

Intentional false responding shares neural substrates with response conflict and cognitive control

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The ability to deceive others is a high-level social and cognitive function. It has been suggested that response conflict and cognitive control increase during deceptive acts but this hypothesis has not been evaluated directly. Using fMRI, we tested this prediction for the execution of an intentional false response. Subjects were instructed to respond truthfully or falsely to a series of yes/no questions that were also varied in autobiographical and nonautobiographical content to further examine the influence of personal relevance when lying. We observed an interference effect (longer reaction times for false versus true responses) that was accompanied by increased activation within the anterior cingulate, caudate and thalamic nuclei, and dorsolateral prefrontal cortex (DLPFC), a circuit that has been implicated in response conflict and cognitive control. Behavioral and neural effects were more robust when falsifying autobiographical responses relative to nonautobiographical responses. Furthermore, a correlation between reaction time and left caudate activity supported the presence of increased response inhibition when falsifying responses. When presented with self-relevant (autobiographical) stimuli regardless of response condition, the mesial prefrontal and posterior cingulate cortices were recruited. Neural activity within these two regions and the anterior cingulate cortex (ACC) also showed correlations with self-report personality measures from the Psychopathic Personality Inventory (PPI). Overall, we conclude that the process of interference is inherent to the act of falsifying information and that the amount of conflict induced and cognitive control needed to successfully execute false responses is greater when dealing with personal information.

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Introduction

Many attempts have been made to define markers of deceptive behavior using both behavioral (body posture, speech patterns, and response latency) (DePaulo et al., 2003; Seymour et al., 2000; Zuckerman et al., 1981) and physiological measures (heart rate, skin conductance, and pupil diameter) (Dionisio et al., 2001; Godert et al., 2001; Podlesny and Raskin, 1977). Nevertheless, the subjective nature of experimenter evaluations and differences in the nature of each individual's level of moral and ethical behavior produce a considerable amount experimental variability for such measures (Ben-Shakhar and Dolev, 1996; Bradley and Cullen, 1993; DePaulo et al., 2003; Kircher and Raskin, 1988). However, the availability of techniques such as functional magnetic resonance imaging (fMRI) allows for a direct examination of the neural activity that underlies deceptive behavior.

Recent functional imaging studies have employed a variety of techniques to identify the neural correlates of deceptive behavior. For example, one study used a modified version of the Guilty Knowledge Test (Lykken, 1959, 1960) in which subjects were asked to lie about their possession of a specific target stimulus while answering truthfully to all other stimuli (Langleben et al., 2002). A second study examined the patterns of neural activity between spontaneous and memorized lies (Ganis et al., 2003), and yet another used a forced choice task in which subjects were asked to feign memory impairment such that some trials were answered incorrectly while others were answered correctly (Lee et al., 2002). These studies have identified a variety of brain regions within frontal, temporal, and parietal cortices yet the regions identified between studies have been highly variable and lacking consistent activation across all studies (Ganis et al., 2003; Langleben et al., 2002; Lee et al., 2002; Spence et al., 2001). This may be due in part to the large variability among experimental designs as well as their broad and behaviorally complex definitions of a deceptive act. Thus, our study attempted to target specific elements of deceptive behavior such as conflict, response inhibition, and higher level cognitive control using an ecologically relevant question and

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answer paradigm in combination with a simple and clearly defined deceptive act.

Our approach was based upon three current theories of deception including information manipulation theory (IMT) (McCornack, 1992, 1997), interpersonal deception theory (IDT) (Buller and Burgoon, 1996), and Zuckerman's four-factor model (Zuckerman et al., 1981). All of these posit that there is an increase in the amount of cognitive control during deceptive behavior and recent fMRI studies have confirmed that there is an increase in neural activity within a number of cortical regions implicated in control during a deceptive act (Ganis et al., 2003; Langleben et al., 2002). The need for increased "controlled behavior" is also featured as one of the four factors in Zuckerman's model and can be viewed as a product of the neural processes of conflict resolution and cognitive control (Botvinick et al., 2001; Braver et al., 2003; Cohen et al., 1990; MacDonald et al., 2000). Interestingly, the processes of conflict monitoring and higher level cognitive control have been associated with the anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (DLPFC), respectively, and both of these regions have been identified as being active during deceptive behavior using fMRI (Ganis et al., 2003; Langleben et al., 2002). Accordingly, deceptive behavior lends itself to study within the context of interference and conflict resolution since when generating a lie or a false response, one must know the truth, resist the impulse to answer truthfully, and further generate an alternative but appropriate response. Although the processes of increased conflict and cognitive control are believed to be inherent to deceptive behavior (Ganis et al., 2003; Langleben et al., 2002; Lee et al., 2002; Spence et al., 2001), they have not been the target of direct study in previous functional imaging work. Furthermore, the presence of an interference effect during deceptive behavior has not been validated with behavioral measures such as reaction time, and thus whether or not interference occurs during a deceptive act remains unconfirmed.

Perhaps the simplest deceptive act as described by Coleman and Kay (1981) is the lie, which is defined by three basic features. The first feature is the falsehood itself, for example, the communication of the falsehood. Second is the awareness that a false act/utterance has been committed, and third that this act has been committed intentionally (e.g., it is not a mistake). Thus, in the current study, we varied true versus false responses while maintaining the basic elements of a lie such that (1) subjects intentionally give a false response, (2) subjects were aware they were answering incorrectly, and (3) their responses were not the result of a mistake.

Although this task may satisfy Coleman and Kay's (1981) definition of a lie, the intentional delivery of false information in and of itself is merely a distillation of the deceptive process, which in real life is often complicated by personal circumstance. For example, one's incentive to lie may vary substantially depending upon whether or not the lie is of no personal consequence versus a scenario in which a successful lie leads to reward or deters punishment. Therefore, we added the additional dimension of personal (autobiographical) and impersonal (nonautobiographical) question types to investigate how self-relevant information interacts with levels of conflict and control processes when falsifying information. Recent functional imaging work has shown that tasks of an autobiographical versus nonautobiographical nature show distinct neural activity, which is indicative of emotional processing, and thus these manipulations afford us a simple entry point into the emotive aspects of deceptive behavior (Fink et al., 1996; Maguire and Frith, 2003; Piefke et al., 2003; Vogeley and Fink, 2003).

Furthermore, within the field of deception, there is interest as to whether or not certain classifiable personality types show a propensity towards deceptive behavior. Thus, we attempted to correlate changes in magnetic resonance signal in brain regions, which exhibited a main effect for false versus true comparisons with various sociopathic personality traits as determined by the Psychopathic Personality Inventory (PPI) (Lilienfeld and Andrews, 1996).

We predicted greater activation in the ACC and DLPFC regions for false over true responses, similar to that seen in classic interference tasks such as the Stroop and flanker paradigms (Botvinick et al., 1999; Eriksen and Eriksen, 1974; MacLeod, 1991; Stroop, 1935), and increased reaction times for false responses indicating the presence of an interference effect. We also predicted an interaction between autobiographical questions and falsifying information such that neural activity within those brain regions, which regulate response inhibition and higher level cognitive control, will show larger increases in neural activity when falsifying autobiographical information (versus nonautobiographical) since personal information is more readily accessible and highly practiced, presumably making it more difficult to suppress prepotent truthful responses. Furthermore, differences in the levels of conflict and cognitive control as indicated by functional activity may correlate with personality traits that are characteristic of high or low levels of self-control or emotionality.

Methods

Subjects

Twenty healthy volunteers (10 males and 10 females) ranging from 20 to 34 years of age (mean age 26.0 years, SD = 4) participated in the functional imaging experiment. Consent procedures were performed according to institutional guidelines and all subjects were right-handed with normal neurological histories and no contraindication for MRI.

Procedure

Stimulus development

One hundred and twenty yes/no questions were generated for pilot testing. All stimuli used for both the piloting and functional experimentation were generated and presented with E-Prime/IFIS (Psychology Software Tools, Inc., Pittsburgh, PA; MRI Devices Corporation, Gainesville, FL) software and hardware. Target stimuli included questions that were easily audible, could be delivered within a 2-s presentation period, and successfully answered within a 2-s response period. Eight subjects, four males and four females (not those referenced for functional scanning), participated in the pilot study. The four different experimental conditions were counterbalanced both within and across runs using a pseudo-randomized Latin square design (Fig. 1A). Only those questions that were answered correctly (as instructed) for 75% of the trials and still retained a content-matched pair were included. The final result was 72 yes/no questions, which comprised two different categories, autobiographical and nonautobiographical, and were represented by 36 content-matched pairs (Table 1).

Experimental design

All subjects provided their truthful responses for the 72 test questions used during the imaging experiments two or more days

prior to the imaging session to reduce priming effects. Within this questionnaire, subjects were also required to rate each question for both its emotional salience as well as their confidence in their answer. During the scanning sessions, the 72 yes/no questions were presented via headphones and were answered using a push-button response pad. Each question was answered once truthfully and once falsely across the experiment yielding four different experimental conditions (Fig. 1A) and 144 total stimuli. Stimuli and question blocks were equally dispersed across three separate functional runs. Each run consisted of eight question blocks, six questions per block, four blocks requiring truthful answers and four blocks requiring false answers (Fig. 1B). All questions within a single question block required the same response type as cued by a rear projection screen, which displayed a “T” to indicate truthful responses and an “F” to indicate false responses. The cue for the desired response type appeared on the screen 2 s prior to the onset of the question block to allow the subject time to prepare and respond appropriately. Each question was presented during a 2-s presentation period, which was followed by a 2-s silent response period in which the subject was instructed to answer either “yes” or “no” using their push-button response pad. For each subject, a visual reminder was presented during all questions blocks to indicate how to respond, for example, the index finger indicates a “yes” response and the thumb indicates a “no” response. In between questions blocks, subjects were presented with 10-s rest periods in which a fixation cross was displayed on the screen. All subjects performed a 2-min practice session in the scanner during their T1 anatomical scans in order to familiarize themselves with the question presentation and response procedures. Questions presented during the practice session were not included in the experimental task.

The four different conditions, true autobiographical (TRUE AUTO), false autobiographical (FALSE AUTO), true nonautobiographical (TRUE NONAUTO), and false nonautobiographical (FALSE NONAUTO), were counterbalanced both across and within runs using a pseudo-randomized Latin square distribution. Once this order was established, question order was held constant

Table 1

Sample of stimulus questions, matched for content

Autobiographical	Nonautobiographical
Do you own a laptop computer?	Is a laptop computer portable?
Have you ever told a lie?	Do people ever lie?
Can you ride a bicycle?	Does a bicycle have six wheels?
Were you born in New York City?	Is New York City in Ohio?

There was a significant difference ($P \leq 0.001$) in salience ratings between autobiographical (1.7 ± 0.07 SEM) and nonautobiographical questions (1.4 ± 0.07 SEM). There was no significant difference ($P \leq 0.683$) in confidence ratings between autobiographical (3.9 ± 0.03 SEM) and nonautobiographical questions (3.9 ± 0.02 SEM).

among subjects and was further counterbalanced to avoid order effects by inverting true and false responses for each question block for half of the subjects tested. Furthermore, “yes” and “no” push-button responses were counterbalanced between the thumb and index fingers across subjects and the orders of both condition and finger assignment were counterbalanced across males and females.

Finally, each subject completed the Psychopathic Personality Inventory (PPI), a self-report questionnaire designed to assess major personality traits associated with psychopathy in noncriminal populations (Lilienfeld and Andrews, 1996). Scored questions from this personality inventory can be divided into eight different subscales, each of which is characterized by different personality traits. For example, subscales of particular interest for this study are those which are characterized by either certain types of deceptive behavior (such as the “Machiavellian egocentricity” subscale, exemplified by frequent “white lies” and manipulative tendencies) or those which are characterized by high or low levels of controlled behavior (such as the “Carefree nonplanfulness” subscale, exemplified by poorly controlled and reckless behavior). Half of the subjects completed this personality styles inventory prior to their scanning session and half completed it following their session.

Image acquisition

All images were acquired using a 1.5-T (General Electric) whole-body MRI scanner with a standard head coil. An initial set of axial T1-weighted images, 19 slices, was acquired in preparation for the acquisition of the axial functional images. T2*-weighted images using a gradient echo, echo planar imaging (EPI) pulse sequence (TR = 2000 ms, TE = 60 ms, FA² = 60°, FOV = 19, 64 × 64 matrix, skip 0 mm, six disabled acquisitions at the beginning of each scan) were then acquired. Functional run duration was 5 min and 14 s during which 19 contiguous, 5.0-mm-thick oblique–axial images, oriented parallel to the anterior–posterior commissural plane, were acquired with a total of 157 brain volumes. The in-plane resolution was 3.0 × 3.0 mm and the approximate size of each volume element, or voxel, was 45 mm³. The 19 slices covered the entire cortex for all subjects. Upon the completion of experimental runs, a 124 slice, three-dimensional axial set (T1-weighted, 3-D spoiled gradient echo images) was acquired to supply a high-resolution structural image.

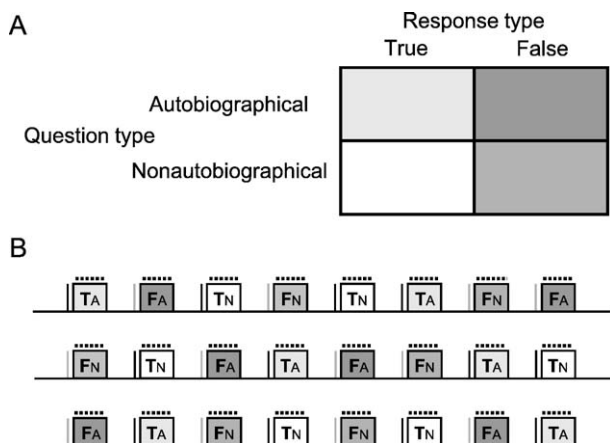


Fig. 1. Experimental paradigm. (A) Conditions were varied as a function of the type of response required (TRUE versus FALSE) and as a function of the type of question presented (AUTOBIOGRAPHICAL versus NON-AUTOBIOGRAPHICAL). (B) Eight stimulus blocks (six yes/no questions per block) were alternated with rest periods across three separate runs. A visual cue directed subject’s responses for each block and was presented 2 s prior to question onset (indicated by gray and black lines). TA, true autobiographical; FA, false autobiographical; TN, true nonautobiographical; and FN, false nonautobiographical.

² Flip angle. In an attempt to improve the MR signal to noise ratio, five individuals were scanned using a TE = 40 ms and a FA = 90°. However, these parameters showed no significant gain in signal to noise as compared to the original TE (60 ms) and FA (60°) indicated in the Methods section. Thus, remaining subjects were scanned according to the original scanning parameters. All other scanning parameters remained constant.

Image preprocessing and analysis

Data were preprocessed and analyzed using Statistical Parametric Mapping (SPM2, Wellcome Department of Imaging Neuroscience, London, UK). Each subject's data were motion corrected and then coregistered with their corresponding high-resolution SPGR T1 image. High-resolution T1 SPGR images were then spatially normalized to the MNI template and transformation parameters were subsequently applied to all functional scans within each subject. Normalized functional images were smoothed with a $6 \times 6 \times 10$ mm Gaussian smoothing kernel (i.e., two times the voxel dimensions originally acquired) and high pass filtered at 204 s. Spatially normalized functional data were first analyzed on an individual level with a general linear model using six experimental regressors (four conditions, error trials, and no-task fixation periods) convolved with the canonical hemodynamic response function. Contrast maps from individual subjects were then entered into a random-effects group analysis to identify regions of interest, which showed significant effects between conditions across all subjects. Activations were required to reach a spatial extent threshold of at least 20 contiguous voxels and all contrasts between conditions were corrected for multiple comparisons using a false discovery rate (FDR) (Genovese et al., 2002) of 0.01.

Post hoc analyses

In order to extract the average MR signal values for each ROI within each subject, all subjects' functional scans underwent a second set of analyses. Functional scans from each subject were spatially normalized to a single template subject using SPM2. Group data were then pooled and analyzed by a voxelwise multifactor ANOVA to examine the main effects based upon significant differences in MR signal change. Regions of interest were identified by F ratios with a $P \leq 0.05$ and a cluster size of five or more voxels (NeuroImaging Software, Laboratory for Clinical Cognitive Neuroscience, University of Pittsburgh, and the Neuroscience of Cognitive Control Laboratory, Princeton University). The average MR signal values obtained from each ROI for each subject were used for all subsequent post hoc analyses including correlations between MR signal changes and behavioral data (i.e., reaction time, accuracy, PPI subscale scores).

Results

Behavioral data

A main effect of response type was evident in the reaction time (RT) data (Table 2; Fig. 2), as the average RT for FALSE

Table 2
Descriptive statistics for behavioral findings

	Reaction time		Percent correct	
	Mean	SD	Mean	SD
True				
Auto	536	±149	95	±3
Nonauto	584	±183	94	±6
False				
Auto	717	±146	95	±3
Nonauto	686	±201	94	±5

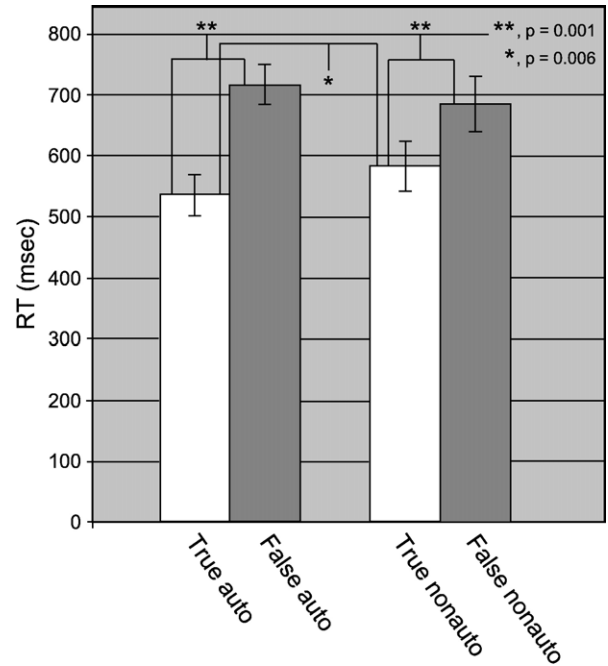


Fig. 2. Differences in reaction times between conditions of interest. All reaction time comparisons between FALSE and TRUE yielded significant differences as determined by paired t test, two tailed. Error bars represent the standard error of the mean.

responses was significantly longer than that for TRUE responses ($F[1,19] = 58.7, P < 0.001$). This main effect was qualified by a significant response type \times question type interaction effect ($F[1,19] = 11.9, P < 0.003$). This interaction was likely due to the fact that while the FALSE $>$ TRUE RT difference was significant for both AUTO and NONAUTO question types ($t = 8.5$ and 4.6 , respectively, $df = 19$ and $P < 0.001$ for both), this interference effect was significantly larger when answering AUTO as compared to NONAUTO questions ($t = 3.4, df = 19, P < 0.003$). Furthermore, individuals showed significantly longer reaction times ($t = 3.1, df = 19, P < 0.006$) when responding truthfully to nonautobiographical as compared to autobiographical questions. There was no main effect of question type nor were there any gender effects between conditions of interest ($P < 0.05$).

Subject's performance accuracy was equivalent across conditions (Table 2). Individuals rated autobiographical questions as having more emotional salience than nonautobiographical questions ($t = 6.6, df = 19, P < 0.001$) but showed no significant difference in the confidence of their responses between personal or impersonal questions.

Imaging results

FALSE versus TRUE responses

Regions more active when comparing FALSE versus TRUE responses included the left anterior cingulate, the superior, medial and middle frontal cortices (DLFPC), bilateral caudate and thalamus, left inferior frontal cortex, and left precentral regions (Table 3; Fig. 3A). All brain regions included in a single cluster of activation are listed together within the tables and clusters are ordered according to the significance of the peak voxel. No

Table 3
Brain areas active when falsifying responses (FALSE > TRUE responses)

Regions contained within cluster	BA	Peak voxel			Cluster size (voxels)	Max. <i>t</i>	Corrected <i>P</i>
		<i>x</i>	<i>y</i>	<i>z</i>			
Left anterior cingulate	32	−10	20	41	827	8.1	0.002
Right and left superior frontal	6						
Right and left medial frontal	6						
Right caudate	NA	16	−5	19	370	7.7	0.002
Right thalamus	NA						
Left caudate	NA	−20	−1	26	277	7.0	0.002
Left thalamus	NA						
Left inferior frontal	44	−57	14	12	341	6.5	0.002
Left inferior frontal	45/47						
Left caudate	NA	−20	11	16	59	6.0	0.002
Left precentral	6	−42	4	43	230	5.8	0.002
Left middle frontal	6/8/9						
Right middle frontal	10	34	42	20	46	5.4	0.003
Right superior frontal	9/10						
Right middle frontal	9	34	32	24	25	5.2	0.004
Right middle frontal	46						

Regions contained within a single cluster are listed together. Peak voxels for each cluster are located within the regions printed in bold. The spatial extent threshold was >20 voxels and an FDR of 0.01 was used to correct for multiple comparisons.

regions were more active when contrasting TRUE versus FALSE conditions.³

AUTO versus NONAUTO questions

When contrasting the AUTO versus NONAUTO conditions, significant activation was observed in the posterior cingulate, precuneus, superior, middle and medial frontal regions (mesial prefrontal), and temporal and parietal cortices (Table 4; Fig. 3B). No regions were more active when contrasting NONAUTO versus AUTO conditions.

Contrasts between the four conditions

When FALSE versus TRUE conditions were contrasted within a question type, activation was observed only in the FALSE AUTO > TRUE AUTO comparison. Regions similar to those seen within the FALSE > TRUE comparison were observed with the addition of right anterior cingulate and right inferior frontal cortices (Table 5; Fig. 3C). At the same threshold of significance, there were no regions more active when contrasting FALSE NONAUTO versus TRUE NONAUTO conditions, suggesting that the strength of the main effect (FALSE > TRUE) was carried predominantly by the difference in the AUTO condition.

When the AUTO > NONAUTO comparison was examined within response types, similar effects were observed for both comparisons, FALSE AUTO > FALSE NONAUTO and TRUE AUTO > TRUE NONAUTO. Overall, the active brain regions were identical to those observed when contrasting the main effect of AUTO > NONAUTO. No brain regions were significantly active when comparing NONAUTO > AUTO within either FALSE or TRUE conditions. Furthermore, analyses examining positive and negative interaction effects among all four conditions revealed no significant activations with an FDR of 0.01. Finally, there were

no observable gender effects for the main effects (FALSE versus TRUE and AUTO versus NONAUTO), nor for comparisons between any of the subconditions at the same level of significance (FDR = 0.01).

Correlation analysis of imaging and behavioral data

There was one brain region, the left caudate, that showed a significant correlation ($r = +0.520$, $P = 0.019$) between the percent change in MR signal between FALSE and TRUE conditions and each subject's corresponding percent change in reaction time between FALSE and TRUE conditions.

Several regions showed a correlation between the percent change in MR signal between FALSE and TRUE conditions and each subject's percent correct (performance). These included motor and supplementary motor cortices such as the postcentral gyrus ($r = +0.690$, $P = 0.001$) and right and left medial frontal gyri (BA 6/8) ($r = +0.639$, $P = 0.002$). The right DLPFC (right inferior frontal and middle frontal) also showed a positive correlation with percent correct ($r = +0.523$, $P = 0.018$).

Correlation analysis of imaging data and PPI subscale scores

Several correlations of interest were observed between individual's scores on various PPI subscales and differences in MR activity between conditions. In the anterior cingulate, an increasing score for "alienation" correlated with an increase in MR signal when answering AUTO over NONAUTO questions regardless of response type (FALSE or TRUE) ($r = +0.455$, $P = 0.044$) and when compared only within TRUE responses this association was even stronger ($r = +0.492$, $P = 0.028$) (Fig. 4A). In the mesial prefrontal cortex, the difference in MR signal between AUTO and NONAUTO question types was correlated with each subject's score for "carefree nonplanfulness" ($r = +0.522$, $P = 0.018$). This association was also stronger when examined only within TRUE responses ($r = +0.644$, $P = 0.002$) (Fig. 4B). And finally, within the posterior cingulate and precuneus cortices, subject's "coldheartedness" score correlated to the percent difference in MR signal between FALSE versus TRUE response conditions when answering nonautobiographical questions ($r = -0.518$, $P = 0.019$).

³ Raw MR signal analysis. All regions of interest identified using SPM2 were verified by comparisons between the four conditions using the MR signal extracted from each ROI using a linear regression model. All ROIs showed significant differences between the main conditions of response and question type but no significant interaction effect was found.

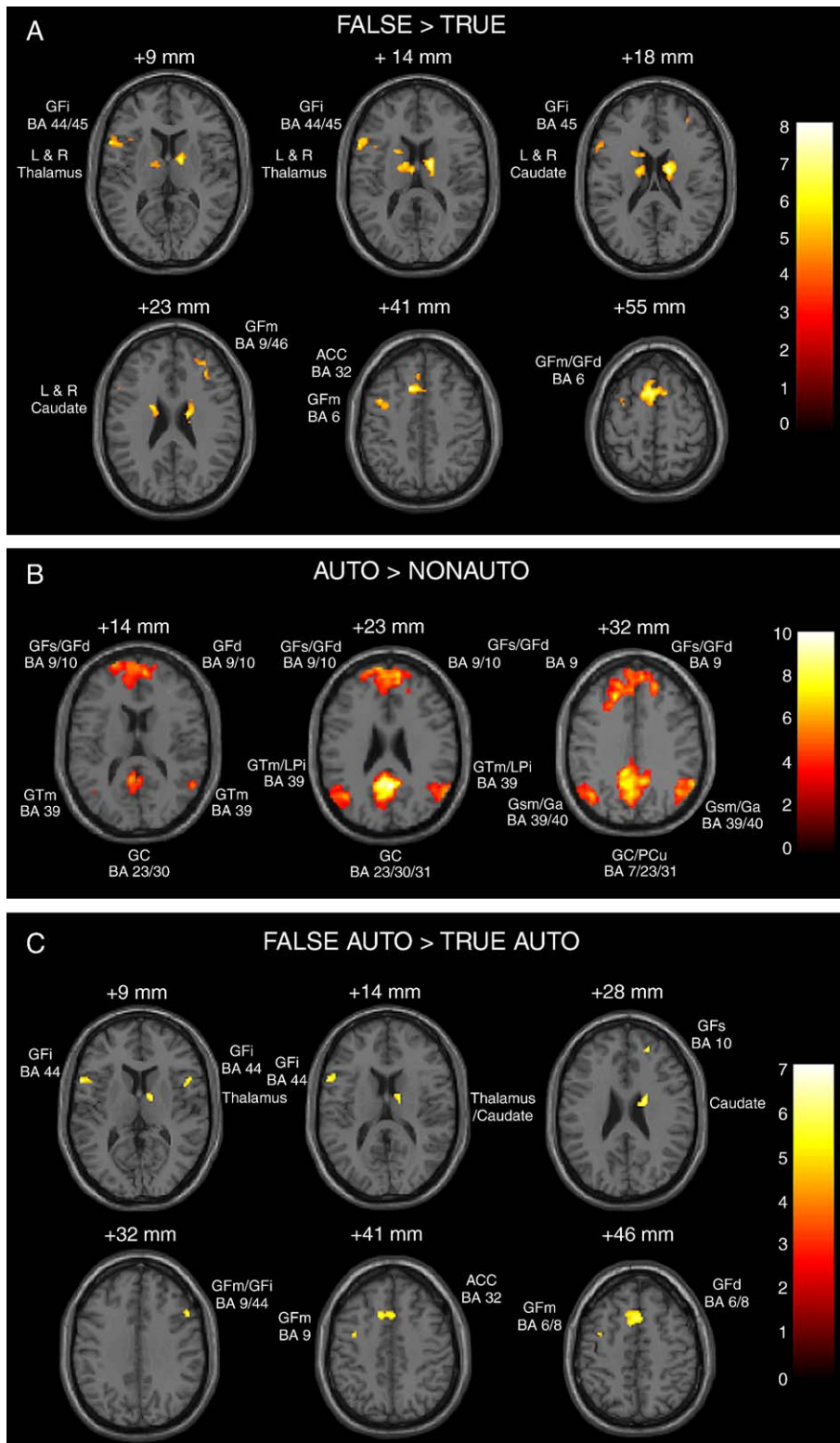


Fig. 3. Brain areas showing differences between conditions. Regions are displayed on standard MNI template brain in axial slices demonstrating clusters listed in accompanying tables. Slice location is given by its respective Talairach z coordinate and images are shown in neurological convention (left side of image is left side of brain). Brain regions and Brodmann's areas are labeled accordingly. Color scale represents t score values for corresponding functional overlays. (A) Main effect for the comparison between all FALSE responses versus all TRUE responses. (B) Main effect for the comparison between all AUTO questions versus all NONAUTO questions. (C) Effect for the comparison between FALSE AUTO and TRUE AUTO subconditions. No activation was observed when comparing FALSE NONAUTO and TRUE NONAUTO subconditions.

Table 4
Brain areas active when answering autobiographical questions (AUTO > NONAUTO responses)

Regions contained within cluster	BA	Peak voxel			Cluster size (voxels)	Max. <i>t</i>	Corrected <i>P</i>
		<i>x</i>	<i>y</i>	<i>z</i>			
Right posterior cingulate	31	4	−51	27	3040	10.1	0.001
Right and left posterior cingulate	23/30/31						
Right and left precuneus	7/31						
Right superior frontal	8	22	45	37	6812	8.7	0.001
Right and left superior frontal	8/9/10						
Right and left medial frontal	9/10						
Right and left middle frontal	8/9						
Right and left cingulate	24/32						
Left middle frontal	6						
Right supramarginal	40	57	−51	36	1015	6.9	0.001
Right middle temporal	39						
Right inferior parietal lobule	39/40						
Right superior temporal	39						
Right angular gyrus	39						
Left angular gyrus	39	−42	−62	34	148	6.7	0.001
Left middle temporal	39						
Left inferior parietal lobule	39/40						
Left superior temporal	39						
Left supramarginal	40						

Regions contained within a single cluster are listed together. Peak voxels for each cluster are located within the regions printed in bold. The spatial extent threshold was >20 voxels and an FDR of 0.01 was used to correct for multiple comparisons.

(Fig. 4C). There were no significant correlations between individual subject's scores on the PPI subscales and subject's reaction times for any of the main conditions nor subconditions.

Discussion

Summary

The presence of an interference effect when falsifying information was confirmed by significantly longer reaction times for FALSE versus TRUE responses in all subjects. Furthermore, our imaging findings indicate that the same brain regions, which are engaged during classical interference tasks (MacDonald et al.,

2000; MacLeod, 1991; Peterson et al., 1999; Stroop, 1935), and the suppression of highly practiced responses (Casey et al., 2001, 2002; Durston et al., 2002, 2003; Mink, 1996; Peterson et al., 2002) are significantly more active when falsifying information as compared to when answering truthfully. Thus, both our behavioral and functional findings support the hypothesis that interference is integral to the act of falsifying responses. Furthermore, the magnitude of the effect between FALSE versus TRUE comparisons for both functional and reaction time comparisons was more robust within the autobiographical as compared to nonautobiographical conditions. This suggests that one experiences a greater amount of conflict and need for increased cognitive control when falsifying information about oneself rather than information of no personal significance.

Table 5
Brain areas active when falsifying responses to autobiographical questions (FALSE AUTO > TRUE AUTO)

Regions contained within cluster	BA	Peak voxel			Cluster size (voxels)	Max. <i>t</i>	Corrected <i>P</i>
		<i>x</i>	<i>y</i>	<i>z</i>			
Left superior frontal	6	−2	12	51	512	7.2	0.005
Right and left superior frontal	6						
Right and left medial frontal	6/8						
Right ^a and left anterior cingulate	32						
Left inferior frontal gyrus	44	−57	14	12	78	6.6	0.005
Right superior frontal	10	22	46	20	28	6.5	0.005
Right caudate	NA	20	−3	22	179	6.4	0.005
Right thalamus	NA						
Right middle frontal	9	50	19	32	30	5.8	0.006
Right inferior frontal^a	44	52	14	9	30	5.6	0.006
Left middle frontal	6	−36	0	41	22	5.1	0.008
Left middle frontal	8						

Regions contained within a single cluster are listed together. Peak voxels for each cluster are located within the regions printed in bold. The spatial extent threshold was >20 voxels and an FDR of 0.01 was used to correct for multiple comparisons.

^a Indicates regions which were unique to the FALSE AUTO > TRUE AUTO contrast as compared to the FALSE > TRUE contrast.

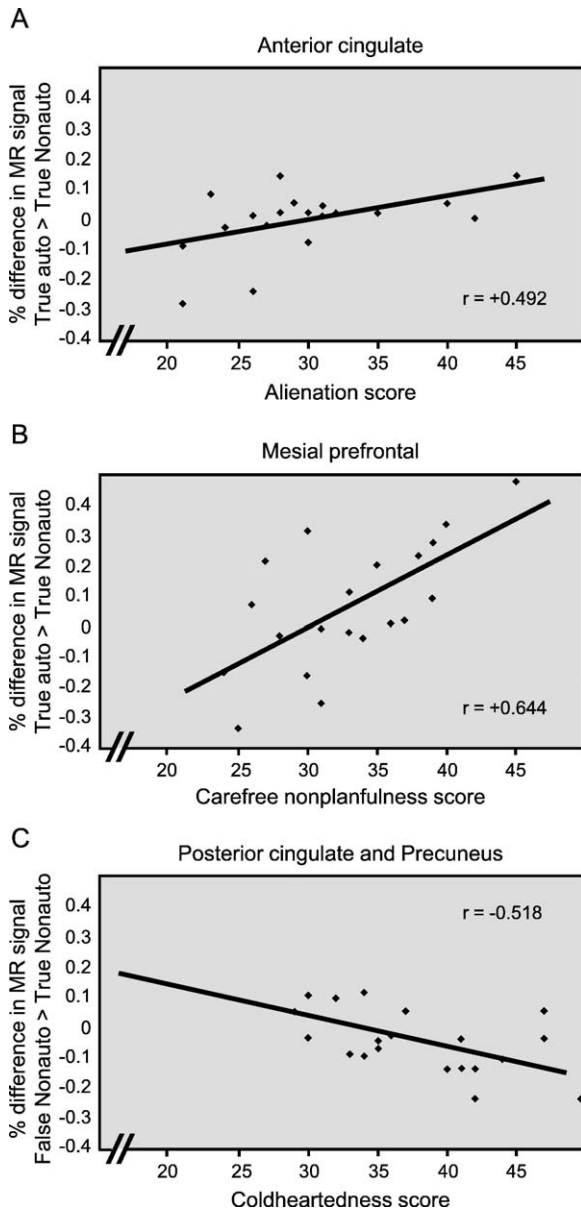


Fig. 4. Correlations between PPI subscale scores and MR signal differences between conditions within regions of interest. Each data point represents a single subject and the regression line was determined by least squares fit. (A) The percent difference in MR signal between TRUE AUTO and TRUE NONAUTO conditions within the right and left anterior cingulate cortex (BA 32) was correlated with each subject's score on the alienation subscale of the PPI. (B) The percent difference in MR signal between TRUE AUTO and TRUE NONAUTO conditions within the mesial frontal (BA 9/10) cortex was correlated with each subject's score on the carefree nonplanfulness subscale of the PPI. (C) The percent difference in MR signal between FALSE NONAUTO and TRUE NONAUTO conditions within the posterior cingulate (BA 31) and precuneus (BA 7) regions was correlated with each subject's score on the coldheartedness subscale of the PPI.

Evidence for cognitive control, conflict, and interference effects

When comparing FALSE versus TRUE responses, we observed functional activation, which reflects that seen during classic Stroop interference tasks (Liu et al., 2004; MacDonald et al., 2000;

Milham et al., 2002; Peterson et al., 1999) including the right and left DLPFC, the right and left inferior frontal gyri, and the anterior cingulate (Fig. 3A). This interference effect was also present at the behavioral level (longer RTs for FALSE responses) and cannot be attributed to differences in question difficulty as not only were all questions counterbalanced across conditions and subjects, but confidence ratings were comparable across questions as well (Table 1). The ACC and DLPFC regions are often jointly active during tasks that require a significant amount of working memory, error monitoring, and task preparation (Courtney et al., 1998a; Courtney et al., 1998b; Garavan et al., 2002; MacDonald et al., 2000; Ruff et al., 2001), but recent studies suggest that activity within these two regions can be dissociated from one another and ultimately implicate the DLPFC and ACC in higher level cognitive control and conflict monitoring, respectively (Carter et al., 1998; Dreher and Berman, 2002; Garavan et al., 2002; Hernandez et al., 2001; Kerns et al., 2004; MacDonald et al., 2000). In addition to cognitive control and decision making, the left middle frontal cortex (BA 9) has also been associated with memory and motor control (Leung et al., 2002; Pedersen et al., 1998). Thus, the increased activation within these areas when falsifying information indicates there are increased levels of conflict and cognitive control during deceptive behavior.

Interestingly, subject performance (accuracy) improved as the difference in MR signal between FALSE versus TRUE conditions increased within several different frontal regions including the bilateral premotor areas (BA 6/8) and dorsolateral portions of the prefrontal cortex (BA 9/44). Increased neural activity within these regions may reflect the need for a greater level of motor and cognitive control when falsifying responses as the impulse to respond truthfully must be suppressed for button press responses as well. Thus, this association is not unexpected and illustrates the presence of an interference effect at both the behavioral (longer reactions for FALSE responses) and neural levels (increased MR signal in regions that exercise motor and cognitive control).

Evidence for response inhibition

The caudate and thalamus also showed more neural activity for FALSE versus TRUE comparisons and these two regions are commonly observed during tasks that require individuals to suppress prepotent or highly practiced responses (Casey et al., 2001, 2002; Durston et al., 2002, 2003; Mink, 1996; Peterson et al., 2002). The basal ganglia have traditionally been implicated in inhibitory motor control but recent research suggests that these nuclei may exert inhibitory control over mental "actions" as well (Casey et al., 2001, 2002; Mink, 1996; Redgrave et al., 1999). Thus, these activations may reflect the inhibition of the impulse to answer truthfully. Interestingly, the left caudate was the only region to show a correlation between the magnitude of change in MR signal between FALSE and TRUE conditions and reaction time differences between FALSE and TRUE responses. Presumably, the increase in neural activity within the left caudate is reflected by increased reaction times due to the greater need to inhibit a prepotent response. Thus, we conclude that there is an increase in the amount of conflict and higher level cognitive control needed when falsifying information. Based upon both the functional imaging and behavioral data, these processes can be labeled as an interference effect.

Augmented conflict and cognitive control for personal information

When analyses were restricted to question type (AUTO and NONAUTO), a significant effect was observed between FALSE > TRUE responses only when comparing autobiographical questions (FALSE AUTO > TRUE AUTO). Thus, an increase in neural activity was observed across both question types when falsifying information but the effect was more robust when examining autobiographical questions alone. This was accompanied by a larger difference in FALSE > TRUE reaction time for autobiographical questions. These results are important for several reasons. First, they provide evidence that the simple element of personal relevance noticeably influences patterns of behavioral and neural activity within the context of deceptive behavior. Second, they suggest that there is a difference in the amount of conflict one experiences when falsifying personal information as well as the amount of cognitive control needed to successfully implement a response. And finally, future functional imaging studies of deception may benefit by exploiting the increased power self-relevant stimuli affords and thus greatly enhance the sensitivity of experimental designs.

Brain areas that are engaged during self- versus non-self-discriminations

Interestingly, when contrasting the AUTO versus NONAUTO conditions, we observed robust and distinct activations in the superior and medial frontal regions (mesial prefrontal), the posterior cingulate, precuneus, and temporal and parietal cortices (Table 4; Fig. 3B). The pattern of functional activation seen for this comparison is strikingly similar to that observed in a recent study (Greene et al., 2001), which contrasted the brain activations evoked when individuals were faced with different kinds of moral dilemmas. The moral dilemmas in Greene's study were divided into "moral–personal" and "moral–impersonal" conditions and each decision was categorized according to how closely (personally) the subject would be involved in committing a morally questionable act. The authors suggest that the different emotional response elicited by each of the dilemma types was responsible for this pattern of neural activity and indeed these regions have all been implicated in emotional processing (Lane et al., 1997a, 1997b; Maddock, 1999; Maddock et al., 2003). Although these regions may be involved during emotional or moral reasoning processes, our experiment employed a task in which the stimuli differed only between self- versus non-self-attributes, and nevertheless we observed the same pattern of neural activity. However, subjects within our study consistently rated autobiographical questions as more emotionally salient than nonautobiographical questions, and thus the possibility remains that the recruitment of these regions could be due to either the self-referential content of the stimuli or their emotional salience. But the difference in emotional salience ratings between the two categories was small (Table 1) and recent imaging studies which have focused on autobiographical processing, not emotional nor ethical content, have produced equally similar results (Vogeley and Fink, 2003; Vogeley et al., 2004). Thus, based upon our findings and recent autobiographical research, the pattern of brain activation seen for AUTO versus NONAUTO comparisons is most likely due to the differences in the self-referential content of the stimuli rather than differences in emotional or moral reasoning.

Relationships between personality traits and imaging findings

Within the regions identified above, three showed correlations with the subscales of the Psychopathic Personality Inventory (Lilienfeld and Andrews, 1996), including the anterior cingulate, mesial prefrontal, and posterior cingulate/precuneus regions. In the anterior cingulate, the difference in MR signal between AUTO versus NONAUTO conditions correlated with each subject's "alienation" score and this association was even stronger when compared within TRUE responses (Fig. 4A) but did not retain significance when compared within FALSE responses. Individuals who score highly on the "alienation" subscale tend to have various paranoid or insecure personality features. For example, they often feel like they have a lot of bad luck or that they are not as successful as they could be because others perceive them unfairly, and in general, they feel misunderstood by others. Increased neural activity within the ACC when answering autobiographical as compared to nonautobiographical questions may reflect the experience of a higher level of conflict when these individuals are faced with questions that are of a self-relevant nature (AUTO) due to their naturally underlying issues with self-perception and tendency towards feelings of persecution.

A similar association was shown within the mesial prefrontal cortex (BA 9/10) for MR signal differences between AUTO versus NONAUTO conditions and subject's "carefree nonplanfulness" scores. This correlation was also stronger when compared within TRUE AUTO and TRUE NONAUTO conditions (Fig. 4B) and did not retain significance when comparing FALSE AUTO and FALSE NONAUTO conditions. The mesial prefrontal area has been implicated in both self-identity and emotional processing (Gilboa, 2004; Lane et al., 1997a, 1997b; Piefke et al., 2003; Vogeley and Fink, 2003; Vogeley et al., 2004) and thus differences in levels of neural activity as a function of self and nonself are expected. A high score for the "carefree nonplanfulness" subscale would be common for individuals who are less inclined to monitor or evaluate their own behavior, generally irresponsible, give up easily, often make the same mistakes over and over again and have very little foresight, planning skills, or thought for others. Thus, subjects who displayed stronger tendencies for these traits showed more neural activity within the mesial prefrontal cortex when having to evaluate truthful statements about themselves versus nonself statements.

Finally, within the posterior cingulate (BA 23/30/31) and precuneus cortices (BA 7), the difference in MR signal between FALSE NONAUTO and TRUE NONAUTO conditions showed a negative correlation with subject's "coldheartedness" scores (Fig. 4C). Individuals who score highly on this scale are relatively unemotional, guiltless, do not have many deep interpersonal relationships or attachments, and are generally not concerned with others' feelings nor their effect on others. Our results support previous studies (Maddock et al., 2001; Vogeley and Fink, 2003; Vogeley et al., 2004), which suggest that these regions are responding to the self-relevance of the stimuli and one possibility is that individuals who score highly on the "coldheartedness" subscale experience a lesser degree of self-identification when lying about matters that do not concern them. Thus, individuals who are generally coldhearted may find it easier to engage in deceptive behaviors when it involves matters that are of no personal consequence. Interestingly, although the mesial prefrontal cortex and posterior cingulate/precuneus regions are often seen jointly active during tasks that incorporate autobiographical versus nonautobiographical stimuli, we observed a dissociation in their

patterns of functional activity and individual's scores on the "coldheartedness" and "carefree nonplanfulness" subscales of the PPI. This suggests that even within the general category of self-referential stimuli, these two regions may be further specialized in either their response to similar stimuli (e.g., AUTO versus NONAUTO when responding truthfully; Fig. 4B) or when different response patterns are required to the same stimuli (e.g., FALSE versus TRUE responding to nonautobiographical questions; Fig. 4C). Thus, although both regions clearly process self-referential stimuli, the mesial prefrontal region appears to be more highly specialized for self- versus non-self-comparisons whereas the posterior cingulate/precuneus region shows broader capabilities for discrimination between stimuli which are not self-relevant.

Conclusion

This study demonstrates that there is increased neural activity within the anterior cingulate, dorsolateral prefrontal cortex, and caudate and thalamic nuclei when individuals answer falsely as compared to truthfully. Based upon these functional results and the behavioral findings (longer RTs for FALSE versus TRUE responses), we conclude that interference, similar to that observed during the Stroop and other tasks that measure various aspects of response inhibition and choice selection, is inherent to the act of falsifying information and thus certain types of deceptive behavior. Furthermore, both functional activity and reaction time data showed greater differences between FALSE and TRUE comparisons for autobiographical stimuli as compared to nonautobiographical stimuli (although the interaction effect was not significant for functional activity). Thus, not only is there an interference effect when falsifying information, but the amount of conflict and cognitive control needed to successfully execute false responses is greater when individuals are faced with self-relevant circumstances. Also, the presence of a correlation for reaction time differences and MR signal differences within the left caudate nucleus between FALSE versus TRUE conditions similarly suggests there is an increased need for response inhibition when falsifying responses. And finally, certain measurable personality traits, as determined by the Psychopathic Personality Inventory, show a relationship to patterns of neural activity within the anterior cingulate, mesial prefrontal cortex, and posterior cingulate/precuneus regions and indicate that regions that are engaged when processing self-referential information (mesial prefrontal cortex and posterior cingulate/precuneus regions) may be further specialized to handle different aspects of autobiographical information. In conclusion, this is the first study to demonstrate the presence of an interference effect at both the behavioral and functional levels using a deception-based paradigm, thus providing a new foundation for future deception research as well as presenting a new medium for the study of conflict and cognitive control processes.

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