

Intelligence and Changes in Regional Cerebral Glucose Metabolic Rate Following Learning

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Positron emission tomography (PET) studies of brain glucose metabolic rate (GMR) in normal volunteers report inverse correlations between GMR and scores on the Raven's Advanced Progressive Matrices (RAPM) and verbal fluency. A new study in eight normal men reports widespread significant GMR decreases following learning a complex task (the computer game "Tetris"). The purpose of this study is to ascertain the correlations between GMR changes following learning "Tetris" and psychometric intelligence scores (RAPM and WAIS-R) to determine whether high-ability subjects show the largest GMR decreases, as predicted by a brain efficiency hypothesis. This hypothesis is supported with significant correlations between the magnitude of GMR change and intelligence scores in many brain areas that changed with learning. Some implications for the role of attention, memory, and speed of processing are discussed in view of the specific brain areas involved.

A series of investigations in normal subjects indicate an inverse relationship between brain glucose metabolic rate (GMR) and psychometric measures of intelligence. Haier et al. (1988) found negative correlations between scores on the Raven's Advanced Progressive Matrices (RAPM; Raven, Court, & Raven, 1983) and cortical brain GMR determined by positron emission tomography (PET) with flurodeoxyglucose (FDG) as the metabolic tracer. Negative correlations were also found for subcortical and medial cortical areas (Haier, LaFalase, Katz, Nuechterlein, & Buchsbaum, 1992). Parks et al. (1988), similarly using PET in normals, found negative correlations between verbal fluency scores and cortical GMRs. Berent et al. (1988) also reported a PET study including normal controls who showed negative correlations between WAIS memory scores and brain glucose use. These studies have been interpreted as evidence for a brain efficiency model of intelligence: Intelligence is not a function of how hard the

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brain works but rather how efficiently it works (see Haier, in press; Parks et al., 1989). This efficiency may derive from the disuse of many brain areas irrelevant for good task performance as well as the more focused use of specific task-relevant areas.

Learning may result in decreased brain metabolic rates. Diamond (1988) reported an audioradiographic study of rats raised in impoverished or enriched environments. The rats raised in the enriched environment had lower brain GMRs, consistent with the PET data in humans.

Recently, we studied normal volunteers ($N = 8$) with PET before and after they practiced a complex task, the computer game "Tetris" (Haier, Siegel, et al., 1992). Each subject was scanned with PET after receiving FDG during the first time they ever had played the game, a test of visuospatial ability and motor coordination. They practiced up to 5 days a week for 1 to 2 months and then were scanned again playing the game. On average, game performance increased sevenfold after practice; cortical and subcortical GMRs decreased significantly (these areas are listed in Tables 4–6, pp. 422–424). This was interpreted as consistent with efficiency: better performance after practice but lower metabolic rate. Some areas showed significant metabolic increases (relative to whole-slice or whole-brain GMR) after practice (see Table 6). These were Area 18 in the right occipital cortex, the right precuneus, the right hippocampus, and the left cingulate cortex. These few areas may be especially salient for good task performance. The widespread decreases, however, indicate that learning may include not using brain areas irrelevant for optimal task performance.

In a large lesion study of learning and problem solving in rats, Thompson, Crinella, and Yu (1990) looked for brain areas implicated in biological and psychometric intelligence. Biological intelligence was defined as the underlying ability common to performance on all the tasks. Factor analyses of brain lesion sites across a variety of tasks revealed eight brain areas necessary for adequate performance on all the tasks. These eight areas were identified with biological intelligence. Psychometric intelligence was defined by areas that loaded on the first factor extracted from a variety of learning tasks performed after lesions at different sites. Six brain areas were implicated in psychometric intelligence (only one of which overlapped with the biological g areas). Haier, Siegel, Crinella, and Buchsbaum (in press) compared the results of Thompson et al. to their own human PET studies. Of the 13 areas identified as sites of biological and psychometric intelligence in rats, four areas were too small for the spatial resolution of PET (posterolateral hypothalamus, substantia nigra, ventral tegmental area, and the median raphe). Of the remaining nine areas, five also showed significant effects in the human PET studies of intelligence and learning (caudate putamen, globus pallidus, superior colliculus, hippocampus, posterior pons).

Reviewing the empirical relationship between learning and intelligence, Jensen (1989) concluded that "Whatever general factor is found among the parameters of the learning curves derived from a number of diverse learning

tasks is essentially the same general factor, *g*, that is found among any large number of diverse tests of mental abilities." (p. 51). Moreover, Jensen pointed out that the same information-processing components are implicated in both learning and intelligence with the variable of speed being the most important for individual differences.

Kyllonen and Christal (1990) reported that general reasoning ability and general working memory are highly correlated factors. They concluded that individual differences in working memory (rather than speed of processing) may be the central components underlying individual differences in reasoning. They cite this as consistent with Ackerman's (1987, 1988) conceptualization that attentional resources underlie general reasoning ability. According to this view, general ability predicts performance during early learning where working memory and attention resources are most critical; the influence of general ability on learning diminishes with practice.

One technique for identifying the brain areas salient for the underlying information-processing components of learning and intelligence in humans is the use of PET to assess cerebral GMR. PET studies can determine whether GMR is related to general reasoning ability and to learning, and can demonstrate any overlap in brain areas used for both. Brain areas thought to be implicated in working memory, attention allocation, and speed of processing can be studied with PET to determine relationships with measures of intelligence and learning. For example, the widespread inverse correlations between GMR and RAPM scores, and the similar findings with verbal fluency, suggest that *g* may not be localized to a large degree. This could be consistent with a speed of processing view because speed of neural transmission would most likely be a characteristic of the brain as a whole rather than of only specific sites. However, these correlations were not entirely uniform; areas associated with attention (the cingulate gyrus) and working memory (especially, the superior frontal cortex, the temporal lobe, and the hippocampus; Haier, LaFalase, et al., 1992) had the highest correlations.

The purpose of this article is to examine the relationship between intelligence scores and metabolic changes in the brain areas where GMR changes after learning the "Tetris" task to determine whether high-ability subjects show the largest decreases in metabolic rate, consistent with an efficiency theory. The overlap in brain areas between the learning results and previous results relating GMR to psychometric intelligence scores are also examined for evidence of the psychometric views that learning and intelligence share the same *g*, and that GMR in memory and/or attention brain areas is related to ability measures.

METHOD

Subjects

The same 8 normal right-handed male volunteers from the "Tetris" learning study (Haier, Siegel, et al., 1992) participated. They ranged in age from 19 to 32

years old ($M \pm SD = 24 \pm 4$). All were recruited by advertisements on the University of California, Irvine campus, and were screened and found to be without any history of psychiatric, neurological, or major medical disorder.

Learning Task

During the 35-min FDG uptake period for both scans, the subjects played the "Tetris" game, which requires the subject, using a computer keyboard, to rotate and move objects, consisting of four square blocks in various configurations (see Figure 1) in such a fashion as to try to create a solid row of blocks. The objects move downward from the top of the screen, and as the game progresses, if performance is good, speed increases. When a solid row is complete, the row disappears, and all the blocks above it drop down to replace the completed row. The score is visible on the screen at all times and equals the number of lines of blocks that are created filling the entire horizontal aspect of the computer screen. Subjects were instructed to try to get the highest score possible. All subjects used the right hand during task performance. The number of button presses and the amount of hand movement were not recorded.

Each of the subjects was scanned with FDG PET on two occasions 4 to 8 weeks apart ($M \pm SD = 38 \pm 8$ days; the variance due to scheduling logistics).

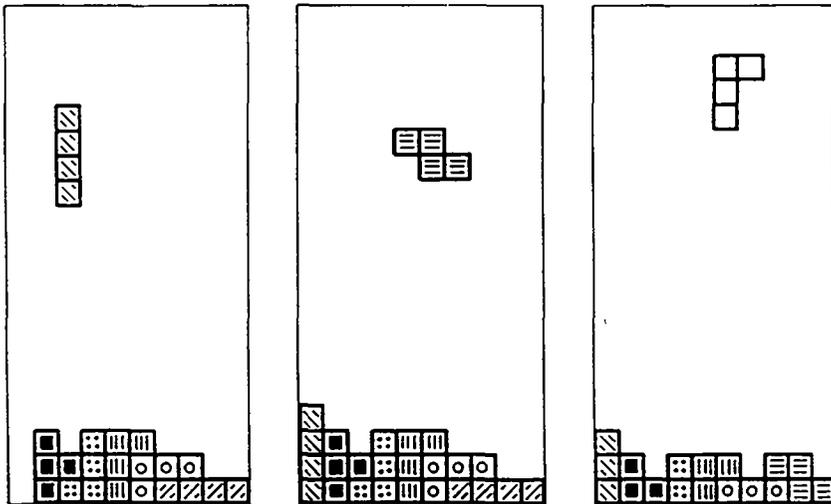


Figure 1. The "Tetris" game in progress from left to right. Subjects attempt to manipulate configurations of four square blocks falling from the top of the screen to produce solid rows of blocks. Once a solid row of blocks is completed, it disappears and is replaced by the row above it. Symbol markings show individual shapes that have already been placed. Note the bottom row of the middle panel is complete; in the panel on the right it has disappeared (1 point is scored) and the rows above moved down.

On the first occasion (naive scan), each subject was injected with FDG after a maximum of 3 min of practice playing the video game, "Tetris," and on the second occasion (practiced scan), after "Tetris" practice sessions of 30 to 45 min in duration, five times/week (maximum). For the group, the mean number of practice sessions was 18.8 ($SD = 5.4$). During the naive scan, the mean number of games played during the uptake period was 7.0 ($SD = 1.8$); during the practiced scan, the mean was 3.4 ($SD = .74$).

Intelligence Testing

Between the first and second scans, each subject completed the RAPM (Raven et al., 1983) during a timed 40-min period. The Wechsler Adult Intelligence Scale-Revised (WAIS-R; Wechsler, 1981) was administered to each subject according to standard procedures by the same tester within 1 week of the RAPM.

PET Procedure, Brain Region-of-Interest Location, and Glucose Quantification

PET scanning technique was identical to that in previous studies, detailed in Haier et al. (1988).

After the 35-min FDG uptake period, subjects were moved to the scanner and 9 or 10 slice planes were obtained parallel to the canthomeatal line at 10-mm increments. Scans were transformed to GMR as elsewhere (Buchsbbaum et al., 1990).

Cortical regions of interest (16 in each hemisphere) were measured using the cortical peel technique (Buchsbbaum et al., 1989) and subcortical structures were located using stereotaxic coordinates derived from a standard neuroanatomical atlas (Matsui & Hirano, 1978). Where slice levels are indicated, they are expressed as percentage of head height, greater percentages of head height indicating higher (more dorsal) regions.

In addition to the 63 bilateral (126 total) regions of interest included in the standard template used in previous studies, in order to locate regions of interest in the pons and cerebellum, we surveyed a set of magnetic resonance images (MRIs) of 10 normal subjects to construct a statistical-stereotaxic outline. The structures were analyzed at the 14% Matsui and Hirano (1978) atlas level, but the anterior-posterior and left-right brain dimensions were taken from a higher slice (28% level) to avoid potential variability in the frontal lobe edges on the PET scan from affecting the position of the template.

Because of the large intersubject variability of whole-brain GMR, we calculated a ratio of regional GMR to whole-brain mean GMR (for surface cortical structures) or to whole-scan-slice mean GMR (for subcortical structures) for each region. This ratio, termed relative GMR, controls for this source of variance. Within-individual comparisons between the naive and practiced conditions for the "Tetris" subjects are reported for both GMR and relative GMR.

Statistics

Correlations between GMR (naive, practiced, and change between practice minus naive) and intelligence test scores were calculated partialling out the number of practice sessions ($M = 18.75$, $SD = 5.4$) for all correlations using practiced or change (practice minus naive) variables.

Bonferroni corrections for multiple comparisons were applied post hoc in any tests of significance where $p < .05$. We are also reporting any $p < .05$ differences uncorrected for multiple tests, because the number of comparisons done in an exploratory PET study is necessarily quite large, making it extremely difficult for any one comparison to reach statistical significance by Bonferroni criteria. Those regions reaching significance prior to Bonferroni correction may be useful for hypothesis generation and comparison to other studies. But, given the large number of comparisons, a $p < .05$ level of significance must be interpreted with caution.

RESULTS

Haier, Siegel, et al. (1992) reported that all 8 subjects showed markedly improved "Tetris" scores from the first to the second scan. The average plus or minus standard deviation number of lines completed during the first scan was 11.2 ± 6.8 with a range of 2.4 to 24.0, and during the second scan, 80.7 ± 20.7 with a range of 52.8 to 110.7.

Table 1 shows the means and standard deviations for age and intelligence scores along with ranges for the sample. Table 2 shows the intercorrelations among the intelligence measures and "Tetris" scores for the naive and practiced conditions as well as for the change after learning (naive minus practice). None of these correlations are statistically significant in this sample of 8 except for the .79 between naive score and practiced score. The same results for the whole matrix were apparent for Kendall and Spearman rank-order correlations.

It should be noted that 1 subject had a 24-point disparity between Verbal IQ

TABLE 1
Age, Intelligence Scores, and "Tetris" Change Score Means
and Standard Deviations for All Subjects

	<i>M(SD)</i>	Range
Age	24.0 (4.0)	19-32
RAPM	26.6 (4.7)	21-35
VIQ	109.1 (14.4)	87-130
PIQ	119.3 (16.3)	106-147
Full-Scale IQ	114.9 (13.9)	101-137
Change in "Tetris" score*	69.5 (20.3)	92.5-38.5

Note. $N = 8$.

*Practiced minus naive.

TABLE 2
Intercorrelations Among Intelligence Scores and "Tetris" Performance Scores

	RAPM	VIQ	PIQ	Naive Tetris	Practiced Tetris	Practiced Minus Naive
RAPM	1	.48 ^a	.59	.36	.41	.20
VIQ		1	.22 ^a	.05	.27	.37
PIQ			1	.52	.19	-.36
Naive				1	.79	.00
Practiced					1	.61

Note. $N = 8$; $r > .707$, $p < .05$, two-tailed. The highest score during the first day of testing and the highest score ever during practice were used.

^aOne subject has a 24-point difference between VIQ and PIQ. Excluding this case increased the VIQ-PIQ correlation to .53 and the RAPM-VIQ correlation to .95; none of the other correlations changed appreciably.

(VIQ) and Performance IQ (PIQ). Deleting this subject increases the VIQ-PIQ correlation from .22 to .53 and the RAPM-VIQ correlation increases from .48 to .95. Nonetheless, this case is not judged to be a statistical outlier (a 24-point disparity is found in about 18% of normals) so this case is not deleted post hoc for the other analyses.

Table 3 (p. 422) shows the correlations or partial correlations between whole-brain GMR (naive, practiced, and change) and intelligence scores. Although only the RAPM and two WAIS-R subtests are significant, almost all of these correlations are inverse; that is, the highest intelligence scores are associated with the largest decreases in GMR. Correlations tend to be higher in the naive rather than the practiced condition.

Table 4 (p. 422) lists the specific cortical brain areas that showed significant decreases in GMR between the naive and practiced scans, that is, areas that changed with learning (Haier, Siegel, et al., 1992). The correlations between change in GMR in these areas (Scan 2 minus Scan 1) and scores on the intelligence tests, partialling out number of practice sessions, are shown. All are negative but only the RAPM-GMR correlations are significant. The subcortical and medial cortical areas show similar results in Table 5 (p. 423). Again, only those brain areas where there was a significant difference after learning are listed in Table 5 (all significant differences were decreases in GMR after practice). All but one of the correlations between change in GMR and intelligence scores (partialling out sessions of practice) are negative. The most significant correlations are for RAPM-GMR and PIQ-GMR.

Table 6 (p. 424) shows the same partial correlation analyses for relative GMR data (GMR within an area divided by whole-slice GMR). Note the two significant positive correlations are in areas (right precuneus, left cingulate) where relative GMR increased with practice. The areas showing increases in relative GMR with practice could be areas especially salient for good task performance.

TABLE 3
Partial Correlations (Controlling for Days of Practice)
Between Intelligence Scores and Whole-Brain GMR in Naive
and Practiced Conditions and Change in GMR After Learning
(Practiced Minus Naive)

	Naive	Practiced	Change
RAPM	.77**	.09	-.68*
WAIS-R			
VIQ	.11	-.49	-.38
PIQ	.59	.25	-.40
FSIQ	.35	-.20	-.43
Information	-.18	-.45	-.09
Digit Span	.23	-.46	-.48
Vocabulary	-.31	-.36	.08
Arithmetic	.31	-.24	-.41
Comprehension	.41	-.47	-.63*
Similarities	-.12	-.36	-.09
Picture Completion	.55	.13	-.42
Picture Arrangement	.64*	.46	-.40
Block Design	.15	.11	-.09
Object Assembly	.61	.15	-.47
Digit Symbol	.33	.11	-.24

Note. $N = 8$.

* $p < .05$, one-tailed. ** $p < .025$, one-tailed.

TABLE 4
Cortical Areas With a Significant Decrease
in GMR After Learning and the Partial
Correlations Between the Change in GMR
(Practiced Minus Naive "Tetris" Conditions)
and Intelligence Scores
(Controlling for Days of Practice)

Cortical Area	RAPM	VIQ	PIQ
l. precentral	-.68	-.36	-.46
r. precentral	-.67	-.38	-.41
l. post. central	-.64	-.32	-.40
r. post. central	-.72*	-.32	-.51
l. angular gyrus	-.69	-.33	-.48
r. angular gyrus	-.72*	-.41	-.52
l. post. temp.	-.65	-.45	-.26
l. area 17	-.67	-.28	-.35
r. area 17	-.63	-.32	-.29

Note. $N = 8$.

* $p < .05$, two-tailed.

TABLE 5
Subcortical and Medial Cortical Regions Showing Significant Decreases
in GMR After Learning and the Partial Correlations
Between GMR Change (Practice Minus Naive "Tetris" Conditions)
and Intelligence Scores (Controlling for Days of Practice)

Region	% ^a	RAPM	VIQ	PIQ
r. paracentral	80	-.58	-.13	-.79*
l. superior frontal	74	-.81*	-.18	-.67
r. superior frontal	74	-.87***	-.23	-.63
l. paracentral	74	-.88***	-.34	-.45
r. paracentral	74	-.71*	-.01	-.65
l. precuneus	74	-.70	-.25	-.58
r. precuneus	74	-.77*	-.31	-.46
l. paracentral	68	-.74*	-.36	-.35
l. superior frontal	61	-.58	-.38	-.11
r. anterior cingulate	54	-.62	-.38	-.52
l. posterior cingulate	54	-.97***	-.33	-.75*
r. posterior cingulate	54	-.82*	-.39	-.64
l. precuneus	54	-.62	-.31	-.12
r. precuneus	54	-.63	-.23	-.41
l. midcorpus coll.	47	-.44	-.12	.05
l. caudate	41	-.27	-.22	-.20
l. anterior cingulate	34	-.81**	-.55	-.43
l. frontal white	34	-.52	-.57	-.29
l. putamen	34	-.53	-.40	-.28
r. putamen	34	-.74*	-.64	-.46
r. globus pallidus	34	-.59	-.08	-.17
l. superior coll.	34	-.53	-.45	-.52
l. fusiform	34	-.58	-.50	-.55
r. fusiform	34	-.66	-.11	-.48
l. anterior cingulate	28	-.80**	-.56	-.41
l. putamen	28	-.37	-.25	.05
r. inferior coll.	28	-.49	-.31	-.12
l. orbital gyrus	21	-.68	-.37	-.79*
l. uncus	21	-.41	-.03	-.53
r. posterior pons	14	-.35	-.30	-.29
r. cerebellar vermis	14	-.12	-.62	-.09
l. mid cerebel. cortex	14	-.16	-.57	.04
l. ant. cerebel. cortex	14	-.33	-.22	.12
r. post. cerebel. cortex	14	-.27	-.78*	-.16

Note. $N = 8$.

^aIndicates percent of head height from CM line of the slice in which the structure is measured according to Matsui and Hirano (1978).

* $p < .05$, two-tailed. ** $p < .02$, two-tailed. *** $p < .01$, two-tailed.

TABLE 6
Cortical, Subcortical, and Medial Cortical Regions
Showing Significant Differences in Relative GMR After Learning
and the Partial Correlations Between Relative GMR Change
(Practiced Minus Naive "Tetris" Conditions) and Intelligence Scores
(Controlling for Days of Practice)

Cortical Regions	% ^c	RAPM	VIQ	PIQ
l. post. central ^a		-.13	-.32	-.32
l. angular gyrus ^a		-.44	-.07	-.79*
r. area 18 ^b		.54	.32	.54
Sub- and Medial Cortical Regions				
r. precuneus ^b	74	.37	.77*	.54
l. superior frontal ^a	61	-.32	-.74*	.05
l. cingulate ^b	61	-.03	.79*	.00
r. posterior cingulate ^a	54	-.54	-.13	-.72*
l. anterior cingulate ^a	28	-.78	-.80*	-.43
r. hippocampus ^b	28	-.55	.27	-.84**
l. mid cerebel. cortex ^a	14	.15	-.54	-.04
l. ant. cerebel. cortex ^a	14	-.56	-.06	-.75*
r. post. cerebel. cortex ^a	14	-.08	-.74*	-.10

Note. $N = 8$.

^aDecreased relative GMR after learning. ^bIncreased relative GMR after learning. ^cIndicates percent of head height from CM line of the slice in which the structure is measured according to Matsui and Hirano (1978).

* $p < .05$, two-tailed. ** $p < .01$, two-tailed.

The decreases in relative GMR shown in some areas may reflect the subject learning which brain areas not to use for good performance.

DISCUSSION

The subjects with the highest scores on the RAPM showed the largest GMR decreases after practice in overall brain GMR and in many specific brain areas where there was a "Tetris" learning effect. This may reflect greater increases in automatic processing in the high-ability subjects after practice, which would result in fewer extraneous brain areas being used for the task, and thus, a greater decrease in GMR. We see this as consistent with the efficiency hypothesis. Moreover, the highest correlations were found for naive rather than practiced GMR and intelligence scores. This supports the view that g is more related to initial, instead of practiced, task performance.

The specific brain areas showing significant correlations between change in GMR and RAPM are: bilaterally, superior frontal cortex, paracentral gyrus (74%), posterior cingulate; the right posterior central gyrus, the right precuneus, the right anterior cingulate (54%), the right putamen; and on the left, the paracentral gyrus (68%) and the anterior cingulate (28%). These areas do not overlap

with the rat lesion results of Thompson et al. (1990) except for the putamen and cingulate. Interestingly, these cingulate and putamen areas also showed significant correlations between RAPM performance and GMR in Haier, LaFalase, et al. (1992). This overlap of brain areas implicated in learning and intelligence suggests some support for the view that both learning and intelligence share the same *g*. The findings in the superior frontal cortex and the cingulate gyrus are consistent with views that attention may play an important role in *g*. Evidence for the role of working memory is less apparent. Only one region of interest in the hippocampus, the primary memory area, changed after practice of "Tetris," and the change was an increase in relative GMR. A significant inverse correlation between relative GMR and PIQ was found in this area (see Table 6); this is difficult to explain. "Tetris" does require attention and speed, but it may not be an adequate probe of working memory. Moreover, the widespread findings using GMR compared to fewer results using relative GMR suggest that *g* is not well localized.

Because the sample size is small, correlations are not stable so the results are interpreted cautiously, especially because PET measures the entire brain and provides data for a large number of comparisons. The overall pattern of inverse correlations between decrease in GMR following learning and intelligence scores suggests that high-ability subjects may have the most gains in automatic processing, especially in putamen and cingulate areas where the correlations are the highest. The lack of findings with WAIS-R VIQ scores may reflect the nature of the learning task.

This study begins to identify the brain sites in humans where individual differences in function are related to intelligence and learning. Future studies incorporating elementary cognitive tasks and PET across a range of intelligence could be especially rich for advancing our understanding of brain-learning-intelligence relationships.

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