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Neural correlates of intelligence as revealed by fMRI of fluid analogies

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It has been conjectured that the cognitive basis of intelligence is the ability to make fluid or creative analogical relationships between distantly related concepts or pieces of information (Hofstadter, D.R. 1995. *Fluid Concepts and Creative Analogies*. Basic Books, New York., Hofstadter, D.R. 2001. *Analogy as the Core of Cognition*. In *The Analogical Mind: Perspectives from Cognitive Science* (D. Gentner, K. J. Holyoak and B. N. Kokinov, Eds.), pp. 504–537. MIT Press, Cambridge, Mass.). We hypothesised that fluid analogy-making tasks would activate specific regions of frontal cortex that were common to those of previous inferential reasoning tasks. We report here a novel self-paced event-related fMRI study employed to investigate the neural correlates of intelligence associated with undertaking fluid letter string analogy tasks. Stimuli were adapted from items of the AI program Copycat (Mitchell, M. 1993. *Analogy-making as Perception: A computer model*. The MIT Press, Cambridge MA.). Twelve right-handed adults chose their own “best” completions from four plausible response choices to 55 fluid letter string analogies across a range of analogical depths. An analysis using covariates determined per subject by analogical depth revealed significant bilateral neural activations in the superior, inferior, and middle frontal gyri and in the anterior cingulate/paracingulate cortex. These frontal areas have been previously associated with reasoning tasks involving inductive syllogisms, syntactic hierarchies, and linguistic creativity. A higher-order analysis covarying participants’ verbal intelligence measures found correlations with individual BOLD activation strengths in two ROIs within BA 9 and BA 45/46. This is a provocative result given that verbal intelligence is conceptualised as being a measure of crystallised intelligence, while analogy making is conceptualised as requiring fluid intelligence. The results therefore support the conjecture that fluid analogising could underpin general intellectual performance.

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Introduction

It has long been argued that all human reasoning, including logical inference, is essentially analogical in nature (James, 1890/1950) and that the essence of intelligent insight lies in making creative metaphors or fluid analogies (French, 2002; Halford, 1992; Hofstadter, 1995, 2001; Holyoak and Thagard, 1995; Mitchell, 1993). Making an analogy is clearly rooted in perceptual experience; however, it goes beyond perception in employing relationships (Mitchell, 1993). For such higher-order categorical relationships, Hofstadter argues that: “categories are quintessentially fluid entities; they adapt to a set of incoming stimuli and try to align themselves with it. The process of inexact matching between prior categories and new things being perceived ... is analogy-making par excellence” (Hofstadter, 2001). Insightful behaviour through fluid analogy making is necessary for success in a wide range of endeavours, including complex pattern recognition, composition of musical variations, producing and appreciating humour, translation between languages, poetry, classroom exercises, and much of everyday speech (Geake, 2003; Goswami, 2001; Hofstadter, 1995, 2001; Holyoak and Thagard, 1995; Mitchell, 1993). Wharton et al. note that since “cognitive processes required for analogical mapping are localised to specific brain regions, ... analogical reasoning is a tractable topic for neuroimaging investigation” (Wharton et al., 2000). Evidence for a neural localisation associated with analogical reasoning, therefore, should contribute to an improved understanding of the neural basis of intelligent behaviour.

Here, we present an fMRI investigation of the neural correlates of fluid analogy making. This study utilises analogical stimuli that capture some degree of fluidity while at the same time affording a tractable investigation. Fortuitously to this end, Hofstadter and Mitchell’s AI program *Copycat* (Hofstadter, 1995; Mitchell, 1993), used in previous psychological studies (Burns, 1996) seemed particularly suitable for adaptation to the testing of humans in fMRI. *Copycat* makes non-exact or ‘fluid’ applications of a transformation rule that is applied to a string of letters. The only internal knowledge required is alphabetical and reverse-alphabetical order, and the boundary conditions of the English alphabet, the

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letters ‘a’ and ‘z’. The task, given the first transformation pair, is to complete the second in an analogous way. As a simple example, to $abc \rightarrow abd, ijk \rightarrow ?$ most people respond “ijl” (increase the last letter by one), although “ijd” (change the last letter to “d”) and other responses are possible. However, examples can be made arbitrarily more complex, such as $abc \rightarrow abd, iijjkk \rightarrow ?$ or $a \rightarrow ab, z \rightarrow ?$ each of which can elicit a number of plausible responses (Burns, 1996).

Adapting *Copycat* as an operationalisation of fluid analogy making is in contrast to previous neuroimaging approaches to seeking neural correlates of analogising that employed either simple analogies (e.g., black is to white as high is to . . . ?) (Luo et al., 2003), or the Ravens Progressive Matrices (RPM), a visuospatial intelligence test presented as 2D multivariate spatial analogies (Christoff et al., 2001; Kroger et al., 2002; Prabhakaran et al., 1997; Wharton et al., 2000). The RPM has been widely used for investigations of the neural correlates of deductive reasoning (Prabhakaran et al., 1997), and reasoning underpinning relational complexity (Christoff et al., 2001; Kroger et al., 2002), each of which report a network of frontal activations. Whereas solving simple analogy problems requires both semantic and content knowledge, the rationale for the focus on the RPM in earlier studies was that it provided valid and reliable measures of the ability to solve novel problems without reference to long-term knowledge. As useful as this concept may be, it is a restricted conceptualisation of analogical reasoning since all responses are only graded either correct or incorrect. In contrast, fluid analogising elicits a range of responses, all of which could be regarded as correct, albeit with differing degrees of plausibility. The novelty of this study arises from our attempt to reflect the inexactness of real-world reasoning by investigating preferred-answer responses, as opposed to correct answers. We hypothesised that the fluid analogy-making tasks in this study would show characteristic spatial (and temporal) patterns of neural activation that were common to the majority of previous inferential reasoning tasks. Hence, for example, we would expect some degree of spatial overlap between our fluid analogy-making task and the PFC activation patterns associated with the RPM, possibly due to a shared reliance on working memory (Baddeley and Sala, 1998). Moreover, it could be argued that, if success at inductive reasoning tasks requires selection and application of relevant generalised properties, then inductive reasoning requires the making of fluid analogies.

Materials and methods

Participants

Twelve right-handed adults (4 men, 8 women; age range 18 to 54 years) with normal or corrected-to-normal vision participated in this study. All participants were recruited from the staff and postgraduate student cohorts of the two Oxford-based universities of the authors. We deliberately targeted participants of above-average intelligence since the literature reviewed above implies that such people would be adept at fluid analogising. Strong right-handedness was verified with a modified form of the Annett Handedness Questionnaire (Annett, 1970) (R-preference >95%). Participants were also screened for any history of dyslexia. All participants were fluent speakers of English; two were bilingual. Participants received explanatory descriptions of the experiment and fMRI procedures and, in particular, of fluid letter string analogy making. The instructions emphasised that for each analogy

item presented there was no correct answer, rather, that participants should choose the completion which they considered to be the best. Furthermore, participants were informed of the total number of experimental stimuli and that the experiment was self-paced. Each participant gave their informed consent prior to their inclusion in the experiment in accordance with the Helsinki Declaration. The study had appropriate research ethics approval from the Oxfordshire Research Ethics Committee.

Experimental tasks and set-up

The analogical stimuli consisted of 55 fluid letter string items of different degrees of complexity, presented visually in a random order. Thirty of these were selected from 80 of the original *Copycat* items (www.cse.ogi.edu/mm/analogy-problems.html). The remaining 25 items consisted of the simplest match letter string analogies, e.g., $abc \rightarrow abc, tsr \rightarrow ?$. This design was chosen to maximise the range of cognitive behaviour of participants across the stimulus items, whilst minimising variance in the non-cognitive aspects of the task, such as visual processing (primary visual cortex), saccadic eye movement (frontal eye field), and motor activity (left motor cortex).

Each of the stimuli had four possible response choices. For the 30 *Copycat* stimulus items, the four choices for completion were selected from the most popular open-ended responses to that item solicited from two classes of secondary school students in an earlier study (J.G. and R. Butera, unpublished data). Importantly, all of the choices were plausible. The simplest match analogy choices included the target, anagrams, and basic variants. None of the letter strings resembled words in English (or any Roman script language that we are aware of). A feature of the original *Copycat* test was the variability in the string length of the exemplars utilised. Here, we recorded the summed total of the number of letters appearing on-screen for each stimulus (summed string length or SSL) for later examination. The SSL measure varied between 7–52 letters, with mean 31. As suggested above, the rationale of plausibility over the usual correct–incorrect paradigm was that it more closely reflected ‘real life’ intellectual demands, at least in analogy making (Dunbar, 2001), and thus could instigate greater consistency of task processing between participants.

The analogy letter strings were always presented 2° above the centre of the screen, with the four response choices in a 2×2 ($7^\circ \times 5^\circ$) grid centred just below. Times New Roman font, with white text on black background, was used throughout. An example is shown in Fig 1.

The order of presentation of individual stimuli was pseudo-randomised such that participants could not anticipate the degree of complexity of successive items and thus needed to treat each stimulus as if it were a complex fluid analogy to be completed. This

abcm \Rightarrow abcn, rijk \Rightarrow ?

(1) rijk (2) rijl

(3) sijk (4) sijl

Fig. 1. An example fluid analogy letter string stimulus. In this particular case, response 2 (rijl) was the most commonly preferred response (11 out of the 12 subjects) even though it had a lower ADR (2) than either response 3 (sijk) (ADR = 3) or 4 (sijl) (ADR = 4).

design was chosen to minimise any order effect for these fluid letter string analogies (Burns, 1996). The stimuli presentation was self-paced and time-locked to the scanner such that each stimulus was on screen until the participant had indicated their response. The stimulus was then immediately replaced by a fixation cross for the time until the next volume acquisition onset plus 6 s (2 TRs) whereupon the next stimulus was presented. The responses were indicated by key presses on a four-button box, activated by digits 2 to 5 of the right hand (a post hoc analysis indicated no significant digit preference). The buttons were aligned along a slight curve to comfortably fit beneath the four active fingers such that digit 2 (index finger) always pressed button 1 to indicate a choice-1 decision, digit 3 (middle finger) always pressed button 2 to indicate a choice-2 decision, and so on. Participants practised using the button box in situ; no one indicated in the post-experiment that they had made any finger-press errors. Participants were asked to fixate on the fixation cross between stimuli presentations; this provided a constant baseline with which to compare all the responses. Cross fixation times ranged from 6.5 to 9 s, permitting attenuation of neural response prior to the presentation of each subsequent item.

The stimuli presentations were coded using the FMRIB Enhanced Stimulus Tool (FEST) 3.1 software (www.fmrib.ox.ac.uk). Button responses and reaction times (RT) were recorded on-line for each stimulus. Prior to the presentation of the stimulus set, a practice set of ~15 analogy letter strings of varying complexity were presented in order to reduce activations due to task learning. During the scanning, participants wore earplugs and were positioned supine in the magnet, with their heads immobilised with padding inside the RF coil. The stimuli were back-projected on to a screen outside of the magnet and were viewed by the participants through prism glasses.

Verbal intelligence

Verbal intelligence (VI) estimates were obtained from scores on the National Adult Reading Test (NART) 2nd Edition (Nelson, 1991). The NART was chosen for both practical and theoretical reasons. The NART has been employed in previous studies into adult neural processing capacity, in particular, cognitive reserve (Stern et al., 2003). More importantly, we were attracted to the NART because its scores, as a theorised measure of crystallised intelligence (g_c) and thus orthogonal to measures of fluid intelligence (g_f), could provide a more challenging test of our hypothesis that fluid analogising underpins all intellectual activity, including g_c through categorisation matching (Hofstadter, 2001). That said, it should be noted that the NART has been found to load 0.85 onto a general intelligence factor g (Freeman and Godfrey, 2000). The NART's main shortcomings are a ceiling effect for VI > 132, which could have affected several participants, and an assumption of English as a first language, which affected two of our participants. Despite the NART's correlation with g , we used the NART scores more conservatively to infer only participants' VI from the NART Manual's regression tables (Nelson, 1991). Participants' NART VIs were used as a covariate in the fMRI analysis.

Image acquisition

Both functional and structural MRI images were acquired on a Siemens/Varian 3T system fitted with a birdcage head coil. Structural scans were obtained with an in-plane resolution of 1 ×

1 mm and thickness of 1.5 mm. For the functional data, as the experiment was self-paced, a variable number of T2* weighted echo-planar imaging (EPI) volumes (ranging from 249 to 812 vols) were acquired over a time period of 13–25 min. Each volume consisted of 24 contiguous axial slices with an in-plane resolution of 3 × 4 mm and a thickness of 5 mm, covering the entire brain (TR = 3 s, 64 × 64 matrix, FOV = 192 × 256 mm, TE = 30 ms, flip angle = 85°).

Behavioural data measures

The response variance was formalised by having a panel rate all of the 220 possible stimuli responses for analogical depth (ADR: scale from 1 to 5) as the number of transformation operations required to get from the prompt to that choice (J.G. and C. Dodson, unpublished data). The transformation operations included letter copy, letter advance, letter retraction, string reversal, letter-place swap, letter insertion, letter deletion, alphabet preservation, alphabet reflection, grouping, numerical increase, numerical decrease, and letter randomisation. For example, possible response choices to abc → abd, pqqrrr → ? would be assigned depth ratings as follows:

pqqrrr ADR = 1: new letter sequence
 pqqrrd ADR = 2: new letter sequence, last letter copy
 pqqrrs ADR = 3: new letter sequence, alphabet preservation, letter advance
 pqqsss ADR = 4: new letter sequence, alphabet preservation, grouping, letter advance
 pqqssss ADR = 5: new letter sequence, alphabet preservation, grouping, numerical increase, letter advance

It should be noted that, for each fluid analogy item, each of the four response choices actually presented could have any value of ADR in the range 1 to 5, depending on its composition. ADRs were used in the design of the stimuli and in the analysis of the data; however, subjects were not aware of the ADRs of the response choices. This rating process was preferred to the solution histograms of *Copycat* which, although providing an objective measure of solution quality, “are not meant to model all the domain-specific mechanisms people use in solving these letter-string problems” (Hofstadter, 1995). From the 55 response choices actually made by each participant throughout the entire experiment, a corresponding set of 55 ADR ratings were generated as a quantitative measure of task performance.

Neuroimaging data analysis

Analyses of the fMRI data were carried out in a multi-parameter GLM using FEAT v5.1 (FMRIB Expert Analysis Tool, www.fmrib.ox.ac.uk/fsl), with motion correction using MCFLIRT, spatial smoothing using a Gaussian kernel of FWHM 5 mm, mean based intensity normalisation of all volumes by the same factor, and nonlinear highpass temporal filtering (Gaussian-weighted LSF straight line fitting), temporal cutoff = 50 s. The individual statistical analyses were carried out using FMRIB's Improved Linear Model (FILM) (Woolrich et al., 2001) with local autocorrelation correction. In our primary ADR-based GLM analysis, three principal covariates of interest were calculated for each participant based on their individual ADR ratings. These covariates were created by partitioning the per-subject histogram of events by ADR

into low, intermediate, and high ADR responses, such that each covariate contained roughly one third of the total events. The covariates were thus parameterised into three increasing levels of analogical depth. The fitted GLM comprised a flat boxcar function for each event within the three principal covariates convolved with a standard Gamma function HRF (mean lag = 6 s, SD = 3 s). The duration of the boxcar function on each event was defined by the stimulus presentation time (i.e., the individual RT for this event). Whilst the covariates were therefore idiosyncratic to each participant, this model made the fewest assumptions about intra-participant processing. Nine other parameters were added as covariates of no interest to each individual GLM. These were the temporal derivatives of the three principal stimulus covariates and the six parameters of motion correction derived from MCFLIRT.

Higher-level group analysis, where the individual results were registered both to the high-resolution morphological MR images and to the MNI 152 standard image (Collins et al., 1994), was undertaken using FMRIB's Local Analysis of Mixed Effects (FLAME, www.fmrib.ox.ac.uk/fsl). FLAME uses an MHMC randomisation technique to infer group level statistics in a random effects model over participants. For the group level analysis, individuals' NART scores were also included as a further covariate. Z (Gaussianised T/F) statistic images were created using clusters determined by a voxel threshold of $Z > 2.3$ and a corrected cluster significance of $P < 0.05$.

Results

Behavioural data

The behavioural data are summarised in Table 1. Data were collapsed across each of the three parametric covariates (corresponding to the low, medium, and high ADR conditions) by computing the mean ADR and median RT per subject. The participants' NART VI scores ranged from 107 to 128 (close to the theoretical ceiling), indicating that the participants comprised an above-average VI sample group. There were no significant correlations between the NART VI scores and the other summary behavioural measures. However, on an individual subject basis, non-parametric Spearman correlations between RT and ADR ($p = 0.44$ to 0.70) were significant at $P < 0.01$ for all subjects. Although the group mean RTs for the high and medium ADR fluid analogy

letter string items (23.95 and 24.68 s) were significantly longer than for the low ADR items (8.83 s, Wilcoxon signed-rank test, $P < 0.01$), the relatively long RTs for the low ADR items indicated the effectiveness of using these simplest analogies in the experimental design. Participants therefore appeared to be treating each item as if it were a potentially difficult fluid analogy. We additionally found significant non-parametric correlations between RT and SSL for each subject ($p = 0.53$ to 0.74), indicating that more time was being taken to read and process the longer strings, as might be expected. The relationships between these three measures (pooled subject RT, ADR, and item SSL) might best be explained by a partial correlation of ADR with RT, controlling for SSL, in which $r = 0.31$ ($P < 0.01$).

Neuroimaging data

A random effects analysis over the subject group was computed using the main ADR-based GLM model. The primary contrast of interest, seeking a positive linear trend over the three parameterised ADR conditions $[-1 \ 0 \ 1]$, found a number of significant and identifiable bilateral neural activations in the superior, inferior, and middle frontal gyri and in the anterior cingulate/paracingulate cortex, all at a voxel threshold of $Z \geq 2.3$, corrected cluster significance $P < 0.05$ [Fig. 2; Table 2]. Additional posterior activations were observed in the precuneus and inferior parietal sulcus. Individual parametric conditions alone also produced strong widespread areas of activation, however, these are not reported in further detail here as they were not of primary interest to this study.

To investigate our main conjecture that fluid analogising underpins general intelligence, we next conducted an analysis at the group level using NART VI as a global covariate in the main ADR-based GLM analysis. This produced two well-defined regions of activation (not separately delineated in Fig. 2), one of 84 voxels in BA 9 (left MFG, MNI coordinates $-28, 32, 40$) and the other of 157 voxels in BA 45/46 (left MFG, MNI coordinates $-39, 32, 26$) [Fig. 3] when covaried against the positive linear trend $[-1 \ 0 \ 1]$ parametric ADR-based contrast (voxel threshold $Z > 2.3$, corrected cluster significance $P < 0.05$).

These two clusters were subsequently used to define regions of interest (ROI) for further analysis. Average %BOLD signal changes for the positive linear trend $[-1 \ 0 \ 1]$ in ADR within each ROI were calculated per subject from the appropriate contrast of parameter estimate (COPE) values at each voxel, after normal-

Table 1

Subject NART, mean analogical depth responses (high, medium, and low ADR), median RTs, and standard errors of the RTs

Subject	NART verbal intelligence	High			Medium			Low		
		ADR	RT (s)	SEM	ADR	RT (s)	SEM	ADR	RT (s)	SEM
1	128	3.56	25.49	0.68	1.43	25.11	0.80	1.00	11.03	0.27
2	119	3.42	28.42	1.39	1.67	19.67	0.48	0.96	7.72	0.10
3	125	3.73	13.77	0.35	1.60	16.06	0.46	1.00	6.87	0.12
4	115	3.50	18.98	0.49	1.70	19.08	0.95	0.96	8.49	0.17
5	125	3.56	6.62	0.14	1.86	6.18	0.19	1.00	4.32	0.07
6	118	3.68	14.82	0.35	1.88	11.86	0.38	1.00	5.57	0.12
7	124	3.53	13.74	0.29	1.45	13.36	0.59	0.84	7.00	0.09
8	107	3.79	33.68	0.41	1.80	45.04	4.69	1.00	12.63	0.18
9	126	3.68	53.25	1.30	1.80	64.99	7.14	0.96	13.66	0.55
10	112	3.38	15.37	0.55	1.71	11.55	0.33	0.92	6.97	0.22
11	117	3.65	46.06	1.03	1.70	45.15	2.21	1.00	13.42	0.34
12	113	3.58	17.15	0.48	1.82	18.12	0.74	1.00	8.31	0.19
Group mean	119.10	3.59	23.95	0.62	1.70	24.68	1.58	0.97	8.83	0.20

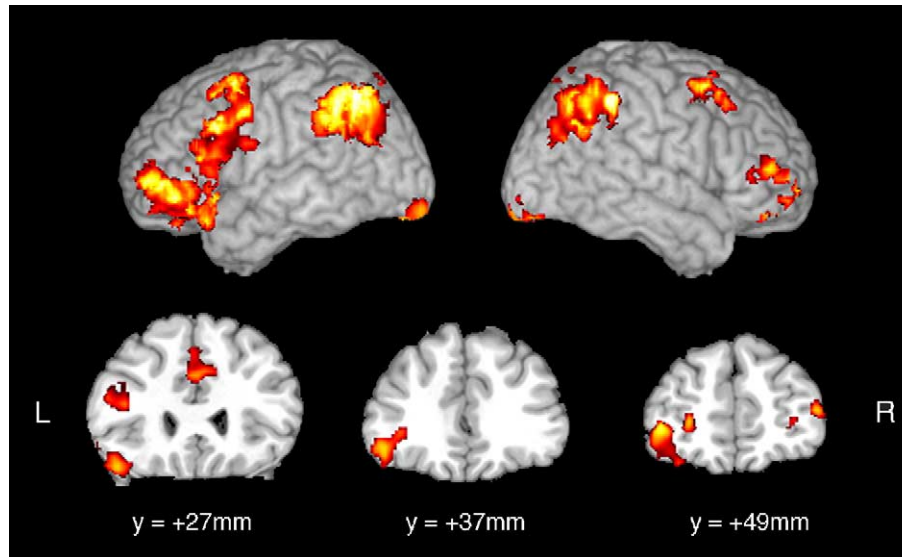


Fig. 2. Significant clusters from group random effects model analysis showing the positive linear trend contrast over ADR conditions, rendered onto a standard brain in MNI space. Voxel threshold $Z > 2.3$, corrected cluster significance $P < 0.05$. Lower coronal sections indicate the frontal activations of interest.

isation by the mean subject EPI time series per voxel, by taking a grand mean spatially across the ROI. Additionally, the standard error per subject was estimated from the voxel-to-voxel variance within each ROI. There was a strong linear relationship across the group for both ROIs between the mean %BOLD signal change within the ROI and NART verbal intelligence ($r = 0.85$ and 0.89 , $P < 0.01$) as shown in Fig. 4.

To satisfy ourselves that our experimental design assumptions were justified, we conducted several separate validity checks. First, all the GLM analyses assumed a relatively flat BOLD response in the time interval between each stimulus presentation and subject button response. We therefore examined the time series of the EPI data for individual participants in a variety of different frontal areas to ensure that this assumption was reasonable. Different participants had similar profiles, differing only in the maximum time for the sustained response. Fig. 5 shows the BOLD response over time, averaged over all subjects, in the left IFG. Adjacent frontal areas were found to have similar sustained HRF profiles. This supports our assumption of sustained activation during the processing of the fluid analogy stimuli.

Second, the behavioural results indicated a significant correlation of around 0.5 on average between ADR and RT per subject. Thus, the extent to which the result of the ADR-based analysis could alternately be explained purely by differences in RT alone needed to be addressed. A further RT-based GLM was therefore constructed (in an identical manner to the ADR-based GLM) by partitioning the histogram of individual events by RT into three new principal RT-based covariates of interest (short, middle, and long RTs) for each participant. Using this, we recomputed the random effects group map for the contrast of increasing linear trend in RT $[-1 \ 0 \ 1]$. No significant activations were found, even at the liberal voxel threshold $Z > 1.8$, uncorrected cluster significance $P < 0.05$. This appears to support the main model assumption that the neural response was contingent on the stimulus-specific ADR, independent of reaction time.

Third, to check that the relationship between task complexity and neural response was indeed linear, we compared the %BOLD change across ADR levels (low, medium, high) in the two IFC ROIs (BA 9 and BA 45/46) (Fig. 6). The linear trend is evident; the %BOLD signal change corresponding to the medium ADR

Table 2
Principal activations for positive linear trend of ADR

Region	Hemis.	BA	MNI x	MNI y	MNI z	Peak Z
Superior frontal gyrus	L	8	-26	22	44	4.2
Superior frontal gyrus	R	8	-30	24	44	4.1
Inferior frontal gyrus (vl PFC)	L	47/12	-50	44	-10	4.7
Inferior frontal gyrus (vl PFC)	R	47/12	48	48	-12	4.0
Inferior frontal gyrus (dl PFC)	L	44/45	-46	18	14	4.3
Inferior frontal gyrus (dl PFC)	R	45/46	52	22	20	3.6
Middle frontal gyrus (vl PFC)	L	47/10	-44	50	2	4.8
Middle frontal gyrus (vl PFC)	R	47/10	48	46	8	4.2
Anterior cingulate/paracingulate	L	32	-4	24	40	4.8
Anterior cingulate/paracingulate	R	32	6	22	42	3.0
Precuneus	L/R	7	0	-60	48	4.3
Inferior parietal lobule	L	40/7	-34	-62	44	5.0
Inferior parietal lobule	R	40/7	30	-60	44	4.8
Lingual gyrus/Occipital pole	L	17/18	-16	-92	-18	3.7
Lingual gyrus/Occipital pole	R	17/18	20	-86	-10	3.7

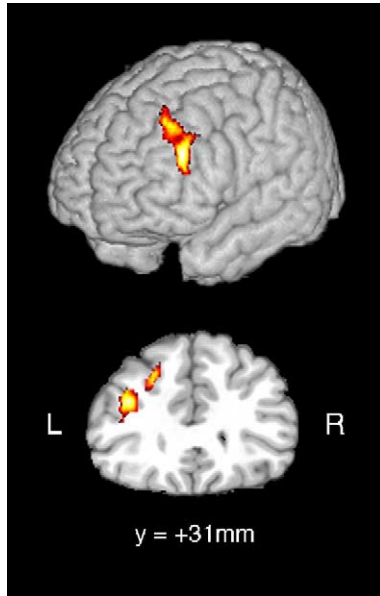


Fig. 3. Left PFC activations in BA 9 and 45/46 produced by group level analysis, covarying the positive linear ADR contrast across subjects with NART verbal intelligence. Coronal section at $y = +31$ mm. Voxel threshold $Z > 2.3$, corrected cluster significance $P < 0.05$.

level is intermediate between the values for the low and high ADR levels. A nonlinear trend analysis was not significant, although it should be noted that the ADR scale was not a priori linearly parametricised.

Fourth, it is possible that some of neural activity might have been due to differences in overt eye movements across levels of task complexity. To evaluate the possible extent of confounds from differentially active saccades, we computed the %BOLD signal change against ADR level (low, medium, high) in ROIs around coordinates reported in the literature as the centres of regions associated with saccadic and pursuit eye movements (Beauchamp et al., 2001; Petit and Haxby, 1999). Within the FEF and SEF, there were no significant differences in activation across the three levels of ADR.

Finally, we expected to find specific areas involved in the early visual processing of the stimuli, not involved with higher order cognition, that were independent of the ADR rating. We therefore conducted a separate ROI examination of the activity of the Visual Word Form Area (VFWA), centred on MNI coordinates $-43, -54, -12$, a region not relevant to our main hypothesis but which is responsive to all letter-like stimuli (McCandliss et al., 2003; Todd and Marois, 2004; Wandell, 1999). As anticipated, this area was significantly activated ($Z > 3.0$) during the low, medium, and high ADR conditions. However, there were no significant differences between the maximum Z values ($P = 0.51$). This result also acted as a general confirmation that our overall model and analytic procedures were robust.

Discussion

This is the first fMRI analogic reasoning study that we are aware of which has employed a multiple-plausibility rather than a correct–incorrect event-related paradigm, and the first neuroimaging investigation of human responses to the *Copycat* fluid analogy

letter strings. One positive feature of employing a plausibility, rather than a correct–incorrect, paradigm was the greater assurance that participants were predominantly on-task and engaged in analogy making, since the commonly used multiple-choice strategy of eliminating wrong answers would have been unproductive. Moreover, employing simplest-match items as minimal analogies provided a parametric design of increasing item difficulty and thus enabled a linear trend analysis of progressive participant task engagement with the analogy items undertaken.

The main findings were that: (1) a distributed network of brain areas were activated by fluid analogy making; and 2) the BOLD signal associated with analogical depth of the stimulus items within two subregions of this network in the left middle frontal gyrus correlated with measures of verbal intelligence. This supports the conjecture that fluid analogising underpins general intellectual performance (Burns, 1996; French, 2002; Goswami, 2001; Hofstadter, 1995, 2001; Holyoak and Thagard, 1995; Mitchell, 1993), and in particular, that crystallised intelligence (g_c) may be underpinned by fluid analogy making (g_f). However, the extent to which the results of this study, utilising only one type of visual stimuli, is generalisable would need to be investigated by expanding the paradigm to include fluid analogies in other domains.

The distributed frontal network found here to be involved in fluid analogising can be related to previous studies in at least two broad ways. First is the degree of overlap between the regions of activation associated with undertaking fluid letter string analogies and those associated with convergent analogising using simple analogies (Luo et al., 2003) or the RPM (Christoff et al., 2001; Kroger et al., 2002; Prabhakaran et al., 1997; Wharton et al., 2000), viz., inferior and superior lateral prefrontal regions. Second is the degree of similarity between the regions of activation associated with undertaking fluid letter string analogies and those associated with high- g correlated items (Duncan et al., 2000), viz., lateral prefrontal and parietal regions. Here, we note that the regions of PFC activation found in the present study fall more or less within the zone identified by Duncan in his meta-analysis (Duncan, 2001; Duncan and Owen, 2000), notably within bilateral inferior frontal sulci and Sylvian fissures (Duncan, 2001; Duncan et al., 2000; Gray et al., 2003) which, he argues, is populated by neurons that are selectively recruited to varying cognitive task demands. The salience of an adaptive account of frontal processing to fluid analogy making can be gleaned from the implications for selectional attention of relational properties over surface features—one of the hallmarks of fluid analogy making. Thus, our results inform these accounts of how frontal areas might solve higher-level problems and contribute to executive functioning. As to any causal relationship between fluid analogising (and its particular task-specific demands) and the executive functioning of the PFC, future studies could investigate this more extensively by extending the experiment to include tasks operationalised for executive functioning. Such studies could help resolve the discrepancy between lateralised models of frontal function, where areas on the left PFC engage in information abstraction, while areas on the right PFC play a more evaluative role (Schacter et al., 1997), and other models where task distribution is not so readily partitioned (Kroger et al., 2002).

To this end, significant activations were found in the left superior frontal gyrus, adding support to the claim that this region is used to retrieve rule-based knowledge, in this case, knowledge of alphabetical order and ordinality (Goel et al., 1997; Parsons and

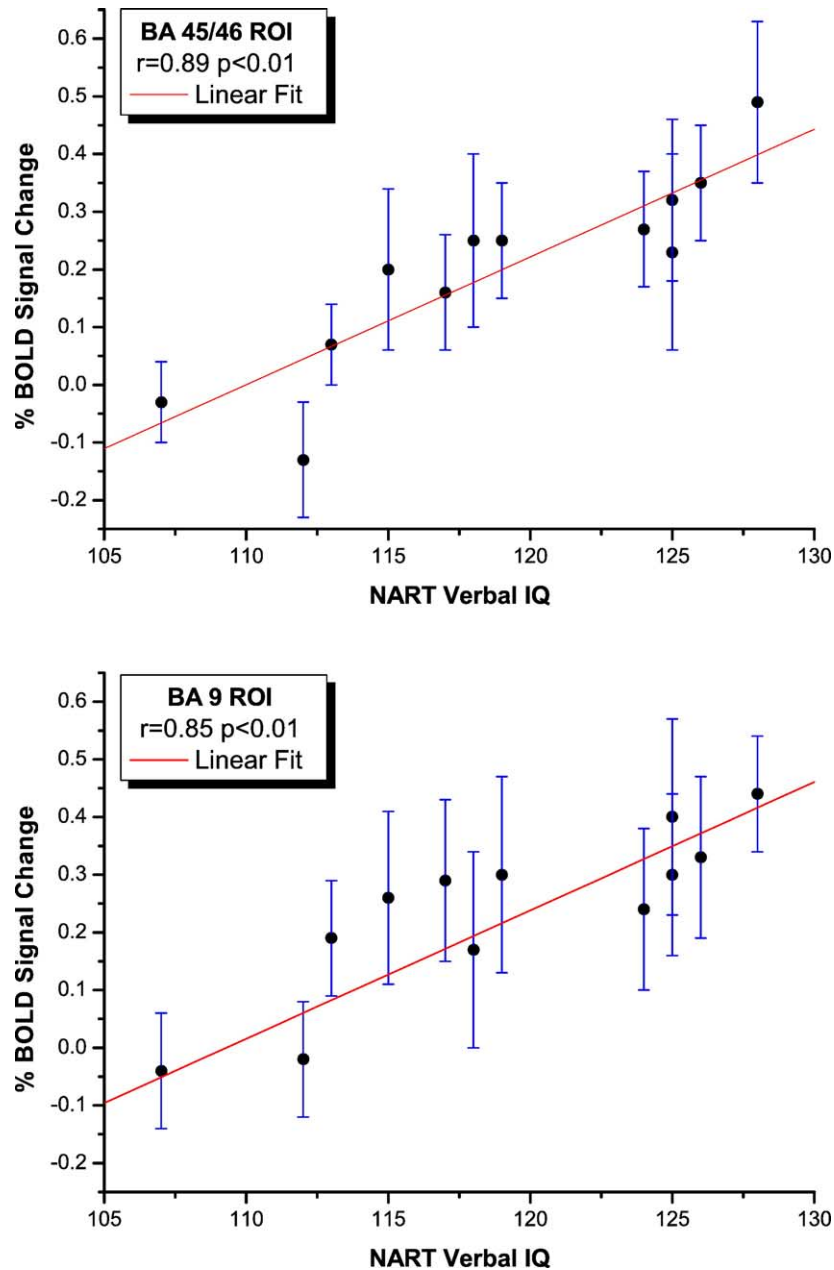


Fig. 4. Scatterplots showing the variation across the sample group of the mean %BOLD signal change of the positive linear trend in ADR within the BA 9 and BA 45/46 ROIs with NART verbal intelligence. Error bars indicate ± 1 SEM.

Osherson, 2001). The involvement of regions in the medial frontal gyri is consistent with previous data showing engagement of the middle frontal gyrus in changes of executive functioning required to learn new rules (Strange et al., 2001); here, a new analogical transformation with each criterion item. Furthermore, activations in the left ventral inferior prefrontal cortex could then be accounted for by an earlier finding that this frontal region is specifically involved in relational integration of task complexity (Christoff et al., 2001), particularly when the task requires selection from competing alternatives (Kroger et al., 2002), a feature of our plausibility paradigm. To this purpose, activations in anterior PFC (BA 47/10) are consistent with an account of this region as being involved in resolving sub-goals (Koechlin et al., 1999), here, comparison amongst plausible response choices. Additional to this

frontal network, activations in the right superior frontal gyrus, and in the adjacent middle frontal areas, are interpretable as supporting models of right hemisphere involvement in the processing of distant associations that may be useful in creative thought and problem solving (Seger et al., 2000). Unsurprisingly, our tasks also activated the anterior cingulate/paracingulate cortex, a region whose role in attention and higher-order decision-making has been well established (Kroger et al., 2002; Parsons and Osherson, 2001), although whether this is done by initiation or inhibition remains equivocal (Knauff et al., 2002).

Significant activations were also found bilaterally in the inferior frontal gyri, which on the left were in or adjacent to Broca's area, and on the other side, in its right homolog. In particular, activations in Broca's area were positively correlated with participants' NART

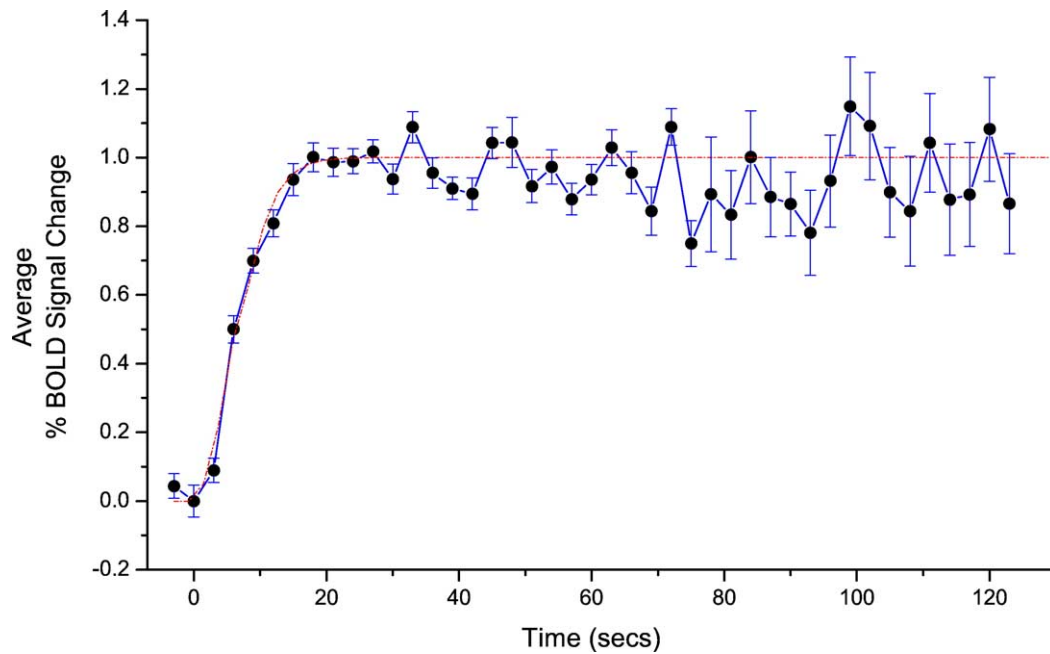


Fig. 5. Group mean time series of %BOLD signal change in response to the high and medium ADR items within an ROI of 81 voxels centred around Talairach coordinates $(-50, 18, 24)$, corresponding to the left IFG. The plot shows the grand average %BOLD signal change over all the items; the blue line indicates the average response, the red dashed line the best convolved HRF fit to the data (the fit has a mean lag of 6.2 s). Error bars indicate ± 1 SEM.

VI scores. However, the precise role of language systems in reasoning abilities is unclear (Embick et al., 2000). While some earlier neuroimaging studies of deductive and inductive reasoning report evidence in support of the hypothesis that language underpins human reasoning (Goel et al., 1997), later investigations found evidence for non-linguistic deductive reasoning, involving an occipito-parietal-frontal network (Goel and Dolan, 2001), in which the anterior cingulate cortex mediates task attention, possibly by inhibiting irrelevant information (Knauff et al., 2002), but which bypasses the linguistic system. Given that the letter strings in

Copycat were deliberately chosen so as not to contain, or to suggest, any words in the English lexicon, this result challenges a simple explanation of the involvement of Broca's area in what is essentially a non-language task. One possible explanation could be that participants were engaging in a degree of sub-vocalisation in response to the task demands of the analogy letter string stimuli. Alternatively, our results could support an interpretation of the role of Broca's area as being involved in processing syntax governing the hierarchical organisation of words and phrases rather than in language knowledge per se (Embick et al., 2000).

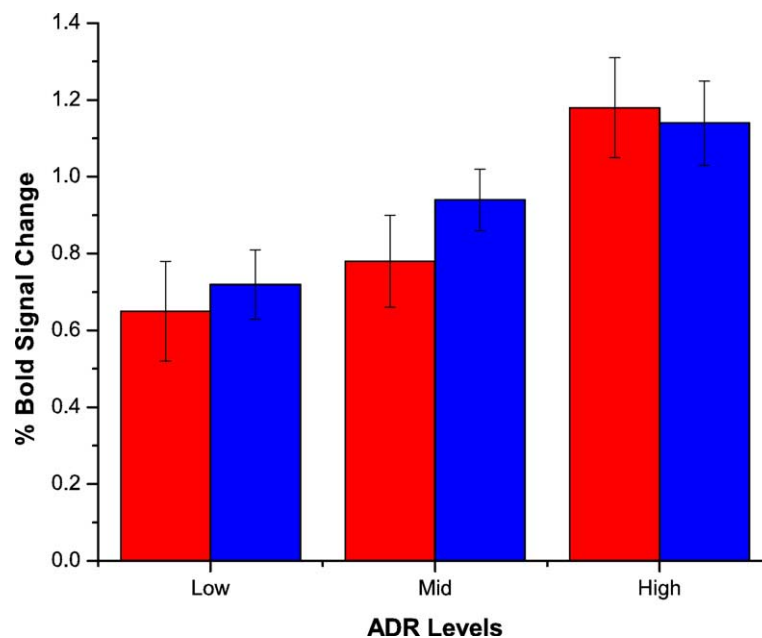


Fig. 6. Group mean %BOLD change across ADR levels (low, medium, high) in the two IFC ROIs (BA 9—red bars and BA 45/46—blue bars). Error bars indicate ± 1 SEM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The activation of non-frontal areas, particularly the inferior parietal lobes including the precuneus, is consistent with previous evidence for involvement of an occipito–parietal–frontal loop in the processing of visually presented, quasi-spatial problems (Goel and Dolan, 2001; Knauff et al., 2002), especially for high-*g* participants (O’Boyle et al., abstract, International Neuroscience Conference, Tokyo, 2002). This is likely to be the case here with analogies which required processing and manipulation of quasi-spatial alphabetic sequence information. However, it is not clear from our data what the temporal order of the involvement of these areas is in such tasks; in particular, whether involvement of the frontal regions represents some end-point of the information processing time-course or part of a feedback loop. Thus, some future understanding of the time course of these activations could be informative, assuming that the question is tractable given the multiple iterative task demands of attention, rehearsal and, meaning making.

Activations in the lingual gyrus are likely to have resulted from the greater modulation of visual attention required for the higher ADR items as compared to the lower ADR items (Knauff et al., 2002). Indeed, this sensitivity of visual areas to attentional modulation has been well documented (for an extensive review, see Wandell, 1999). In contrast, there was no significant activation of the fusiform gyrus in the main group comparison map [Fig. 2], whereas the separate group maps for the high, medium, and low ADR conditions (not reported here) showed significant bilateral fusiform gyri activations, including in the VWFA in the lateral fusiform gyrus. The VWFA is an area known to be involved with the processing, not of words per se, but of generic orthographic sequences (McCandliss et al., 2003; Todd and Marois, 2004). The other visual cortical activations in the main group map [Fig. 2] were attributed, not from differences in duration (Christoff et al., 2001), but from attentional factors not entirely controlled for across conditions.

The absence of any significant activations in the RT-based GLM suggests that participants were indeed involved in determining the best analogy response, rather than some associative or peripheral aspect of the task. For example, the analogy item $a \rightarrow b, z \rightarrow ?$ is more complex than the item $aabbcc \rightarrow aabbdd, ppqqr \rightarrow ?$, which had more letters but was simpler; each had similar average RTs, even though there was a general trend (as demonstrated by the significant correlation with SSL) for RT to increase with string length. This demonstrates the constraint on the correlation between RT and ADR due to the contribution to RT, both from processing the analogy as well as reading the letter strings multiple times in order to complete the task. Consequently, we would not have expected to see RT highly correlated with the event demands. Rather, our results are consistent with earlier studies showing that activations in the middle frontal gyrus are correlated with reasoning complexity rather than task duration (Christoff et al., 2001; Kroger et al., 2002).

In the context of studying the neural correlates of intelligence, it should be noted that the NART has also been used as a behavioural measure in previous fMRI investigations of neural processing capacity, conceptualised as “cognitive reserve” (Stern et al., 2003). It has been argued that cognitive reserve allows individuals to cope with the general (rather than just pathological) cognitive challenge associated with neural changes in response to moving from low to high task demand. The significant linear correlation we have demonstrated between neural activation strength and NART VI found in the BA 9 and BA 45/46 ROI analyses, all the more notable for the restricted (high) range of verbal intelligence scores in our

sample, is similar to previously reported associations of BOLD activation strength with intelligence using the NART (Stern et al., 2003), and in other studies (Gray et al., 2003; Rypma et al., 1999). Whereas the ROIs we have identified are centred some distance from that of Christoff et al.’s (2001) ROI analysis centred on BA 44 (MNI coordinates $-44, 4, 33$) of convergent analogising employing the RPM, it is closer to Gray et al.’s (2003) reported largest frontal activation (BA 46/45: MNI coordinates $-46, 18, 24$) in their RPM study of neural correlates of *g*. Interestingly, Rypma et al. (1999) have shown activity in an almost identical area to the larger of our ROIs (at Talairach coordinates $-37, 29, 20$) in a working memory task involving an extended array of letters, suggesting that this region mediates high WM processing load. Additionally, the results of a recent ERP study of individual differences in Visual WM capacity of a graphic colour array (Vogel and Machizawa, 2004) are strongly consistent with our findings. Vogel and Machizawa (2004, see Fig. 3b) report a linear relationship ($r = 0.78$) between the amplitude of ERP contra-lateral-delay as a measure of RH neural activity and Visual WM capacity within the range of individual differences for their criterion memory array task.

Clearly, our study can only be a first step towards an evidential base for understanding the putative contribution of fluid analogy making to intellectual functioning. Nevertheless, the neural correlates reported here are readily interpretable in conjunction with the findings of others, whilst offering a new perspective with which to inform these earlier results. Our analysis using NART VI as a global covariate identified PFC areas in which g_c measures correlated with activations on our g_f task. While causation cannot, of course, be attributed to such a correlative result, there is at least consistency with the conjecture that crystallised intelligence may be underpinned by fluid analogy making (French, 2002; Hofstadter, 1995, 2001; Holyoak and Thagard, 1995; Mitchell, 1993). Moreover, as activations in these PFC areas have been previously associated with variance in WM load, our results add to a growing literature which indicates a critical role for WM in all intellectual functioning, and thus its candidature as a neurobiological correlate of *g* (Gray and Thompson, 2004), the meta-factor of common variance between g_c and g_f (Carroll, 1993; Macintosh, 1998). In conclusion, therefore, this study offers support for the conjecture that fluid analogising underpins general intellectual performance and indicates a possible direction for future studies.

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References

- Annett, M., 1970. A classification of hand preferences by association analysis. *Br. J. Psychol.* 61, 303–321.
- Baddeley, A., Sala, S.D., 1998. Working memory and executive control. In: Roberts, A.C., Robbins, T.W., Weiskrantz, L. (Eds.), *The prefrontal cortex: executive and cognitive functions*. Oxford Univ. Press, Oxford, pp. 9–21.
- Beauchamp, M.S., Petit, L., Ellmore, T.M., Ingelholm, J., Haxby, J.V., 2001.

- A parametric fMRI study of overt and covert shifts of visuospatial attention. *NeuroImage* 14, 310–321.
- Burns, B.D., 1996. Meta-analogical transfer: transfer between episodes of analogical reasoning. *J. Exper. Psychol., Learn., Mem., Cogn.* 22, 1032–1048.
- Carroll, J.B., 1993. *Human cognitive abilities: a survey of factor-analytic studies*. Cambridge Univ. Press, New York.
- Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J.K., Holyoak, K.J., Gabrieli, J.D., 2001. Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *NeuroImage* 14, 1136–1149.
- Collins, D., Neelin, P., Peters, T., Evans, A.C., 1994. Automatic 3D inter-subject registration of MR volumetric data in standardized Talairach space. *J. Comput. Assist. Tomogr.* 18, 192–205.
- Dunbar, K., 2001. The analogical paradox: why analogy is so easy in naturalistic settings, yet so difficult in the psychological laboratory. In: Gentner, D., Holyoak, K.J., Kokinov, B.N. (Eds.), *The analogical mind: perspectives from cognitive science*. MIT Press, Cambridge, MA, pp. 313–334.
- Duncan, J., 2001. An adaptive coding model of neural function in prefrontal cortex. *Nat. Rev., Neurosci.* 2, 820–829.
- Duncan, J., Owen, A.M., 2000. Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci.* 23, 475–483.
- Duncan, J., Seitz, R.J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., Newell, F.N., Emslie, H., 2000. A neural basis for general intelligence. *Science* 289, 457–460.
- Embick, D., Marantz, A., Miyashita, Y., O'Neil, W., Sakai, K.L., 2000. A syntactic specialization for Broca's area. *Proc. Natl. Acad. Sci. U. S. A.* 97, 6150–6154.
- Freeman, J., Godfrey, H., 2000. The validity of the NART-RSPM index in detecting intellectual decline following traumatic brain injury: a controlled study. *Br. J. Clin. Psychol.* 39 (Pt. 1), 95–103.
- French, R.M., 2002. The computational modeling of analogy-making. *Trends Cogn. Sci.* 6, 200–205.
- Geake, J.G., 2003. Adapting middle level educational practices to current research on brain functioning. *J. N. Engl. League Middle Schools* 15, 6–12.
- Goel, V., Dolan, R.J., 2001. Functional neuroanatomy of three-term relational reasoning. *Neuropsychologia* 39, 901–909.
- Goel, V., Gold, B., Kapur, S., Houle, S., 1997. The seats of reason? An imaging study of deductive and inductive reasoning. *NeuroReport* 8, 1305–1310.
- Goswami, U., 2001. Analogical reasoning in children. In: Gentner, D., Holyoak, K.J., Kokinov, B.N. (Eds.), *The analogical mind: perspectives from cognitive science*. MIT Press, Cambridge, MA, pp. 437–470.
- Gray, J.R., Thompson, P.M., 2004. Neurobiology of intelligence: science and ethics. *Nat. Neurosci. Rev.* 5, 471–482.
- Gray, J.R., Chabris, C.F., Braver, T.S., 2003. Neural mechanisms of general fluid intelligence. *Nat. Neurosci.* 6, 316–322.
- Halford, G.S., 1992. Analogical reasoning and conceptual complexity in cognitive development. *Hum. Dev.* 35, 193–217.
- Hofstadter, D.R., 1995. *Fluid concepts and creative analogies*. Basic Books, New York.
- Hofstadter, D.R., 2001. Analogy as the core of cognition. In: Gentner, D., Holyoak, K.J., Kokinov, B.N. (Eds.), *The analogical mind: perspectives from cognitive science*. MIT Press, Cambridge, MA, pp. 504–537.
- Holyoak, K.J., Thagard, P., 1995. *Mental leaps: analogy in creative thought*. The MIT Press, Cambridge MA.
- James, W., 1890/1950. *The principles of psychology*. Henry Holt, New York.
- Knauff, M., Mulack, T., Kassubek, J., Salih, H.R., Greenlee, M.W., 2002. Spatial imagery in deductive reasoning: a functional MRI study. *Brain Res. Cogn. Brain Res.* 13, 203–212.
- Koechlin, E., Basso, G., Pietrini, P., Panzer, S., Grafman, J., 1999. The role of the anterior prefrontal cortex in human cognition. *Nature* 399, 148–151.
- Kroger, J.K., Sabb, F.W., Fales, C.L., Bookheimer, S.Y., Cohen, M.S., Holyoak, K.J., 2002. Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: a parametric study of relational complexity. *Cereb. Cortex* 12, 477–485.
- Luo, Q., Perry, C., Peng, D., Jin, Z., Xu, D., Ding, G., Xu, S., 2003. The neural substrate of analogical reasoning: an fMRI study. *Brain Res. Cogn. Brain Res.* 17, 527–534.
- Macintosh, N.J., 1998. *IQ and human intelligence*. Oxford Univ. Press, Oxford.
- McCandliss, B.D., Cohen, L., Dehaene, S., 2003. The visual word form area: expertise for reading in the fusiform gyrus. *Trends Cogn. Sci.* 7, 293–299.
- Mitchell, M., 1993. *Analogy-making as perception: a computer model*. The MIT Press, Cambridge, MA.
- Nelson, H.E., 1991. *National adult reading test (NART) test manual*. NFER-Nelson Publishing, Windsor, UK.
- Parsons, L.M., Osherson, D., 2001. New evidence for distinct right and left brain systems for deductive versus probabilistic reasoning. *Cereb. Cortex* 11, 954–965.
- Petit, L., Haxby, J.V., 1999. Functional anatomy of pursuit eye movements in humans as revealed by fMRI. *J. Neurophysiol.* 81, 463–471.
- Prabhakaran, V., Smith, J.A., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1997. Neural substrates of fluid reasoning: an fMRI study of neocortical activation during performance of the raven's progressive matrices test. *Cognit. Psychol.* 33, 43–63.
- Rypma, B., Prabhakaran, V., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1999. Load-dependent roles of frontal brain regions in the maintenance of working memory. *NeuroImage* 9, 216–226.
- Schacter, D.L., Buckner, R.L., Koustaal, W., Dale, A.M., Rosen, B.R., 1997. Late onset of anterior prefrontal activity during true and false recognition: an event-related fMRI study. *NeuroImage* 6, 259–269.
- Seger, C.A., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 2000. Functional magnetic resonance imaging evidence for right-hemisphere involvement in processing unusual semantic relationships. *Neuropsychology* 14, 361–369.
- Stern, Y., Zarahn, E., Hilton, H.J., Flynn, J., DeLaPaz, R., Rakitin, B., 2003. Exploring the neural basis of cognitive reserve. *J. Clin. Exp. Neuropsychol.* 25, 691–701.
- Strange, B.A., Henson, R.N., Friston, K.J., Dolan, R.J., 2001. Anterior prefrontal cortex mediates rule learning in humans. *Cereb. Cortex* 11, 1040–1046.
- Todd, J.J., Marois, R., 2004. Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature* 428, 751–754.
- Vogel, E.K., Machizawa, M.G., 2004. Neural activity predicts individual differences in visual working memory capacity. *Nature* 428, 748–751.
- Wandell, B.A., 1999. Computational neuroimaging of human visual cortex. *Annu. Rev. Neurosci.* 22, 145–173.
- Wharton, C.M., Grafman, J., Flitman, S.S., Hansen, E.K., Brauner, J., Marks, A., Honda, M., 2000. Toward neuroanatomical models of analogy: a positron emission tomography study of analogical mapping. *Cogn. Psychol.* 40, 173–197.
- Woolrich, M.W., Ripley, B.D., Brady, M., Smith, S.M., 2001. Temporal autocorrelation in univariate linear modeling of FMRI data. *NeuroImage* 14, 1370–1386.