

Neural correlates of deception: lying about past events and personal beliefs

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Abstract

Although a growing body of literature suggests that cognitive control processes are involved in deception, much about the neural correlates of lying remains unknown. In this study, we tested whether brain activation associated with deception, as measured by functional magnetic resonance imaging (fMRI), can be detected either in preparation for or during the execution of a lie, and whether they depend on the content of the lie. We scanned participants while they lied or told the truth about either their personal experiences (episodic memories) or personal beliefs. Regions in the frontal and parietal cortex showed higher activation when participants lied compared with when they were telling the truth, regardless of whether they were asked about their past experiences or opinions. In contrast, lie-related activation in the right temporal pole, precuneus and the right amygdala differed by the content of the lie. Preparing to lie activated parietal and frontal brain regions that were distinct from those activated while participants executed lies. Our findings concur with previous reports on the involvement of frontal and parietal regions in deception, but specify brain regions involved in the preparation *vs* execution of deception, and those involved in deceiving about experiences *vs* opinions.

Key words: deception; fMRI; episodic memory; beliefs; lie

Introduction

For reasons of both security and justice, there is considerable interest in applying neuroimaging methods to detect deception so that deception can be identified with increasing reliability (Vrij *et al.*, 2006; Sip *et al.*, 2008; Abe, 2009). Delineating the brain basis of lying *vs* truth-telling can also be used to inform a general understanding of cognitive and neural mechanisms involved in deception (Abe, 2009; Christ *et al.*, 2009; Ganis *et al.*, 2003, 2009; Ganis, 2015). Studies using neuroimaging methods to detect deception have underscored the notion that deception is a complex and cognitively demanding task. These studies identified several brain regions that show increased activation when people lie compared with when they tell the truth (Langleben *et al.*, 2002; Ganis *et al.*, 2003; Spence, 2004; Kozel *et al.*, 2005; Johnson *et al.*, 2007; Abe *et al.*, 2008; Lisofsky *et al.*, 2014).

Deception-related activations were identified in regions that are involved in cognitive control processes such as frontal and parietal cortex (Christ *et al.*, 2009), and regions that are involved in evaluating social context such as the superior temporal cortex and temporal poles (Lisofsky *et al.*, 2014). In recent years, attention has been directed to generate experimental designs that take into account the intention of the person and the context in which the lie is executed (Sip *et al.*, 2008). In this report, we supplement these efforts by providing evidence for differentiation in the neural correlates of deception based on the type of information one is asked to lie about. We also further investigate whether preparatory activation that is irrespective of the content of the lie is related to the effectiveness by which a lie is being executed.

The definition of the verb 'lie' according to the Merriam-Webster dictionary is 'to make an untrue statement with intent

Received: 21 September 2015; Revised: 8 October 2016; Accepted: 11 October 2016

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to deceive'. Implicit in this definition are three facets of the act of lying. First, an individual must know or determine the truth in order to lie about it. Depending on the nature of the lie, this step could involve remembering specific details of an event or past experiences, or assessing one's opinion or emotional state. Second, a deceiver must then prepare an untrue statement, and finally, respond by providing the statement that is contrary to his or her determined truth. On a cognitive level, these last two steps may involve cognitive control so as to inhibit the truthful response or manipulate the true information to convert it into a lie. Indeed a meta-analysis conducted by Christ et al. (2009) suggest remarkable overlap between region involved in executive control and working memory, and this notion is supported by additional empirical work (Lisofsky et al., 2014).

Much of the prior neuroimaging work on deception has focused on how participants lie about episodic knowledge, or the detailed memory of past experiences. Detecting memory-related activation is critical for approaches to lie detection when an individual is presumably concealing personally available information about the past. Deception regarding past experiences may specifically involve brain regions supporting retrieval and maintenance of episodic memories, such as regions in the medial temporal lobes and prefrontal cortex (Rissman et al., 2010). While this type of deception may be most relevant for lie-detection in a criminal setting, it is not the only kind of lie a person can tell. For instance, other work has focused on identifying the neural correlates of people's choices to lie about their personal opinions based on the social pressures and norms of those around them (Falkiewicz et al., 2015; Volz et al., 2015). It is not well understood whether the same or a different neural circuit is engaged to deceive about memory for an experience vs a moral belief or opinion. Regions associated with moral reasoning include frontal and parietal cortex, medial frontal cortex, as well as regions in the superior temporal sulcus and the temporal parietal junction (Pascual et al., 2013).

Prior neuroimaging work on deception has also focused on detecting differential brain responses during the execution of a lie. Although it is likely that the most distinctive signature of lying will occur during its execution, it may also be possible to detect differential activation when one prepares to lie compared to preparing to tell the truth. To our knowledge, only one published report has examined the neural correlates of preparing to lie (Ito et al., 2012). That study did not find significant differences in brain activation between preparing to tell the truth and preparing to deceive, yet it did identify regions that were overall more active during a preparation to either tell the truth or lie. We hypothesized that there are different neural circuits engaged for the preparation compared with the execution of deception and that there would be individual differences in the magnitude of 'preparatory' lie activation that would be related to individuals' behavior when delivering a lie.

Thus, in this study, we aimed to further characterize the neural mechanisms of deception by examining two fundamental questions about the brain basis of deception. First, we asked if there are different neural circuits engaged for deception about personal experiences (episodic memory) or opinions. Second, we investigated if there are different neural circuits engaged for the preparation of deception vs the execution of deception, and whether individual differences in the magnitude of 'preparatory' lie activation would be related to individuals' behavior when delivering a lie.

We asked people to either tell the truth or lie about either experiences or opinions. Participants were asked yes/no questions about two distinct types of personal knowledge: episodic experiences and beliefs or opinions. For episodic knowledge,

questions probed the recollection of specific but commonplace events. For beliefs or opinions, questions focused on moral or societal topics about which most participants would have an opinion. Unlike many other studies of deception (Langenben et al., 2002, 2005; Davatzikos et al., 2005), each question was unique and did not repeat during the scan session. This was important so that response to any of the questions could not be rehearsed or directly influenced by prior responses to the same question during the scan session. We employed a second aspect of the design aimed to contextualize the experimental task in a more ecologically relevant setting. Participants were told that we would be monitoring their brain activation and that they should try to lie in a way that we could not detect by looking at the images of their brain. These instructions were intended to put the participants' deception in a social context, a factor that is known to affect the process of lying (Abe et al., 2007; Sip et al., 2012; Lisofsky et al., 2014).

We predicted that regions previously identified in a meta-analysis of deception activation (Christ et al., 2009) likely support more common aspects of deception and thus would similar profile of activation during deception regardless of the type of questions one is lying about. We also hypothesized that other regions would show differential activation when lying about episodic questions compared to lying about opinions. Specifically, regions supporting episodic memory would uniquely support lying about episodic content, whereas regions associated with processing of beliefs, or moral judgments would specifically support lying about beliefs or opinions. Finally, we hypothesized that preparing to lie will engage regions involved in voluntary allocation of attention (Ito et al., 2012) and that regions that are recruited during the preparation period would have direct influence on behavioral patterns during the execution of a lie.

Methods

Participants

Eighteen volunteers (nine males, mean age = 19.7 ± 1.0 years, range 18–21 years) were recruited from the Stanford University community. All participants were right-handed, had normal visual acuity and were screened for a history of psychiatric or medical illnesses. Participants were paid \$20 per hour for their time and gave informed consent in accordance with the guidelines of the Stanford Medical Human Subjects Committee.

Materials

One hundred and thirty yes/no questions were created for the experiment. Half of the questions were designed to tap episodic knowledge (episodic questions; mean length = 7.6 ± 1.5 , range 4–11 words; mean propositional idea density calculated with SPIDR[®] = 0.4 ± 0.1 , range 0.3–0.7). Examples include: *Have you ever ridden a horse?* *Did you watch the last Super Bowl?* The other half of the questions assessed personal beliefs and opinions (belief questions; mean length = 6.9 ± 1.7 , range 4–11 words; mean propositional idea density = 0.4 ± 0.1 , range 0.2–0.7), e.g. *Should same sex marriage be legal?* *Do you believe the death penalty is justifiable?* The assignment of questions to Lie or True condition was fully counterbalanced across participants (see below). Episodic questions were constructed with the intention to elicit a recollection of a specific episode and a time frame was added such that there will be roughly an equal distribution of yes and no answers. Belief questions were constructed to elicit reflection on a personal belief or opinion such that there would be a roughly equal

proportion of agreement and disagreement with the statements. Importantly, to minimize the confounding effects of specific response-matching patterns and the remapping of practiced responses, no items were repeated during the scan session.

Procedure

Participants were given 10 practice trials prior to entering the MR scanner. Inside the scanner, 120 trials were presented in 4 blocks of 30 trials each. Each trial began with an instruction cue word ('Lie' or 'True') presented in the center of the screen for 2 s, followed by a fixation cross that was presented for a variable duration between 3 and 5 s. Participants were instructed to use the cue and the fixation periods to prepare to either tell the truth or lie, in accordance with the cue word. A yes/no question was then presented on the screen for 4 s followed. Each trial was followed by a blank screen presented for a variable duration between 9 and 11 s to complete a total of 20 s total between the start of each trial. Participants were instructed to respond to the question as accurately and as rapidly as possible. Half of the trials were cued with 'Lie' and the other half were cued with 'True'. The specific assignment of each question to 'Lie' or 'True' conditions was counter-balanced across participants. The location of the 'yes' and 'no' response buttons was indicated at the bottom of the screen and randomized across trials to prevent simple mapping of the response options. Sixty episodic and 60 belief questions were presented in a pseudo-randomized order. Responses (yes/no) were recorded and response times were used to calculate each individual's deception cost score [$\text{deception score} = 100 \times (\text{mean reaction time to lie} - \text{mean reaction time to respond truthfully}) / \text{mean reaction time to respond truthfully}$] that was used as an indirect measure of the effort of lying across subjects.

Immediately following the scanning session, participants were presented with all 120 questions and asked to give the true responses. Inconsistencies between responses in the scanner and the post-scan review were used to define error trials that were eliminated from analyses. Participants were asked to indicate the strength of their belief for each belief question (strong or weak). Participants were asked to indicate whether, during their response for each of the episodic questions, they recollected a specific detail of an episode (remember), or whether they 'simply knew' the answer but did not recollect any specific details of a specific episode when answering the question (know). This procedure follows remember/know procedure used in memory studies to gain information about subjective memory phenomenology. Participants also filled out a brief questionnaire about their performance on the task, and completed two personality questionnaires (NEO FFI, REF and Psychopathy Personality Inventory PPI; Lilienfeld and Andrews, 1996). These questionnaires are not discussed further.

Image acquisition

Scanning was conducted with a 3.0T GE Signa scanner (General Electric, Milwaukee, WI, USA) using a custom-built volume head coil. Head movement was minimized using a bite bar, formed with the subject's dental impression. T1-weighted whole-brain anatomical images (256×256 voxels, 0.86 mm in plane resolution, 1.2 mm slice thickness) were collected for the purpose of creating a subject-specific mask of the functional data. Functional images were obtained from 24 slices aligned to the anterior-posterior commissure covering the entire brain using a spiral in/out T2* pulse sequence (Glover and Law, 2001) (TR = 2 s,

TE = 30 ms, 60° flip angle 64×64 voxels, 3.75 mm in plane resolution, 6 mm slice thickness with no slice skip). Three hundred and four volumes were acquired per functional run; the first four images were discarded to allow signal stabilization.

Data quality assessment and preprocessing

Data were visually inspected and reviewed for artifacts and motion using custom software (<http://web.mit.edu/swg/software.htm>). Functional data were subjected to artifact detection: images were defined as artifactual if movement between consecutive acquisitions exceeded 0.5 mm in any direction, or if the average image intensity was more than 3 s.d. away from the mean global intensity of the run. Data from one participant were excluded because of overall large standard deviation in the global intensity leading to sustained image artifacts. SPM2 (Wellcome Department of Imaging Neuroscience, London, UK; <http://www.fil.ion.ucl.ac.uk/spm/spm2.html>) was used for all analyses. Images were corrected for motion using sinc interpolation and adjusted for the acquisition time (to the middle); functional images were then spatially normalized based on parameters determined by normalizing the mean functional image to the T1 Montreal Neurological Institute template (MNI). Finally, images were spatially smoothed with an isotropic Gaussian kernel of 6-mm full width at half maximum.

Statistical analysis

First-level general linear model-based analyses were conducted in MNI space. Models included regressors of interest, generated by convolving task events with a canonical model of the HRF, as implemented in SPM2. The preparation period (5–7 s) and the stimuli (4 s) were modeled separately by regressor functions. This resulted in six regressors of interest: two preparation regressors (preparation-lie, preparation-true), four stimuli regressors (belief-lie, belief-true, episodic-lie, episodic-true) for each of the four runs. We used only two regressors for the preparation period because the specific question type was not available for the participants during this period. Cue presentation, error trials, motion parameters (three rotation and three translation parameters), and individual artifact images were also modeled. First-level model estimation was done using an explicit mask created by combining grey and white segments of subjects' high-resolution anatomical brain images. Linear combinations of regressors were used to define contrasts of interest: (i) belief-lie > belief-true, (ii) episodic-lie > episodic-true, (iii) preparation-lie > preparation-true. Contrasts constructed at the first level were then input into a second-level group analysis using a random-effects model. Group level activation maps were computed using a one-sample t-test. Regions that showed deception-related activations (lie > true) for both episodic and belief questions were determined by conjunction analysis of group maps for (i) belief-lie > belief-true, and (ii) episodic-lie > episodic-true (each map uncorrected voxel-level $P < 0.005$, cluster > 100 contiguous voxels). Regions in which deception effects differed by question type were identified by paired t-test across all participants using: (i) belief-lie > belief-true, and (ii) episodic-lie > episodic-true (uncorrected voxel-level $P < 0.005$, cluster > 100 contiguous voxels). Regression analysis was used to examine the relation between activations during lie preparation and deception cost score as continuous variable across subjects. All reported clusters survived uncorrected voxel-level P threshold of 0.005, and consisted of 100 or more contiguous voxels

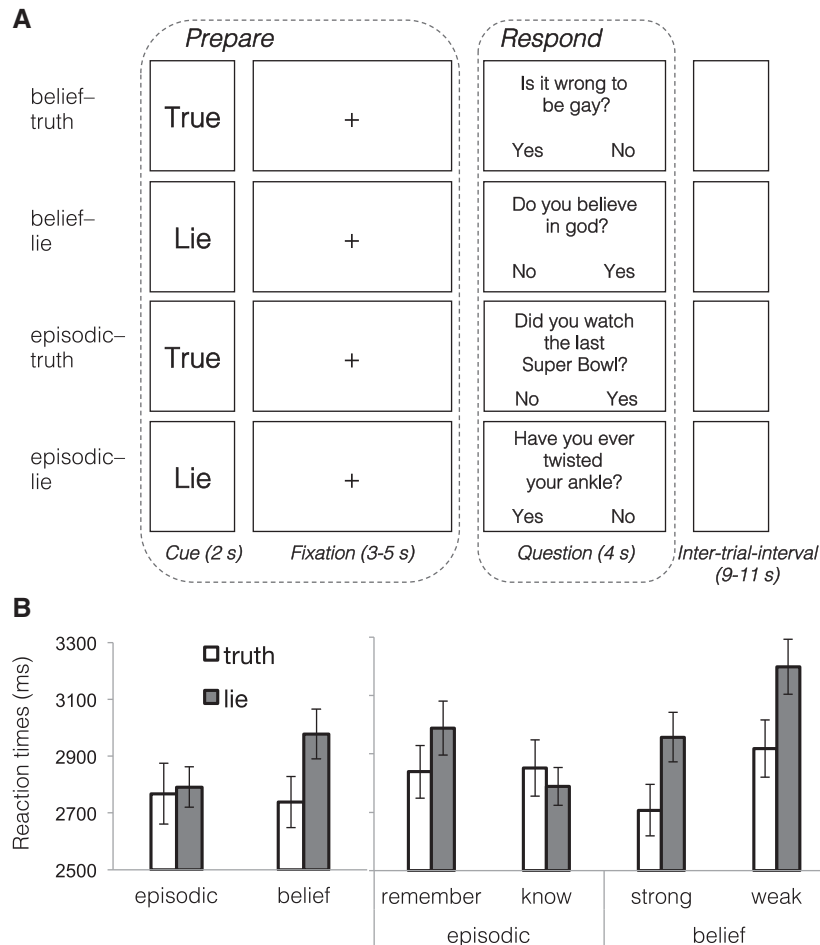


Fig. 1. Paradigm and behavioral results. (A) Example of a trial in each of the four experimental conditions: belief-true, belief-lie, episodic-true and episodic-lie. Each trial began with a LIE/TRUE cue presented on the screen for 2 s, followed by a jittered time for preparation 3–5 s, followed by the question presented for 4 s and a jittered inter-trial-interval ranging between 9 and 11 s. Trial timing information is depicted in seconds. (B) Mean reaction times across participants for responses in the four experimental conditions and in the eight conditions defined by post-scan ratings. Bars represent standard error.

(well within the recommended threshold by Lieberman and Cunningham, 2009).

In addition to clusters identified from the group's activation maps, we examined deception effects in a set of regions of interest (ROIs) identified in a meta-analysis of deception effects (Christ et al., 2009). These literature-based ROIs were created using a 6-mm sphere around the peak voxel of clusters reported in the meta-analysis. Mean individual subjects' contrast values for task conditions were extracted from clusters identified in these analyses and from literature based ROIs. We entered these values into a 2×2 repeated measures analysis (deception: lie/true, question type: episodic/belief) and performed follow-up t-tests with all reported effects significant at P thresholds of 0.05.

To examine effects of participants' post-scan ratings of the questions ('remember' or 'know' for episodic questions and 'strong' or 'weak' for belief questions) we created an additional first-level general linear model with eight stimuli regressors (episodic-remember-lie, episodic-know-lie, belief-strong-lie, belief-weak-lie, episodic-remember-true, episodic-know-true, belief-strong-true, belief-weak-true). With the exception of the number of stimuli regressors, this model was identical to the model used in the main analysis described above. Mean individual subjects' contrast values for eight stimuli conditions were extracted from the clusters and ROIs defined above. We entered

these values into two separate 2×2 repeated measures analyses (deception: lie/true, episodic: remember/know; deception: lie/true, belief: strong/weak).

Results

Behavior

Accuracy was measured by comparing the answers given in the scanner to the honest answers in the post-scan review. Accuracy was high overall ($83.0 \pm 8.2\%$, mean \pm SD), and did not vary by condition [lie: $81.6 \pm 9.8\%$; truth: $84.4 \pm 8.6\%$, $t_{(16)} = 0.19$, $n.s.$], or by the type of question participants were asked [episodic: $83.7 \pm 9.0\%$, belief: $82.3 \pm 9.3\%$, $t_{(16)} = 0.32$, $n.s.$]. Reaction times across conditions were compared using a repeated-measures analysis (2×2 model; deception: lie/true, question type: episodic/belief; Figure 1). Participants were slower when lying relative to telling the truth [deception cost effect: $F_{(1,16)} = 8.6$, $P < 0.01$]. There was a trend to answer belief questions more slowly than episodic questions [question type: $F_{(1,16)} = 4.3$, $P = 0.06$], and there was a significant deception by question type interaction [$F_{(1,16)} = 9.8$, $P = 0.007$]. Follow-up comparisons confirmed that participants were slower when lying relative to telling the truth about their personal beliefs [$t_{(16)} = 4.9$, $P < 0.001$], but not for episodic memories. Furthermore, reaction times did not

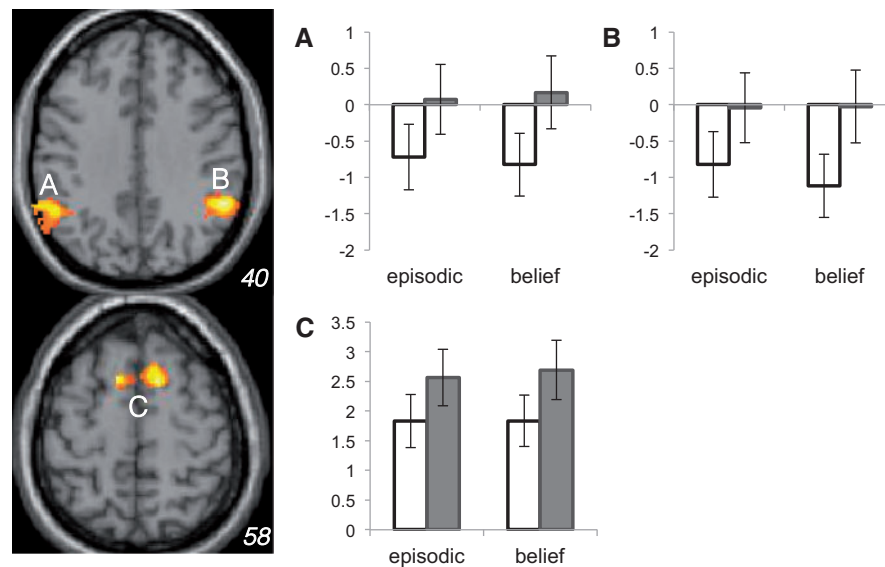


Fig. 2. Deception effects common to episodic and belief questions. Activation maps (conjunction of activation maps for the contrasts episodic lie > true and belief lie > true questions) are rendered on standard brain horizontal sections (middle). MNI coordinates are presented at the bottom of each section. Group mean parameter estimates for lie and true activation in episodic and belief questions (arbitrary units). (A) Left parietal cortex; (B) right parietal cortex; (C) superior frontal gyrus. Bars represent standard error.

differ between episodic and belief questions in the truth conditions.

In post-scan ratings, participants indicated that $48.6 \pm 9.0\%$ of the episodic questions evoked a specific memory ('remember' as opposed to 'know') and $65.7 \pm 6.2\%$ of the belief questions tapped a personal belief that participants rated as 'strong' (as opposed to 'weak'). Two participants had fewer than 10 responses in one of the post-scan rating categories and were thus omitted from further analyses that included the post-scan ratings. A 2×2 repeated-measures analysis was conducted separately for episodic (deception: lie/true, memory type: remember/know) and belief (deception: lie/true, belief strength: strong/weak) questions. For episodic questions, there was no deception cost, but there was a trend for a main effect of memory type [$F_{(1,14)} = 4.3$, $P = 0.06$], and an interaction of deception cost by memory type [$F_{(1,14)} = 4.6$, $P < 0.05$], indicating that participants were slower when lying relative to telling the truth only for episodic questions later rated as 'remember'. For belief questions, there were main effects of deception cost [$F_{(1,14)} = 19.0$, $P < 0.001$], as well as a main effect of belief strength [$F_{(1,14)} = 11.6$, $P = 0.004$], and no interaction of deception cost by belief strength, indicating that participants were overall slower when lying relative to telling the truth and overall slower in responding about personal beliefs rated as 'weak' compared to those rated as 'strong'.

Imaging

Common regions for lying about episodic and belief questions. Regions that showed deception-related activations (lie > true) for both episodic and belief questions were determined by conjunction analysis (group maps for belief-lie > belief-true and episodic-lie > episodic-true, each map uncorrected voxel-level $P < 0.005$, cluster > 100 contiguous voxels). Bilateral lateral parietal and bilateral medial superior frontal regions were activated more when responding with a lie compared to giving an honest response for both episodic and belief questions as determined by a conjunction analysis (Figure 2 and Table 1A). In all clusters

identified by this conjunction analysis, there was a main effect of deception [$F_{(1,16)} > 13.1$, $P < 0.003$] with no interaction of deception by question type [$F_{(1,16)} < 2.9$, $P > 0.11$]. We examined activation in these regions based on the participants' post-scan ratings of questions by either the episodic memory type it evoked ('remember' vs 'know') or the strength of the personal belief it addressed ('strong' vs 'weak'). Both analyses revealed a main effect of deception without interactions between either memory type [$F_{(1,16)} < 2.7$, P 's > 0.12] or belief strength [$F_{(1,14)} < 3.1$, P 's > 0.1]. In sum, bilateral lateral parietal and medial superior frontal regions were consistently activated when a participant lied (compared with truth-telling) irrespective of the type of information they lied about.

Distinct regions for lying about episodic or belief questions. We conducted a second analysis to identify regions in which deception effects differed by question type (paired t-test: belief-lie > belief-true and episodic-lie > episodic-true; uncorrected voxel-level $P < 0.005$, cluster > 100 contiguous voxels). We identified regions in the right temporal pole, precuneus, right amygdala and right precentral gyrus (Figure 3 and Table 1B). These regions were used as functional ROIs to further investigate the nature of the activation modulation by question type. Activation in these regions was extracted across conditions and a significant interaction of deception by question type was confirmed [$F_{(1,16)} > 15.3$, P 's < 0.002]. Below we present the findings across conditions and question types separately in each of these regions.

Activation in the right temporal pole seemed to reflect lying about episodic content, however, it is possible that differential effect for lying about personal beliefs was masked by this region being actively engaged in all conditions relating to personal beliefs. This was evident by a main effect of deception (lie > true) for episodic questions [$F_{(1,16)} = 7.6$, $P = 0.01$] that did not differ by the memory type, remember vs know [$F_{(1,16)} = 3.0$, $P = 0.10$]. In contrast, activation in this region was only marginally related to lying vs responding truthfully about personal beliefs [$F_{(1,14)} = 3.7$, $P = 0.08$]. Prior studies have implicated the temporal pole in reasoning about belief-laden material (Goel and Dolan, 2003;

Table 1. Common (A) and distinct (B) activations for lying (lie > true) about episodic or belief questions

		BA	x	y	z		No. voxels
(A) Deception effects common to episodic and belief questions–conjunction analysis							
L	Supramarginal gyrus	39	−62	−52	28		1030
	Inferior parietal lobule	40	−54	−54	30		
	Superior temporal gyrus	22	−58	−62	26		
R	Supramarginal gyrus	39	56	−48	30		543
	Inferior parietal lobule	40	56	−42	44		
R	Superior frontal gyrus	6/8/32	14	12	58		405
L	Superior frontal gyrus	6	−10	14	58		
(B) Interaction of deception effects by question type							
						T	
R	Precentral gyrus	6/4	46	−10	42	5.24	221
R	Middle/superior temporal gyrus	21	54	4	−40	4.40	168
		38	46	12	−30	4.20	
R	Globus pallidum	n.a.	26	−18	2	3.97	234
	Amygdala	n.a.	30	−2	−14	3.68	
R/L	Precuneus/cuneus	7	6	−78	40	4.25	235

Notes: Peak coordinates (x y z) are based on MNI brain. BA, Brodmann's area; L, left; R, right.

Cunningham et al., 2004). Thus we tested whether the right temporal pole activations seen in the present study were higher overall for belief compared with episodic questions. Activations in this region were higher for belief compared to episodic questions [as evidenced by a main effect for question type: $F_{(1,16)} = 7.6$, $P = 0.01$]. Furthermore, in line with a role for this region in the processing of belief-laden material, right temporal pole activation was greater overall for beliefs judged as 'strong' compared with those judged as 'weak' [$F_{(1,14)} = 5.7$, $P = 0.03$]. We also found a trend towards an interaction between deception and belief strength in this region [$F_{(1,14)} = 3.6$, $P = 0.08$], with a larger effect of deception for weak beliefs.

In contrast, in the *precuneus* there was higher lie > truth activation when lying for personal beliefs. This was evident by a main effect of deception for belief questions [$F_{(1,14)} = 12.2$, $P = 0.004$], that did not differ by belief strength [$F_{(1,14)} = 0.1$, $P = 0.91$]. In contrast, activation in this region showed no effect of deception for episodic questions [$F_{(1,16)} = 0.1$, $P = 0.76$], and no interaction of deception for episodic questions by memory [$F_{(1,16)} = 0.1$, $P = 0.72$].

An *anterior medial temporal lobe* region that included the right amygdala showed reduced activation for all experimental conditions compared with baseline [$t'_{s(16)} > 2.3$, $P's < 0.04$], however the pattern of activation across these conditions revealed a deception effect for episodic questions. Specifically, we identified a main effect of deception for episodic questions [$F_{(1,16)} = 8.0$, $P = 0.01$], that did not differ by memory type [$F_{(1,16)} = 2.0$, $P = 0.17$]. There was no main effect for deception for belief questions [$F_{(1,14)} = 1.4$, $P = 0.25$], or modulation of deception belief strength [$F_{(1,14)} = 1.9$, $P = 0.19$], however, activation in this region was marginally higher (closer to baseline) for 'strong' compared with 'weak' beliefs [$F_{(1,14)} = 4.5$, $P = 0.05$].

Deception activations in a priori defined ROIs. We tested deception effects in a set of 11 literature-based ROIs identified in a meta-analysis of deception studies (Christ et al., 2009). In the majority of these regions, we identified a main effect of deception [$F'_{s(1,16)} > 5.7$, $P < 0.03$] with no interaction of deception by question type [$F'_{s(1,16)} < 2.7$, $P's > 0.2$]. These included bilateral lateral parietal cortex, bilateral inferior frontal gyrus and bilateral anterior prefrontal cortex. Moreover, there was no interaction of deception and either episodic memory type [$F'_{s(1,16)} < 3.8$,

$P's > 0.07$] or belief strength [$F_{(1,14)}'s < 1.3$, $P's > 0.27$] in these regions, further supporting the general role of these regions in deception.

Activation in the left and right *insula* ROIs also identified main effects of deception [left: $F_{(1,16)} = 5.0$, $P = 0.04$; right: $F_{(1,16)} = 6.5$, $P = 0.02$]; however, these effects differed by question type [left: $F_{(1,16)} = 5.7$, $P = 0.03$, trend in the right: $F_{(1,16)} = 3.9$, $P = 0.06$]. Follow-up examinations showed deception effects when subjects responded to belief questions [$t_{(16)} > 2.9$, $P < 0.01$], but not to episodic questions [$|t_{(16)}| < 1.6$, $P > 0.14$]. Deception effects in the insula for belief questions did not differ by belief strength [$F'_{s(1,14)} < 0.25$, $P's > 0.63$].

In three of the ROIs identified in the meta-analysis, we were unable to identify a deception effect or an interaction of deception by question type. These include the anterior cingulate cortex, right intraparietal sulcus, and an anterior right insula region [deception: $F'_{s(1,16)} < 2.1$, $P's > 0.1$; interaction: $F'_{s(1,16)} < 0.1$, $P's > 0.7$].

Preparing to lie. Brain activation in bilateral parietal and occipital regions was greater when participants prepared to lie compared with when they prepared to tell the truth (contrast: preparation-lie > preparation-true) (Figure 4A and Table 2A). None of these regions showed deception effects when participants responded to the questions [$F'_{s(1,16)} < 1.9$, $P's > 0.2$]. These findings suggest that the brain regions recruited when a person is preparing to lie are distinct from those engaged when the person generates and delivers the specific lie.

Lie preparation effects in a priori defined ROIs. Of all the ROIs defined based on the deception-related meta-analysis (Christ et al., 2009), only the anterior right insula showed differential activation during the period of lie preparation [$t_{(16)} = 2.3$, $P = 0.03$; other ROIs: $|t'_{s(16)}| < 1.1$, $P's > 0.3$]. This ROI was one of the three that did not show a deception effect during the response period, suggesting that this region's involvement in lie preparation contributed to its identification in the meta-analysis.

Activations during lie preparation linked to deception cost score. We investigated the behavioral correlates of regional brain activations during the preparation to lie (preparation-lie > preparation-true) by assessing the relation of activations during the

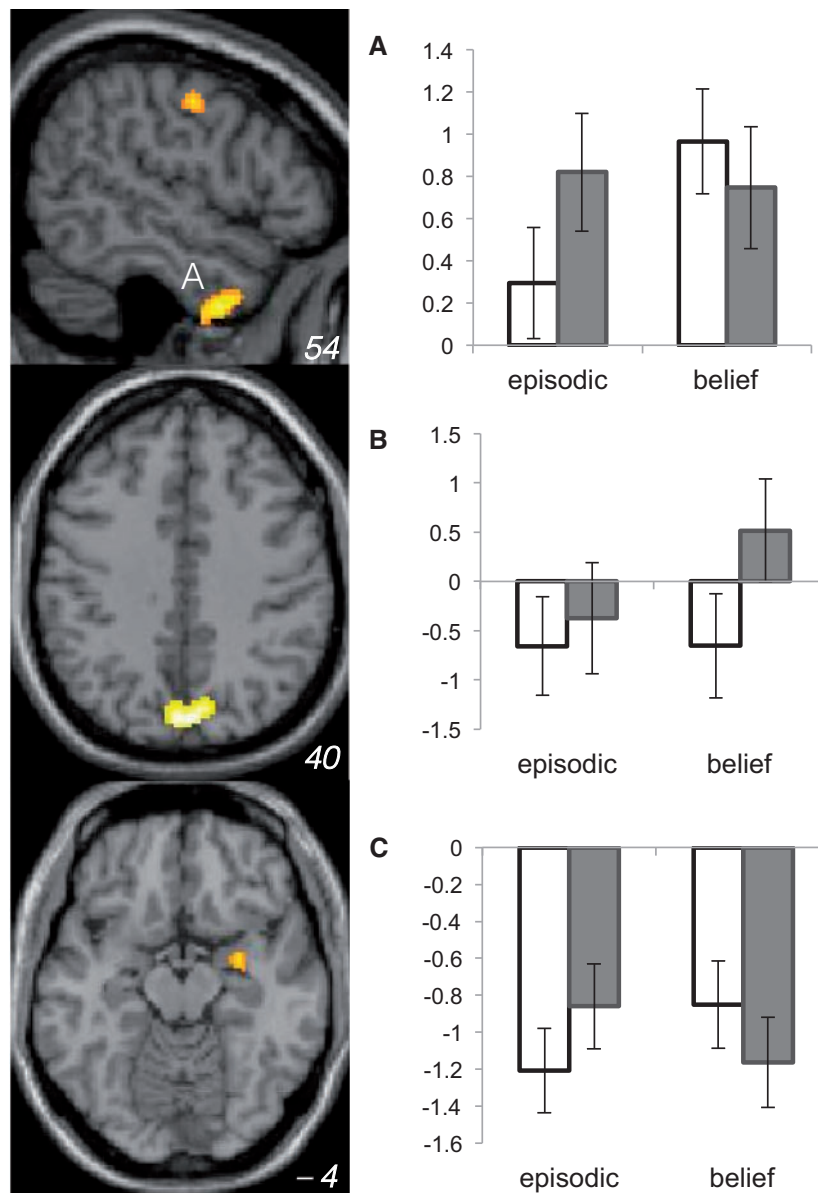


Fig. 3. Distinct deception effects for episodic or belief questions. Activation maps (paired *t*-test of activation maps for contrasts episodic lie > true from and belief lie > true questions) are rendered on standard brain sagittal and horizontal sections (left). MNI coordinates are presented at the bottom of each section. Group mean parameter estimates for lie and true activation in episodic and belief questions (arbitrary units). (A) right temporal pole; (B) precuneus; (C) right amygdala. Bars represent standard error.

preparation to lie to deception cost scores [calculated as: $100 \times (\text{mean reaction time to lie} - \text{mean reaction time to respond truthfully}) / \text{mean reaction time to respond truthfully}$] (Figure 4B and Table 2B). Across participants, the magnitudes of activations during the preparation to lie in the posterior cingulate and in the left temporal and frontal cortices were correlated with lower deception cost scores (Figure 4C, see additional information provided in Supplementary data, Figure S2). This means that participants who recruited these brain areas more when preparing to lie than when preparing to tell the truth also tended to show less deception cost, suggesting that recruitment of these regions during lie preparation was linked to lying more efficiently. Across all participants, activations in these regions were not different in preparation for lie compared with true conditions [$|t|_{(16)} < 2.0$, P 's > 0.07]. Moreover, across all

participants in only one of these regions, the left dorsolateral prefrontal cortex (BA 46), there was a significant deception effect [increased activation for lie than truth during the response: $F_{(1,16)} = 6.2$, $P = 0.03$]. The deception effect in the left dorsolateral prefrontal cortex did not differ by question type [$F_{(1,16)} = 1.6$, $P = 0.22$].

Distinct regions for responding truthfully to episodic or belief questions. Although not the focus of this report, the present experiment allowed us to compare brain activations associated with two distinct types of personal knowledge. We found striking dissociations in the brain regions involved in responding truthfully to questions about personal episodic knowledge compared to personal beliefs and opinions (described in detail in Supplementary materials).

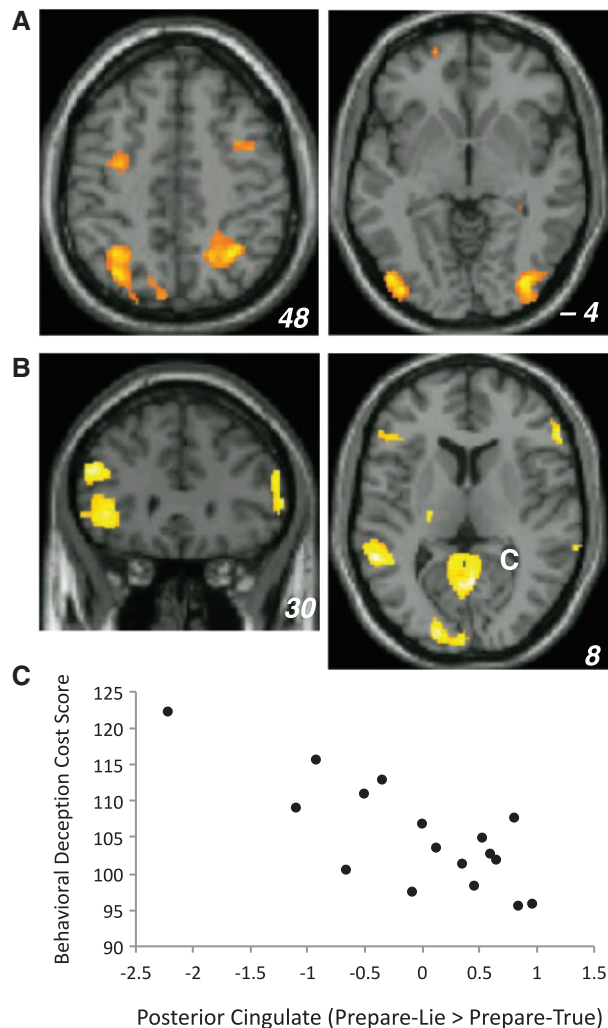


Fig. 4. Neural correlates of lie preparation. (A) Activations during lie preparation (contrast preparation-lie > preparation-true). (B) Activations during lie preparation that were correlated with deception cost score across participants (see text for details). MNI coordinates are presented at the bottom of each section. (C) Scatterplot of the correlation depicted in B from one of the clusters located in the posterior cingulate cluster. The data in the scatterplot depicts the correlation between activation during the preparation to lie and the behavioral deception cost score, calculated as ratio between reaction time when responding with truth compared to lie. Increased activation in this region was related to smaller deception cost score.

Discussion

Using a novel paradigm to assess the neural correlates of deception, we identified three major findings. First, consistent with previous reports (Christ et al., 2009; Lisofsky et al., 2014), we found that frontal and parietal regions are engaged during the execution of a deceptive response. Frontal and parietal brain regions support processes related to cognitive control and executive functioning. Thus our findings are consistent with the involvement of cognitive control and executive functioning in deception. Second, we identified regions that showed a differential deception contrast (Lie > Truth) when lying about episodic knowledge or personal beliefs, suggesting that deception-related neural correlates are sensitive to the content one is lying about (Greene and Paxton, 2009). Finally, we identified regions that may be involved in 'preparatory' processes and whose engagement accounts for some individual differences in

behavioral measures of the lie response (Ito et al., 2012). Taken together, these findings further elucidate the neural correlates of several important aspects of deception and highlight the importance of considering the content one is lying about as well as the processes involved in preparing to lie, as those aspects are linked to unique neural correlates.

In an act of deception, one allegedly first determines the truth, and then engages cognitive effort in suppressing the urge to make a truthful response (Spence, 2004). This process is widely referred to as response inhibition and it occupies a central role in the mental toolkit known as cognitive control. We observed a deception cost-effect in participant response times, such that lie responses were overall slower compared with truth responses. This deception cost-effect suggests that participants in this experiment either employed more cognitive control or performed additional computations (e.g. response reversal) when lying compared with telling the truth.

Although there was an overall deception effect in response times, interestingly this effect was almost entirely driven by the slower deceptive responses when asked about personal beliefs, whereas participants responded equally quickly when lying or telling the truth about past personal experiences. Interpreting this differential behavioral effect in the context of the broader deception literature is difficult. Although most studies of deception find that lying is slower than truth telling, this is not the case for all types of lies. Faster responses for lies are sometimes reported (Langleben et al., 2005) and may reflect a more automatic, repeated and rehearsed lie response. In this study, it is possible that the participants were less invested in lies about episodic memory, or that these questions were simply less cognitively complex compared with belief questions and therefore altering the response was not accompanied by a noticeable increase in reaction time. In the current design, each question was presented only once, eliminating the possibility of an automatic lie response. Under these circumstances, truth should be the more automatic, and thus faster, response when considering either personal experiences or beliefs. The differential behavioral effect may reflect a differential ability to monitor cognitive effort when lying about personal experiences vs beliefs. The participants in our study were asked to try to lie in such a way that the experimenter would not be able to tell whether they were lying or telling the truth. In informal interviews conducted after the test period, a few of the participants indicated that they had been deliberately trying to equate the reaction times between the lie and true conditions as a strategy to make it harder for the experimenter to detect deceptive trials. This deliberate attempt to equate reaction times may have been more successful when responding to episodic questions. It is therefore possible that participants were overall better able to monitor their own responses during episodic but not during belief trials. Alternatively, it is possible that differences in the nature of evaluating episodic knowledge vs personal beliefs accounted for the differences in deception reaction time. By this account, the greater deception cost in response time for belief questions is due to difficulty espousing a moral opinion that is contradictory to one's own. Overall, the finding of a deception cost effect in participants' reaction times suggests that the manipulation we used in the current design effectively required participants to engage additional cognitive resources when lying compared to telling the truth, at least in the case of belief statements.

In line with a general role for cognitive control in deception, we found robust deception effects in frontal and parietal regions that did not differ by the type of knowledge (episodic or

Table 2. Activations related to lie preparation (prepare-lie > prepare-truth) across participants (A) were related to behavioral index of deception cost (B) (see text for details)

		BA	x	y	z	T value	No. voxels
(A) Preparation-lie > preparation-true							
L	Superior/inferior parietal lobule	7	-26	-56	36	7.06	1188
	Precuneus	39	-30	-70	50	4.52	
R	Middle/inferior occipital lobe	18	36	-84	-4	5.47	314
L	Middle/inferior occipital lobe	18	-44	-92	-8	5.14	322
			-46	-82	-2	5.07	
R	Superior parietal lobule	7	34	-56	50	4.86	918
	Precuneus	7	26	-70	32	4.15	
	Inferior parietal lobule	40	28	-64	38	3.88	
L	Caudate	n.a.	-22	-24	24	4.98	446
	Middle frontal/precentral gyrus	6	-32	-4	50	4.06	
R	Middle frontal/precentral gyrus	6	34	4	44	4.31	461
	Caudate	n.a.	22	10	26	3.97	
L	Superior/medial frontal gyrus	10	-18	60	8	4.28	139
(B) Correlation with deception cost index							
R	Posterior cingulate cortex	30/29/23	4	-50	14	5.31	1015
L	Superior temporal gyrus	22	-56	-44	8	5.11	505
	Middle temporal gyrus/fusiform	37	-52	-56	-2	4.64	
L	Middle/inferior frontal gyrus	46/9	-50	30	26	4.85	519
R	Middle/superior temporal gyrus	22	70	-38	4	4.80	163
L	Thalamus/midbrain	n.a.	-18	-22	-4	4.77	314
L	Cuneus/middle occipital gyrus	18/17	-16	-94	8	4.48	392
R	Inferior/middle frontal gyrus	46/45/10	58	32	8	4.50	234
L	Lingual gyrus/inferior occipital gyrus	17/18	-16	-96	-14	4.45	117
L	Inferior frontal gyrus	47/46	-44	32	0	4.40	297
L	Medial/superior frontal gyrus	10	-8	62	16	3.88	142

Notes: Peak coordinates (x y z) are based on MNI brain. BA, Brodmann's area; L, left; R, right.

personal belief) about which participants lied. Regions in the frontal and lateral parietal cortex are typically recruited during tasks that require participants to exhibit high levels of cognitive control (Bunge, 2004; Ridderinkhof et al., 2004; Aron and Poldrack, 2006; Dosenbach et al., 2006). Prior neuroimaging studies of deception have implicated the involvement of brain regions linked to cognitive control (Abe et al., 2006; Christ et al., 2009). Indeed, we identified deception effects within the majority of regions that were previously identified in a meta-analysis.

Different brain regions responded specifically for deception about episodic vs belief knowledge. The right temporal pole was activated only for deception about episodic, personal experience. This may reflect the recruitment of this region in retrieval of complex detailed memories. Consistent with evidence about this region being involved in reasoning about beliefs (Goel and Dolan, 2003; Cunningham et al., 2004), we found that it was active during both lie and truth conditions when participants evaluated their personal beliefs. In contrast, the precuneus was active only for deception about personal beliefs. Another fMRI study also found activation of the precuneus when participants lied about personal information (Marchewka et al., 2012). The amygdala, a region linked to fear, anxiety and emotion (LeDoux, 2007), displayed a deception effect in our study. However, the amygdala was less active in all four conditions than at baseline, suggesting that this region may have been inhibited throughout the task. Finally, we also identified a question type difference in the left and right insula when using ROIs from a prior meta-analysis (Christ et al., 2009). The insula has been implicated in certain emotional states (Klucken et al., 2012; Sip et al., 2012), and it is possible that these activations indicate an increased sense of

disgust with ones' lie about a personal belief that is not as evident when one lies about past events.

The study also included a period of preparation on each trial during which participants prepared to either tell the truth or to lie before they knew the material they would be asked to lie about. The inclusion of a preparatory period in the experimental design allowed us to test whether the processes involved in deception could be dissociated from the processes involved in determining a specific truth and selecting a particular lie response. We were able to identify regions in the superior parietal lobule that were more active during preparation of a lie compared with preparation of a truth response. These regions were distinct from the parietal and frontal regions that showed increased activation during the execution of the lie response. To our knowledge, only one published report has examined the neural correlates of preparing to lie (Ito et al., 2012). That study did not show significant differences in brain activation between preparing to tell the truth and preparing to deceive. However, several differences in the design make a direct comparison difficult. Ito and colleagues (Ito et al., 2012) included a condition in which no preparation is possible, and the main findings as for activation specific for preparation were observed when comparing certain to uncertain cue. In our design, participants were given a specific cue. Second, the instruction to either deceive or not was in only limited context of the participant's memory for previously studies pictures of objects, whereas in the current study we included two different types of questions in both the participant was to reflect on their past experiences or beliefs beyond the context of specific experimental induced mnemonic content. Finally, the cue used by Ito et al. (2012) was a colored

circle and therefore a possible difference between the studies is in the more direct instruction and possible associations that go along with processing the cue word 'Lie' or 'True'. Indeed, in this study we identified regions in the occipital lobe that were more active during preparation of a lie compared with preparation of a truth response. One possible explanation is that this occipital activation is reflecting the different visual properties of the cue words. Nonetheless, our results are consistent with the aforementioned paper in that we have identified preparatory activation in regions in the prefrontal cortex, however, unlike these prior findings we have identified differential preparatory responses for lying compared with truth-telling in several regions including the superior frontal gyrus.

Separating the assessment of neural correlates that support lie preparation from the assessment of those supporting lie response allowed us to make an additional unique contribution to the literature by identifying a specific role for a portion of the right anterior insula in lie preparation. The right anterior insula is one of the regions that was identified in meta-analysis (Christ et al., 2009) as involved in deception, but in this study activation in this specific region only differed between the lie and truth conditions during the preparation period and not during the response. Thus, the design may have succeeded in dissociating some of the processes involved in normal deception.

Moreover, we found that activation during lie preparation correlated across participants with individuals' ability to lie efficiently. We approximated efficient lying with reduced behavioral deception cost scores. Thus, we found that individual behavioral deception costs (measure of reaction time increase during lie vs true conditions) correlate inversely with individual neural activation during lie preparation. Specifically, greater preparatory activation in left dorsolateral cortex, a region previously linked to both working memory (Curtis and D'Esposito, 2003; Funahashi, 2006) and deception (Nunez et al., 2005; Priori et al., 2008; Mameli et al., 2010) was associated with more efficient deception. One limitation of our design pertains to the ecological validity of the preparation period. Specifically, deception in the real world does not typically involve preparing to lie before one has determined what he or she will be lying about. Nonetheless, our findings of regions in which the level of lie preparation activation correlated with a behavioral index of lying suggests that the processes carried out during this period may indeed contribute to the act of lying.

In this study, we used a novel paradigm to assess the neural correlates of deception. The most obvious limitation of this and other studies with this goal is the limited ability of experimental manipulations to truly mimic real-life deception. Participants were explicitly asked to lie (or tell the truth) and thus even when they lied they were, in fact, complying with the experimenter's instruction. In this regard, we greatly minimized the emotional component in deception. In fact, the lie detection techniques widely in use today rely on physiological measures (Lykken, 1959) that reflect sympathetic arousal, such as skin conductance response. These measures are believed to reflect the emotional component of lying. We took measures against this limitation by instructing the participants to try to respond in such a way that we would not be able to tell whether they were lying or telling the truth (Uncapher et al., 2015). Moreover, we found deception effects in the amygdala and anterior insula, regions typically associated with emotional processing (LeDoux, 2007; Wagner, N'Diaye et al., 2011; Hamann, 2012; Klucken et al., 2012).

Another limitation is that we ultimately chose a small set of questions (total of 120) to elicit memories of specific past experiences or judgments about specific personal beliefs. To a large extent the findings of this study are limited by our choice of

specific example questions. The comparison between episodic and belief questions, for example, is limited by minimal control of the strength or emotional valence that was evoked in the selected sets of questions. Relatedly, the findings regarding deception about past experiences may have been specifically limited by weak memories of some of those past events. If a participant, for example, had only a weak memory when evaluating a question (e.g. 'Have you received a parking ticket in the last month?'), it may be difficult for him or her to engage in intentional deception about this event. Although a possible limitation, we argue that the intention to deceive would remain a critical driver of what we observed even in cases when the actual memory is weak. Support for this notion comes from a study demonstrating that the active aspect of deception is critical for engaging frontal-parietal regions; when participants were asked to feign memory impairment, only intentional faked responses, and not errors committed unintentionally, were associated with activation in prefrontal and parietal regions (Lee et al., 2009).

Conclusions

The findings described here suggest that the brain signature of a lie is influenced by the type of knowledge one is lying about. The open question for those interested in developing techniques for lie detection is whether lying evokes a reliable neural signature that cannot be manipulated by the deceiver and yet can be reliably detected with neuroimaging. The cumulative evidence suggests that a few brain regions are consistently more active when a person is lying. However, these regions also appear to be engaged by other cognitive tasks, making their use in lie detection algorithms susceptible to false alarms. We believe that the importance of deception studies is in identifying the underlying cognitive processes, as they may be linked to specific brain networks that play a role in deception. Here we identified differential contributions of brain regions to lying about personal past experiences and personal beliefs. Moreover, our findings suggest that preparatory processes are directly related to behavioral responses and are supported by regions that are distinct from those that support the actual act of lying. These findings add to a growing body of knowledge about the underpinnings of deception in the human brain.

Acknowledgments

We wish to thank Max E. Gray and J. Ben Hutchinson for help with data collection and analyses, Paul Mazaika, Heesoo Kim and Boris Volfson for help with data analysis, and Asaf Bachrach and Itamar Kahn for helpful discussions.

Supplementary data

Supplementary data are available at SCAN online.

Funding

This work was supported by the Defense Advanced Research Projects Agency to JDEG.

Conflict of interest: None declared.

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