressive Matrices.

^aGroup \times Condition, $F(1, 26) = 7.04$, $p = .013$; Group \times Condition \times Hemisphere; $F(1, 26) = 5.16$, $p = .03$.

effect of condition (easy–hard span difficulty level). Several significant interactions did emerge, however. First, there was a significant Group \times Condition interaction, $F(1, 26) = 7.04, p = .013$. An examination of Table 1 indicates that for the average RAPM group, metabolic rate for every brain region decreased during the harder digit-span condition, whereas for the high-RAPM group, metabolic rates increased during the harder digit-span condition. There was also a significant Group \times Condition \times Hemisphere interaction, $F(1, 26) = 5.16, p = .03$, indicating that for the hard task the right-greater-than-left asymmetry was larger in the high-RAPM group than in the average-RAPM group. For the easy task, the right-greater-than-left asymmetry was the same in the high- and average-ability groups (see Table 1).

The same ANOVA design computed for relative GMR (region of interest divided by the whole-slice GMR) data showed a significant effect for group, $F(1, 26) = 4.72, p = .04$; the high-RAPM group had high relative GMR. The relative GMR Condition \times Group interaction was neither significant ($p = .86$) nor was the Condition \times Hemisphere \times Group interaction ($p = .11$).

DISCUSSION

Several previous studies (e.g., Boivin et al., 1992; Charlot et al., 1992; Haier et al., 1988; Haier, Siegel, Maclachlan, et al., 1992; Haier, Siegel, Tang, et al., 1992; Parks et al., 1988) found that high aptitude is associated with low brain glucose utilization during problem solving. Different results were found in our study (i.e., high intelligence was associated with relatively high cortical metabolic rate during cognitive task performance). The details of the experimental design would seem to provide the most obvious explanation of why past and present results diverge. Whereas previous research involved the use of standardized cognitive tests or tasks in which all participants received identical items, this article utilized items that were tailed to participants' own ability levels, thereby standardizing difficulty. This allowed task-evoked cortical activity to be examined free of individual differences in the effort required to achieve criterion performance. Our goal was to evaluate the hypothesis that high-aptitude participants exhibited lower cortical activity in previous studies simply because they were required to work less hard and not because of other endogenous variables. Although our results indicate that standardizing task difficulty leads to unique results, no clear picture of the effects of mental effort on cortical activity was obtained.

Group differences in problem-solving strategies provide a possible explanation for why the harder backwards digit-span task caused increased activation in high-intelligence participants and decreased activation in average-intelligence participants. The difficulty of interpreting PET data from groups with heterogeneous strategies has been previously noted by several authors, including Parks et al. (1989) and Volkow and Tancredi (1991). Moreover, previous research indi-

cates that there are at least two strategies for backwards digit-span items: internal visual scanning (Black, 1983; Gardner, 1981) and verbalization. Use of a visual strategy may be consistent with the increased right-greater-than-left asymmetry for the high-RAPM group in the hard condition. Previous research suggests, however, that visual backwards digit-span strategies not associated with advanced intellectual or developmental levels. For example, visual strategies are common in school children (Black, 1983; Rudel & Deckla, 1974), indicating that their use may not explain the Group \times Condition \times Hemisphere interaction. Nonetheless, the finding that the high-RAPM group shows a particularly high right hemisphere activation in the hard condition suggests that some strategy effects may be present.

A motivation-based explanation for these results seems implausible. For example, backwards digit-span performance was completely in line with expectations based on RAPM scores and experimental conditions. The mean digit-span lengths for the high-RAPM group was higher than that for the average-RAPM group, a finding consistent with the previous research on group differences in intelligence and backwards digit span (e.g., Banken, 1985; Jensen & Figueroa, 1975). There is no evidence to suggest that one group tried harder than the other; indeed, the experiment was designed to ensure that effort expenditure was equivalent for the two groups.

Despite some unexpected results, there are several noteworthy implications of these findings. First, if low cortical activity implies brain efficiency as suggested by Haier et al. (1988), then high-RAPM individuals are not invariably more neurally efficient. We think it unwise at this point, however, to directly pit these studies against one another and make "either-or" generalizations. For example, a neural efficiency explanation may be applicable to previous studies that drew participants primarily from the middle part of aptitude distribution but not for studies (e.g., this research) that include a large number of high-aptitude participants. It is possible that the relation of cerebral glucose use and cognitive ability is quite sensitive to participant selection, task selection, or both. In that light, our study suggests that PET outcomes partly depend on choice of item-difficulty level for the uptake task, and that tasks which are tailored to subjects' own ability levels provide different results than tasks where all participants receive identical item sets.

Finally, it seems appropriate to address implications for the broader intelligence literature. For example, if brighter participants do indeed exhibit high cortical activity during problem solving, what does this say about the nature of intelligence? Interestingly, our findings may support theories that link individual differences in cognitive ability to the activation capacity of working memory (e.g., Cantor & Engle, 1993; Just & Carpenter, 1992; Woltz, 1988). In discussing language processing, for example, Just and Carpenter (1992) proposed that individuals vary in the amount of activation they have available for computation

and temporary storage in working memory. Similar explanations have been given for performance on general intelligence tests, such as RAPM (Carpenter, Just, & Shell, 1990). If level of cortical activity correlates with the amount of activated information in working memory, and if brighter participants have the capacity to activate more information, then one may anticipate positive correlations between cortical metabolism and intelligence rather than negative correlations. Such relations may have been obscured in the past by differences in relative task difficulty of the type discussed herein. Until further work is done, however, such interpretations will remain speculative.

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