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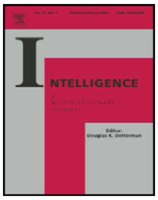

# Exploring possible neural mechanisms of intelligence differences using processing speed and working memory tasks: An fMRI study

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ABSTRACT

To explore the possible neural foundations of individual differences in intelligence test scores, we examined the associations between Raven's Matrices scores and two tasks that were administered in a functional magnetic resonance imaging (fMRI) setting. The two tasks were an *n*-back working memory ($N$=37) task and inspection time ($N$=47). The subjects were members of the Aberdeen Birth Cohort 1936, aged in their mid–late 60s when tested for this study. Performance on both tasks was correlated significantly with scores on Raven's Matrices. In the inspection time task there were regions with significant correlations between the neural activity (BOLD response) and performance but not between BOLD response and scores on Raven's Matrices. In the working memory task there were no significant correlations between BOLD response and either performance or scores on Raven's Matrices. Moreover, there was almost no mediation of the Raven's Matrices versus n-back and inspection time scores correlations by the respective BOLD response. These findings partially replicate important aspects of a prominent report in this field [Gray, J.R., Chabris, C.F., & Braver, T.S. (2003). Neural mechanisms of general fluid intelligence. Nature Neuroscience, 6, 316–322.], but have also extended the those finding into both a unique population and a novel functional task.

## 1. Introduction

Attempts to understand the causes of individual differences in cognitive abilities (intelligence) have involved a large range of explanatory variables from the sociological to the biological. Would-be reductionistic biological research on intelligence differences is guided and limited by the tools that are available to examine the human brain's structures and functioning. For the last two decades or so, apart from genetic studies, the principal toolkit for investigating the biological basis of intelligence differences has been the various types of brain imaging, and especially structural and functional magnetic resonance imaging (MRI).

Structural MRI-based studies of human intelligence differences have made considerable progress. In vivo measures of regional and overall brain size are modestly correlated with intelligence test scores, including the general cognitive factor (*g*) (McDaniel, 2005; MacLullich, Ferguson, Deary, Seckl, Starr, & Wardlaw, 2002). Studies using voxel-based morphometry show that correlations between *g* and grey matter volume are found distributed throughout the brain rather than located solely in the frontal regions (Colom, Jung, & Haier, 2006). Genetic covariance studies indicate that there are some shared additive genetic contributions to both brain size and intelligence differences (Thompson et al., 2001; Posthuma, De Geus, Baare, Hulshoff Pol, Kahn, & Boomsma,

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2002). More detailed work has revealed regions of grey (especially frontal, occipital, and parahippocampal) and white (especially superior occipitofrontal fascicle) matter in which the density is genetically correlated with IQ-type scores (Hulshoff Pol et al., 2006). Work on both grey matter (e.g. cortical thickness, Shaw et al., 2006) and white matter (e.g. fractional anisotropy using diffusion tensor imaging, Deary et al., 2006) finds associations with intelligence differences.

The present study utilises a functional MRI (fMRI) design to explore possible foundations of individual differences in intelligence test scores. Structural and functional MRI studies in intelligence are not entirely independent. For example, Jung and Haier (2007) collated findings from these and other brain imaging modalities to formulate their ‘parieto-frontal integration (P-FIT) theory of intelligence’. Among functional imaging studies there have been different designs. For example, using positron emission tomography, some have found that certain frontal brain regions that are more metabolically active in high versus low *g*-loaded tasks (Duncan et al., 2000). Some have examined the amount of neural activation—using the blood oxygen level dependent (BOLD) response in fMRI—in certain brain regions in response to low and high *g* tasks and compared these in average and high ability subjects (Lee et al., 2006). The latter study implicated that differences in functioning of the prefrontal cortex, anterior cingulate cortex, and posterior parietal cortex were relevant to intelligence differences.

The study which provided the model for the present investigation was conducted by Gray, Chabris, and Braver (2003). Their elegant design comprised three quantitative measures: first, a behavioural measure of fluid intelligence (Raven's Advanced Progressive Matrices); second, a behavioural measure of a task (correct detection of lures in an n-back working memory task) that was used in an fMRI setting; and, third, a measure of the relative neural activity (BOLD signal) from a pre-specified brain region in response to the n-back lure detection task. They hypothesised that Raven scores would correlate significantly with both the ability to correctly detect lures, and with the BOLD signal in, for example, the prefrontal cortex. Both correlations were significant. However, the key finding was that the correlation between Raven and lure-detection accuracy was attenuated by up to about 90% when the correct lure detection-based neural activity was partialled out. Of course, this result is open to a variety of interpretations, but a tenable account is that individual differences in the function of the prefrontal (and some other) region(s) are one biological foundation of intelligence differences.

The Gray et al. (2003) study design was extended, using two tasks. The starting point for the design was to choose tasks that: assessed an important mental capability in which there were individual differences; could be used in an fMRI setting; came with prior published data concerning the specific brain regions likely to be activated when subjects performed them; were known to be associated with intelligence differences. One was n-back, which assesses working memory, and is widely used in fMRI settings, including Gray et al. (2003). The second task was inspection time—an assessment of the early stages of visual information processing—which correlates significantly with intelligence (Grudnik & Kranzler, 2001) and has a known functional anatomy (Deary, Simonotto et al., 2004; Waiter et al., 2008). The aims were: to describe the correlations between intelligence test scores and performance on the two tasks; to describe the correlation between the BOLD response to each task and intelligence test scores, and the BOLD response to each task with its relevant behavioural performance score; and, finally, to test whether adjusting for the respective BOLD response heavily attenuated the correlation between intelligence test scores and the behavioural performance scores on the fMRI tasks.

We examined individuals within a uniquely valuable cohort whose cognitive ability was assessed at age 11 and then again in their middle-to-late 60s: the Aberdeen Birth Cohort 1936 (e.g. Deary, Whiteman, Starr, Whalley, & Fox, 2004; Whalley et al., 2005). Briefly, the design of the experiment was as follows. We examined a group of non-demented people in their seventh decade who, at age 11, had relatively similar general cognitive ability. We examined whether, in older people with relatively successful cognitive ageing, their BOLD activation patterns, while they performed an inspection time task and a working memory task, were responsible for the correlation seen between intelligence at age 70 and accuracy on the behavioural tasks performed.

## 2. Materials and methods

### 2.1. Subjects

The local medical ethics committee granted permission for the study and all participants gave informed, signed consent. The functional anatomy of the inspection time task has been reported elsewhere (Waiter et al., 2008). Results from the working memory task are currently under review. Their recruitment and selection are summarized here. Participants were recruited to the study from the surviving participants of the Scottish Mental Survey 1947 (SMS1947; Scottish Council for Research in Education [SCRE], 1949). This was a Scotland wide study including almost all schoolchildren born in 1936 and attending school on June 4th 1947, i.e. aged 11 ($N=70{,}805$). In the SMS1947 they sat a version of the Moray House Test No. 12 (MHT), which is a 45-minute, group-administered general mental test with a preponderance of verbal reasoning items. Five hundred and eight Aberdeen residents who had taken part in the SMS1947 were recruited to the Aberdeen Birth Cohort 1936 (ABC1936).

### 2.2. Intelligence testing

Three waves of testing took place every 2 years from around 2000, when cohort members were approximately 64, 66, and 68 years old, respectively. Participants undertook a number of medical and cognitive assessments (Deary, Whiteman et al., 2004). The current study was conducted as part of the third wave of assessment. The cognitive assessment on each of these occasions included a test of non-verbal reasoning (Raven's Standard Progressive Matrices test [RPM]; Raven, Court, & Raven, 1977).). The RPM is known to load highly on the general cognitive ability factor, making it a good indicator of general mental ability (Carroll, 1993). From the ABC1936 sample, 79 individuals (aged 69/70, 28 female) with an age 11 IQ (calculated from MHT scores) between 85 and 115 were invited to do the Inspection Time task; i.e., at age 11 they were within 1 SD of the sample mean. From this sub-group 52 also performed the working memory task. RPM scores obtained in old age correlate with MHT scores from age 11 (Deary, Whiteman et al., 2004), and in the present ABC1936 sample, the two-tailed Pearson correlation between MHT at age 11 years and RPM at age about 68 years (wave 3, $N=294$) was .56 ($p<.001$).

### 2.3. Functional imaging data acquisition and analysis

#### 2.3.1. Inspection time

The inspection time task employed was replicated as closely as possible from those described in Deary, Simonotto et al. (2004) and detailed in Waiter et al. (2008). The participants were required to make a simple visual discrimination, i.e. they were asked to indicate which of two parallel, vertical lines of markedly different lengths, was longer (Fig. 1).

Participants who volunteered for the present functional imaging study had previously undertaken the inspection time task as part of their cognitive testing and immediately before brain imaging the participants practiced the inspection time task again to make sure they were completely familiar with the task demands. Two inspection time sessions took place in the MRI scanner (imaging inspection time test sessions 1 and 2). In the imaging inspection time sessions, twenty trials were presented at each of eight durations: 6, 12, 25, 37, 50, 75, 100, and 150. Paradigms were programmed in Presentation (Neurobehavioral Systems Inc., CA) with instructions and stimuli being presented visually on the computer monitor and viewed via the mirror on the head coil. The eye-to-screen distance was about 5 m. Visual acuity was assessed immediately before scanning and corrected with MR compatible lenses as necessary. Participants were provided with pushbutton units to allow their responses to be logged by the software. Participants indicated the position of the longer line by pressing a key with the left index finger (for 'left') or a key with the right index finger (for 'right'). The same optimal ISI sequence was used for all sessions. The same random sequence of stimulus durations was presented to all subjects.

#### 2.3.2. n-back

Versions of the *n*-back working memory task were created, as blocked design, to manipulate load. There were two conditions—high-load, and low-load. The verbal stimuli consisted 18 English letters (B, C, D, F, G, H, J, K, M, N, P, Q, R, S, T, V, X, and Z). For the *n*-back task, items were presented every 3 s. In the low-load version of the *n*-back (0-back) task, participants were asked to press a button with their right index finger if a specific target appeared. The target was the letter 'X'. If any other item besides the target appeared on the screen, participants were asked to press a button with their left index finger. In the high-load version of the *n*-back task (2-back), participants determined whether an item was the same as one at two trials back. If the item was the same, participants pressed the button under their right index finger. Participants pressed the button under their left index finger if the item was different from the one presented two trials back. Participants were encouraged to rehearse the letters presented in the last two trials while continuously updating their list as each new letter appeared. Items were visible for 500 ms and were followed by a fixation cross that appeared for 2500 ms. Twelve items were presented in each block of trials, so that each block lasted 36 s. The probability of an item being a target was 33% (i.e. 4 targets per block), whereas new distracters and repeated distracters appeared 47% and 20% of the time, respectively. Each participant in the scanner performed one run of the *n*-back task. A run was composed of four epochs—containing a combination of the high-load condition, low-load condition and one fixation control block. For the fixation block, participants were instructed to fixate on the cross presented in the center of the screen. Load was counterbalanced across participants so that half began each run with the low-load conditions and half began with the high-load conditions. The fixation block was always the third block in the run. Thus, a run for the *n*-back task might be (1) 2-back, (2) 0-back, (3) Fixation, or (1) 0-back, or (2) 2-back (3) Fixation. All participants received one training block on the working memory task before being scanned.

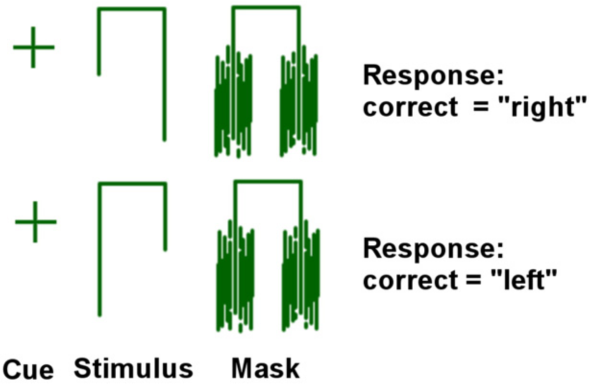

**Fig. 1.** The cue, stimuli, and backward mask for the inspection time task. See text for procedure.

#### 2.3.3. Brain imaging

Scanning was performed on a 1.5-T GE Signa NVi scanner (General Electric Healthcare, Milwaukee, WI), using the standard head coil. Participants began and ended the fMRI imaging session with inspection time tests. Between the two inspection time tests, the working memory task was carried out. Following the second inspection time task a T1-weighted structural scan was acquired. Contiguous T2*-weighted gradient-echo echo-planar images (EPI) were acquired in the axial orientation with TR/TE of 2500/40 ms, matrix 64×64, field of view of 24 cm$^2$, thickness of 5 mm, 30 slices per volume. In total, 292 volumes per inspection time fMRI test, and 222 volumes for the working memory task, were collected, of which the first 4 volumes of each were discarded. The total scanning time was 12 min and 10 s for each inspection time fMRI test and 9 min 15 s for the working memory task.

Post-processing was performed off-line on a workstation using SPM2 (http://www.fil.ion.ucl.ac.uk/spm. Firstly correction for the acquisition delay between slices was applied. Intrasubject registration was then performed by aligning all volumes of each session to the first volume of that session using a 6 parameter rigid body linear registration algorithm. The analysis then proceeded along two different routes. The first, to determine the group response to the stimulus,

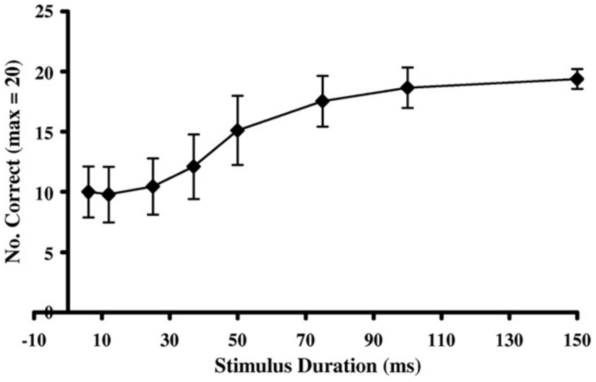

**Fig. 2.** Relation between accuracy and stimulus duration in the inspection time task.

included a normalisation step to the standard SPM2 EPI template by intersubject registration using a 12 parameter affine transformation, warping each participant's images into a standard template with a voxel size of 2×2×2 mm. The second path, to determine the individual variability in response to the stimulus, proceeded directly from intrasubject registration to Gaussian smoothing, at 6 mm FWHM.

Data analysis for the first route was performed in a two-stage mixed-effects analysis (equivalent to a random effects analysis) to determine group response. Data analysis for the second route was a simple fixed effects analysis to determine individual response to the tasks. For the Inspection Time tasks event-related functional activity was modeled using one regressor for trials with correct responses and one for trials with incorrect responses. All the regressors were obtained by convolving the vector of stimulus onsets with a standard hemodynamic response as defined in SPM2. This resulted in 16 predictors of brain activity for each experimental run, 8 for the inspection time trials with correct responses and 8 for the inspection time trials with incorrect responses. Regions of positive and negative correlation of brain response with inspection time difficulty were determined by computing a linear weighting of all eight stimulus durations used in the imaging inspection time test sessions. The computation of contrasts was limited to the eight predictors of brain activity associated with inspection time trials with correct responses. For each participant, we averaged the two contrast maps for the imaging inspection time sessions; the average maps were entered in the second-level random-effects analysis for group analysis.

For the working memory task the observed time series for each voxel was compared to a model created from a box car function representing the three working memory loads (rest, low and high), which was convolved with a standard hemodynamic response. A *t*-test was performed on the average signal intensities comparing any two conditions of interest. Subject-specific linear contrasts on the parameter estimates (high load minus low load) were then entered into a second-level random-effects analysis for group analysis.

Results were thresholded at $p<.05$ corrected for multiple comparisons at the voxel level. Coordinates are quoted in standard Talairach and Tournoux space following application of a conversion factor (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html), from the MNI space employed by SPM. Regional designation of grey matter differences was determined by the Talairach Daemon (Lancaster et al., 1997, 2000) and confirmed by comparison of local anatomy with a standard atlas (Ono, Kubik, & Abernathey, 1990).

### 2.3.4. Statistical analysis

To investigate individual differences in the neural response to the two tasks, regions of interest generated from the second-level group analysis of inspection time and working memory were inverse normalized to the native space of each individual, using algorithms provided by the SPM package.

The correlations between BOLD signal activity, RPM score, and accuracy, were then found by averaging together the brain activity estimates (beta values) from all voxels within these inverse normalised regions determined from the second-level group analysis for the two tasks, inspection time and working memory. For the inspection time task the difference in mean beta values between hard (25, 37, 50 and 75 ms trials) and easy (100 and 150 ms) trials was determined as well as the mean beta during hard trials only (25, 37, 50 and 75 ms trials). Hard trials were defined as those where response levels were above chance (10 out of 20) and below the threshold for inclusion (18 out of 20 at a trial duration of 100 ms). Easy trials were then defined as ceiling durations (100 and 150 ms) (Fig. 2). For the working memory task the difference in mean beta values between high load (2 back) and low load (0 back) trials was determined as well as the mean beta values in the high load task alone. These measures were then entered into a multiple regression model to test formally whether brain activity in each identified region could mediate any association between RPM and behavioural performance. Statistical significance was calculated using a bootstrap method (Preacher & Hayes, 2004).

## 3. Results

Of the 79 members of the ABC1936 group invited for fMRI, 32 were excluded from further data analysis for reasons such as being unable to correct vision, falling below a predetermined threshold for the inspection time task of 18 correct responses out of a total of 20 for the 150 ms duration

**Table 1**
Mean (SD) of patient characteristics

| | Whole ABC1936 sample at wave 3 | IT sample | *n*-back sample |
|---|---|---|---|
| Moray House Test IQ score at age 11 | 103.7 (13.1) | 106.5 (9.85) | 104.9 (6.62) |
| Raven's Progressive Matrices | 37.8 (7.6) | 37.65 (3.85) | 39.01 (4.80) |
| % Correct responses (out of 16) in the high load task | – | | 68.8 (1.38) |
| % Correct responses (out of 320) in the two imaging inspection time sessions | – | 76.4 (12) | |
| Age at scanning | – | 69.96 (0.4) | 69.80 (0.4) |

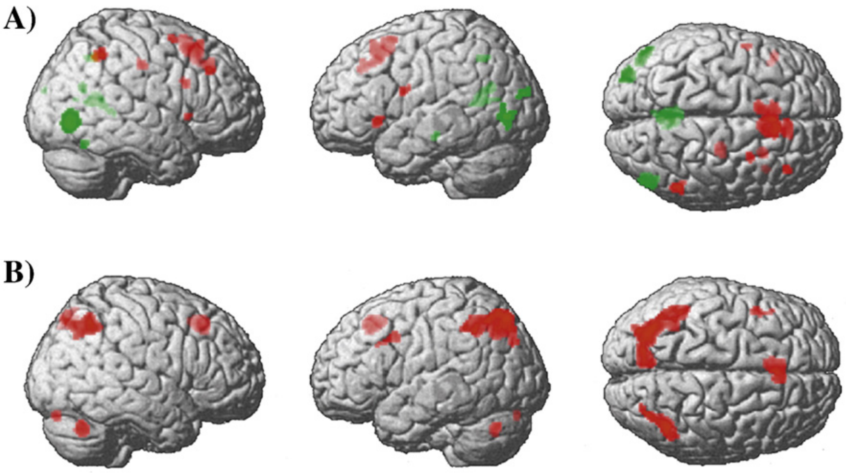

**Fig. 3.** Right lateral, left lateral, and superior views of neural activity associated with: A) positive (red) and negative (green) correlations between inspection time stimulus duration and BOLD effect, for the inspection time sample as a whole ($N$=47); and B) a positive correlation of BOLD effect and working memory load, for the working memory sample as a whole ($N$=37).

in both scanning sessions, or feeling unwell. A further 10 of this group failed to achieve above chance, i.e. 8 out of 16 correct responses, in the high load working memory task. Therefore there were 47 participants (24 male) that had fMRI data available for analysis in the inspection time task, and 37 of those (20 male) had fMRI data available for analysis in the working memory task (Table 1). The significant areas of group brain activation associated with each task in this sample are shown in Fig. 3.

Across individuals, higher RPM score correlated positively with accuracy on both the inspection time ($r$=.445, $p$=.002) and n-back working memory ($r$=.386, $p$=.018) tasks.

In brain regions where there was a positive correlation of BOLD activity with stimulus duration in the inspection time task (Fig. 3A; cf. Waiter et al., 2008) we found no statistically significant correlations between the difference in average BOLD activity between hard and easy stimulus durations and either RPM or accuracy in the inspection time task (Table 2). However, in brain regions where there was a negative correlation of BOLD activity with stimulus duration in the inspection time task (Fig. 3A; cf. Waiter et al., 2008) we found statistically significant positive correlations between the difference in average BOLD activity between hard and easy stimulus durations and accuracy in the inspection time

**Table 2**
Regions where there was a positive or negative correlation of BOLD activity with inspection time stimulus duration

| Talairach coordinates | | | Region | $t_{46}$ | Extent | Correlation with behaviour | | Mediator |
|---|---|---|---|---|---|---|---|---|
| *X* | *Y* | *Z* | | | | RPM | Accuracy | %$R^2$ |
| *Positive correlation* | | | | | | | | |
| 6 | 16 | 47 | R Medial Frontal Gyrus BA6 | 6.26 | 377 | .049 | .130 | .50 |
| 55 | −46 | 47 | R Inferior Parietal Lobule BA40 | 5.32 | 35 | −.109 | .195 | 6.07 |
| −8 | 12 | 55 | L Superior Frontal Gyrus BA6 | 5.00 | 39 | .261 | .197 | −7.074 |
| 30 | 7 | 55 | R Middle Frontal Gyrus BA6 | 4.77 | 12 | −.078 | .183 | 5.62 |
| 26 | −18 | 38 | R Cingulate Gyrus BA24 | 4.66 | 35 | −.1282 | .200 | 7.41 |
| 40 | 33 | 32 | R Middle Frontal Gyrus BA9 | 4.58 | 18 | −.128 | .266 | 6.07 |
| −46 | 21 | −3 | L Inferior Frontal Gyrus BA47 | 4.32 | 29 | −.041 | .118 | 2.02 |
| −53 | 3 | 18 | L Inferior Frontal Gyrus | 4.29 | 17 | −.140 | .001 | 1.12 |
| 40 | 16 | 1 | Insula | 4.20 | 10 | .022 | .058 | 0.00 |
| *Negative correlation* | | | | | | | | |
| 50 | −72 | 2 | R Inferior Temporal Gyrus BA37 | 6.79 | 141 | −.095 | .302 [a] | 12.4 |
| −2 | −52 | 14 | L Posterior Cingulate BA29 | 5.44 | 287 | .093 | .323 [a] | .90 |
| −44 | −75 | 6 | L Middle Occipital Gyrus BA19 | 5.39 | 76 | .0140 | .354 [a] | −5.84 |
| −30 | −84 | 21 | L Middle Occipital Gyrus BA19 | 4.52 | 38 | .040 | .397 [a] | −5.17 |
| 2 | −52 | 45 | R Precuneus BA7 | 4.38 | 28 | −.033 | .249 [b] | −5.17 |
| 32 | −61 | −14 | Declive | 4.25 | 16 | −.0395 | .269 [c] | 6.29 |
| −26 | −22 | −11 | L Parahippocampal Gyrus | 4.21 | 11 | −.158 | .168 | 8.99 |

[a] Correlations are significant (i.e. $p$<.05).

[b] $p$=.091.

[c] $p$=.067, all other correlations are non-significant (i.e. $p$>.1).

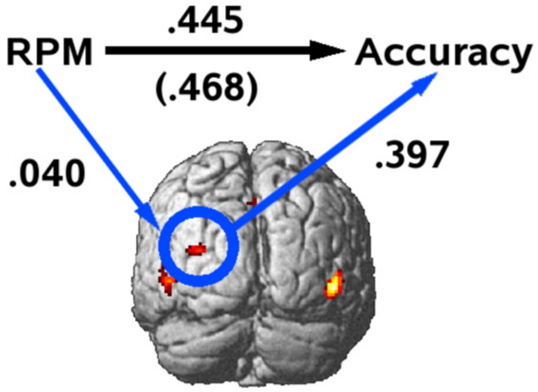

**Fig. 4.** Effects of inspection time-related neural activity in BA19 (left middle occipital cortex) on the association of RPM score with inspection time accuracy. The mediated correlation between RPM and Inspection Time accuracy appears in parentheses below. Thus, although there is a significant correlation between Raven scores and accuracy and between neural activation (BOLD response) and accuracy in the inspection time task, there is no evidence of mediation of the Raven-inspection time correlation by neural activation.

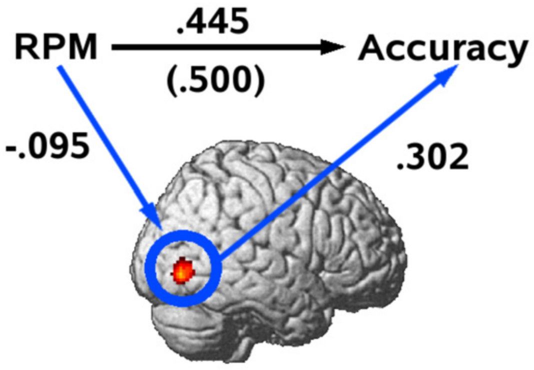

**Fig. 5.** Inspection time-related neural activity in BA37 (left inferior temporal cortex) mediates the association of RPM score with inspection time accuracy. The mediated correlation between RPM and inspection time accuracy appears in parentheses below. There is a significant correlation between Raven scores and accuracy in the inspection time task. There is a significant correlation between Raven and inspection time scores and neural activation (BOLD response), however, there is no significant mediation (12%) of the Raven-inspection time score correlation by neural activation.

task (Table 2) in the right inferior temporal, left posterior cingulate and left middle occipital regions. No significant correlations were found between BOLD activity between hard and easy stimulus durations and RPM. For each region, when controlling for the difference in BOLD functional activity between hard and easy durations within the region (as a hypothesized mediator variable), the shared variance between RPM (ability, predictor variable) and accuracy (performance, dependent variable) showed no significant change. Results based upon one of the brain areas most consistently activated during inspection time, BA19, are shown for illustration in Fig. 4.

In regions where there was a positive correlation of BOLD activity with working memory load (Fig. 3B) we found no statistically significant correlation between the difference in average BOLD activity between high and low load tasks and either RPM or accuracy (Table 3). A trend towards significance was however found in the medial frontal gyrus BA8 (Table 2 and Fig. 3A). For each region, when controlling for the difference in BOLD functional activity between low and high load tasks within the region (as a hypothesized mediator variable), the shared variance between RPM (ability, predictor variable) and accuracy (performance, dependent variable) showed no significant change (Fig. 5).

For both tasks, no significant correlation between BOLD activity and either RPM or accuracy was found for the hard task only (data not reported).

## 4. Discussion

In this group of older individuals, inspection time and working memory performance showed the expected significant correlations with intelligence as measured by the Raven's Progressive Matrices test (Grudnik & Kranzler, 2001; Oberauer, Sub, Wilhelm, & Wittmann, 2008). In regions where there was a positive correlation between inspection time duration and BOLD activity, consisting of a predominantly frontal network, as previously described, (Deary, Simonotto et al., 2004; Deary, Whiteman et al., 2004; Waiter et al., 2008), including the medial aspect of BA6, and the middle and frontal aspect of BA6 bilaterally and a region in the inferior parietal lobe, there were no significant correlations between the difference in BOLD activity during hard and easy durations and intelligence as measured by RPM, nor were there any significant correlations between BOLD activation and accuracy, as defined by the number of correct responses. However, in regions where there was a negative correlation between inspection time duration and BOLD activity, consisting of a

**Table 3**
Regions where there was greater BOLD activity with the high load versus the low load *n*-back working memory task

| Talairach coordinates | | | Region | $t_{36}$ | Extent | Correlation[a] with behaviour | | Mediator |
|---|---|---|---|---|---|---|---|---|
| *X* | *Y* | *Z* | | | | RPM | Accuracy | $\%R^2$ |
| −2 | 25 | 41 | L Medial Frontal Gyrus BA8 | 8.58 | 206 | −.008 | −.186 | 1.30 |
| −14 | −73 | 50 | L Precuneus BA7 | 8.25 | 808 | .128 | .193 | 9.33 |
| 30 | −65 | −24 | R Cerebellum Uvula | 7.70 | 116 | −.054 | −.221 | 6.74 |
| 44 | −56 | 49 | R Inferior Parietal Lobule BA 40 | 7.65 | 282 | −.053 | −.230 | .52 |
| 10 | −82 | −14 | R Cerebellum Declive | 7.14 | 29 | .201 | −.287 | −8.55 |
| −32 | −67 | −24 | L Cerebellum Uvula | 6.70 | 51 | .194 | −.019 | −3.37 |
| −44 | 11 | 33 | L Middle Frontal Gyrus BA9 | 6.22 | 34 | .237 | −.210 | 6.48 |

[a] All correlations are non-significant (i.e. $p > .05$).

predominantly posterior network, including the posterior cingulate and bilateral occipital lobe, we found regions of significant positive correlation between the difference in BOLD activity during hard and easy durations and accuracy. The region with the strongest correlation of BOLD activity and accuracy was the left middle occipital gyrus, Fig. 4. We did not, however, find any correlation between BOLD activity and intelligence.

When comparing regions where there was a significant difference in BOLD activity between hard (high load, 2-back) and easy (low load, 0-back) tasks during the working memory task, including regions in the frontal and parietal lobes and the cerebellum, we found no regions where there was a significant correlation between the difference in BOLD activity between hard and easy tasks and either intelligence or accuracy.

By measuring the difference in BOLD activity between hard and easy tasks for two tasks that are well known to be correlated with measures of intelligence—and which assess psychological constructs that have been used to try to understand intelligence differences better—we were able to examine the possible mediating effects of neural activity on the correlation between intelligence and accuracy (cf. Gray et al., 2003). Comparing all regions identified as being significantly active for our two tasks we found no significant mediating effect of BOLD signal on the correlation. The region of maximum mediating effect was found to be left inferior temporal cortex BA37 (cluster maximum $x=50$, $y=-72$, $z=2$) when accounting for inspection time activity (Fig. 5).

Positive findings from this study are that, in a field where students are often used as the subjects, we found significant associations between processing speed and working memory tasks and intelligence test scores in a sample of relatively healthy older people. Moreover, we found that the processing speed and working memory tasks, in the fMRI setting, were associated with activation in similar brain areas to those found in younger people. Our goal was not to replicate all of the findings reported by Gray et al. (2003), since we were unable to replicate their analysis exactly, however we were able to partially replicate their finding of no significant association between BOLD signal and task and Raven performance when analysing target trials only. We did, however, find positive correlations between accuracy and BOLD activity in regions found to have a negative correlation between inspection time stimulus duration and the difference in BOLD response between hard and easy tasks. This did not result in any mediating effect of the BOLD signal on the Raven-fMRI task performance correlation. Therefore, we were not able to generalise Gray et al.'s (2003) result beyond their use of lure detection in a *n*-back working memory task. It is likely that one of the reasons they used lure detection was that the relatively high ability subjects they tested had near to ceiling effects on target detection in the *n*-back. This was not the case in the present study and, because target detection showed a good distribution and correlations with Raven scores in our sample, it seemed appropriate to use that variable in a design similar to that by Gray et al. (2003). Thus, our design met the necessary preconditions for examining BOLD versus performance correlations, and BOLD mediation of mental test-fMRI task score correlations, and we did find some evidence of BOLD versus performance correlations but these did not result in mediation of mental test-accuracy correlations.

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