

# Representation of attitudinal knowledge: role of prefrontal cortex, amygdala and parahippocampal gyrus

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## Abstract

It has been proposed that behavior is influenced by representations of different types of knowledge: action representations, event knowledge, attitudes and stereotypes. Attitudes (representations of a concept or object and its emotional evaluation) allow us to respond quickly to a given stimulus. In this study, we explored the representation and inhibition of attitudes. We show that right dorsolateral prefrontal cortex mediates negative attitudes whereas left ventrolateral prefrontal cortex mediates positive attitudes. Parahippocampal regions and amygdala mediate evaluative processing. Furthermore, anxiety modulates right dorsolateral prefrontal activation during negative attitude processing. Inhibition of negative attitudes activates left orbitofrontal cortex: a region that when damaged is associated with socially inappropriate behavior in patients. Inhibition of positive attitudes activates a brain system involving right inferior frontal gyrus and bilateral anterior cingulate. Thus, we show that there are dissociable networks for the representation and inhibition of attitudes.

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*Keywords:* Social cognition; Brain; Prefrontal cortex; Amygdala

## 1. Introduction

Attitudes are a type of predisposition toward behavior (Rosenberg & Hovland, 1960; Yucker, 1965) that provide a fast route from a stimulus to the associated behavior (Wood, 2003). Thus, attitudes are biases towards or against behaviors or decisions that influence our decision-making and behavior in social situations. These may be considered one component of behavioral control—other components likely include action representations and event knowledge (Wood, 2003; Wood & Grafman, 2003). If we are to understand how these components are interrelated to influence behavior, we must first understand the individual components. There has been relatively little cognitive neuroscientific research into attitude representation. Identification of the neural correlates of attitudes will enable us to consider, at a systems level, the relationship between networks representing attitudinal knowledge and those representing other types of knowledge

as described above. This may lead to better understanding of how these different knowledge representations may interact in controlling behavior. Taken together, such research may provide insight into the behavior of patients who exhibit abnormal or inappropriate behavioral control.

Attitudes have been explored extensively in social psychological research (Ajzen, 2001; Bargh, Chaiken, Gvender, & Pratto, 1992; Breckler, 1984; Fazio, 1986, 1989; Fazio, Sanbonmatsu, Powell, & Kardes, 1986). An attitude comprises an attitude-object (the target or subject of the attitude, e.g., landlord) that is associated with an evaluation and behavioral response (Breckler; Pratkanis, 1989; Wood, 2003). The evaluation may be simple (e.g., a particular food is good versus bad) or complex (e.g., favoring versus opposing certain political ideas). The present study is concerned with attitudes towards positive and negative attitude-objects that are associated with simple good or bad evaluations. These evaluations may be considered similar to Damasio and co-workers' concept of somatic markers (Damasio, 1995, 1996, 1998) by providing tags that bias behavior based on emotional memories of past experiences.

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In social psychology, attitude research has focused on accessibility and automaticity of attitudes (Bargh et al., 1992; Bargh, Chaiken, Raymond, & Hymes, 1996; Fazio, 1993; Fazio, Chen, McDonel, & Sherman, 1982; Fazio et al., 1986). Bargh et al. have proposed that presentation of an attitude-object *always* leads to automatic activation of the associated attitude evaluation; Fazio et al., on the other hand, have proposed that this automatic attitude activation occurs *only* for strongly held attitudes. The majority of these studies have suggested that there is a continuum of accessibility with accessible attitudes being automatically activated and characterized, for example, by faster categorization as ‘good’ or ‘bad’. However, this view of the relationship between accessibility and automaticity may seem rather circular and the present study is not intended to discriminate between these positions. Attitude studies generally consist of two phases. In Phase 1, people’s attitudes toward attitude-objects (single words, e.g., landlords, chocolate) are assessed using a good–bad classification paradigm. In Phase 2, the attitude-objects associated with the fastest Phase 1 responses are then presented paired with emotional adjectives. The selection of the items associated with the fastest responses in Phase 1 ensures that the items with the most automatic attitudes are used in Phase 2. Generally, people respond faster to adjectives of the same valence as their attitude and slower to those of the opposite valence to their attitude (Bargh et al.; Fazio et al.). These data are interpreted as showing that the attitude has facilitated or interfered with the response to the emotional adjective. However, it is unclear whether the task distinguishes attitude processing from a more generic semantic priming mechanism.

In terms of the neural correlates of attitudes, patients with medial temporal lobe damage exhibit intact attitude change (Lieberman, Ochsner, Gilbert, & Schacter, 2001) and similar findings have been reported for attitude formation and change in patients with Korsakoff’s syndrome (Johnson, Kim, & Risse, 1985; Lieberman et al.). These findings suggest that episodic memory and attitudes may be selectively impaired and thus may be represented independently in the brain. Although these studies demonstrate that medial temporal structures *are not* necessary for attitude representation, they do not inform as to which brain structures *are* necessary. A recent neuropsychological study reported impaired priming of stereotypes (a type of attitude, Wood, 2003) in patients with lesions of the ventromedial prefrontal cortex, relative to patients with dorsolateral lesions and healthy controls (Milne & Grafman, 2001). A single case study, using the social psychology paradigm described above, demonstrated impaired priming of negative, but not positive, attitudes in a patient with bilateral frontal and temporal damage (Park et al., 2001). This indicates that positive and negative attitudes may be selectively impaired, suggesting possible emotion-specific differences in brain networks that mediate attitudes. The present study compares attitudes towards positive and negative attitude-objects.

Any single attitude-object is likely to activate several, possibly contradictory, attitudes, e.g., chocolate may activate a positive attitude related to its pleasant taste and a negative attitude related to its caloric value. This conflict between attitudes and between different responses to the same attitude-object must be resolved. We propose that resolution is achieved by competing attitude representations inhibiting each other with the winner determining the behavioral response to the attitude-object. Other theorists have proposed that there is a general inhibitory mechanism that is composed of a distributed network of regions across both hemispheres (Garavan, Ross, & Stein, 1999; Konishi et al., 1999; Leung, Skudlarski, Gatenby, Peterson, & Gore, 2000; MacDonald, Cohen, Stenger, & Carter, 2000) (e.g., dorsolateral prefrontal cortex, right inferior prefrontal cortex and anterior cingulate), although some studies have implicated orbitofrontal cortex in inhibitory tasks (Jentsch, Olausson, De La Garza, & Taylor, 2002; Wallis, Dias, Robbins, & Roberts, 2001).

The present study directly addresses hypotheses about the localization and inhibition of positive and negative attitudes in the prefrontal cortex and limbic system. Subjects underwent functional MRI (fMRI) while performing a task in which they had to give responses that were consistent or inconsistent with their own attitudes. The attitude-consistent responses were intended to result in activation of their attitudes (attitude activation for a subject who likes parties, e.g., ‘Chris likes parties’ paired with ‘parties are good’), whereas the attitude-inconsistent responses were intended to result in inhibition of their attitudes (attitude inhibition for a subject who likes parties, e.g., ‘Chris dislikes parties’ paired with ‘parties are bad’). The task was to decide whether the two phrases were consistent, irrespective of the subject’s own attitude.

Although we refer to the latter condition as the inhibition condition, it is possible (given the nature of the task) that there are components of both response conflict and inhibition in the “inhibition” condition. In this task, it seems that inhibition may be unnecessary in the absence of conflict and conflict may be unresolvable in the absence of inhibition. Therefore, this task is agnostic with respect to whether inhibition or response conflict mediates the results and it is possible that both are involved. As discussed above, it is unclear whether the effects observed in previous attitude research studies are due to attitude activation or mediated by general semantic priming mechanisms. In the present task, a general semantic priming effect would lead to no differences between the response time to the attitude activation and inhibition conditions, as the prime–target pairs were always of the same valence and associated with “yes” responses in these conditions. An attitude-based effect would lead to slower responses in the attitude inhibition than activation condition.

We have recently proposed that attitudes are stored in distributed networks that represent the attitude-object together with its associated evaluations (Wood, 2003; Wood & Grafman, 2003). According to this framework, the amyg-

dala is implicated in simple emotional evaluations of an attitude-object—due to its association with emotional processing (Aggleton, 1992; Breiter et al., 1996; Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003; Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002; Hart et al., 2000; Phelps et al., 2000, 2001; Wood, 2003). In addition, attitudes were expected to be associated with ventromedial prefrontal cortex regions (Milne & Grafman, 2001; Wood & Grafman, 2003). However, it is possible that these networks may be modulated by the type of attitude-object that is presented, with attitudes towards social attitude-objects (e.g., landlords, parties and adoption) being associated with greater ventromedial prefrontal cortex activation than attitudes towards non-social attitude-objects (e.g., algebra, science and horses). Finally, it has been proposed that there is a ‘general inhibitory network’ involving dorsolateral prefrontal cortex, right inferior frontal gyrus and anterior cingulate (Garavan et al., 1999; Konishi et al., 1999; Leung et al., 2000; MacDonald et al., 2000)—we anticipated that this network should be implicated in attitude inhibition.

## 2. Methods

### 2.1. Subjects

Twenty-three right-handed (Oldfield, 1971) subjects aged 21–42 years (mean, 30.13 years; 12 men) participated. All had normal or corrected-to-normal vision, were native English-speakers, and gave informed consent to a protocol that had been approved by the Institutional Review Board. They reported no history of neurological or psychiatric problems and were determined to have had a normal neurological examination by an NINDS neurologist during the previous 12 months.

### 2.2. Stimuli and presentation conditions

There were two within subject factors: valence (positive and negative) and attitude condition (activation and inhibition). Neutral attitude-objects were included as fillers between blocks of emotional stimuli of opposing valence to allow the hemodynamic response to return to baseline. Dependent variables were response times for correct responses and blood-oxygen-level-dependent response. Consistent with previous attitude research, the study had two phases (Bargh et al., 1992; Fazio et al., 1986). Phase 1 evaluated subjects’ attitudes towards the attitude-objects. Phase 2 presented phrase pairs, the first phrase stated a certain person’s attitudes and the second phrase was either (a) consistent with that person’s attitude and compatible with the subject’s own attitude (e.g., ‘Chris likes chocolate’ with ‘chocolate is good’) or (b) consistent with that person’s attitude but incompatible with the subject’s own attitude (e.g., ‘Chris dislikes chocolate’ with ‘chocolate is bad’).

### 2.3. Phase 1

Subjects classified 800 attitude-objects (single words) as good or bad, as positive, negative, or neutral and as social or non-social (the social–non-social distinction was used for a study that will be reported elsewhere). The words were selected from Bargh et al.’s study (Bargh et al., 1992) and the MRC Psycholinguistic database (Coltheart, 1981). Four hundred of these were selected (J.N.W.) to be positive, negative or neutral (100, 100 and 200 words, respectively; the remaining stimuli were used in a study that will be reported elsewhere). Words were randomly assigned to eight blocks and presentation order counterbalanced across subjects. For all classifications, words were presented in a randomized order in the center of a computer screen until the subject responded; the inter-stimulus interval was 300 ms.

### 2.4. Phase 2

Eighty positive, 80 negative and 160 neutral words to be classified fastest as good/bad were selected for Phase 2—all categorization in Phase 2 was based on the subject’s own responses. Selection of the items associated with the fastest responses ensured that items with the strongest attitudes were used for Phase 2. The phrase pairs stated a person’s attitude towards an attitude-object together with an evaluation of that attitude-object, e.g., ‘Chris likes chocolate’ paired with ‘chocolate is good’ and ‘Chris dislikes murder’ paired with ‘murder is bad’.

Subjects decided whether phrase pairs were consistent, *irrespective of their own attitude towards the attitude-object* (as assessed during Phase 1). In the experimental trials, subjects responded ‘yes’ if the phrase pairs were consistent. Pairs were manipulated such that subjects’ responses were compatible (attitude activation) or incompatible (attitude inhibition) with their attitudes. *Note: the classification of the phrase pair as compatible or incompatible with the subjects’ attitudes was based on the subjects’ own responses in Phase 1 and not on the experimenter’s classification of the stimuli.* Examples are shown below—all of these are associated with ‘yes’ responses as the phrase pairs are consistent with each other:

- *positive attitude activation*: ‘Chris likes parties’—‘parties are good’;
- *positive attitude inhibition*: ‘Chris dislikes parties’—‘parties are bad’;
- *negative attitude activation*: ‘Chris dislikes murder’—‘murder is bad’;
- *negative attitude inhibition*: ‘Chris likes murder’—‘murder is good’.

If semantic priming or matching produced effects in this task, then there should be no differences between the activation and inhibition conditions, as the phrase pairs were always consistent in these conditions. In the attitude activation condition, subjects make an attitude-congruent response whereas in the attitude inhibition condition, subjects make an attitude-

incongruent response—the attitude-incongruent response requires inhibition of the attitude-congruent response. There were also filler trials in which the phrase pairs were inconsistent (e.g., ‘Chris likes death’—‘death is bad’): these were equivalent across the attitude activation and attitude inhibition conditions. Across the experiment, all attitude-objects were presented in both the activation and inhibition conditions.

Attitude-objects of each valence were randomly assigned to one of four runs. Repetition of attitude-objects was separated by at least one intervening run. In each run, there were eight types of block: activation and inhibition versions of positive, negative, neutral A and neutral B (for counterbalancing purposes, neutral words were randomly assigned to set A or B). Block order was counterbalanced across runs, with the constraint that neutral blocks were always presented between positive and negative blocks. Each block contained 10 trials. Half of the trials in each block were experimental (consistent prime–target pairs) and half filler (inconsistent prime–target pairs). Each block was of one valence and contained experimental trials of one type (activation/inhibition). Prime–target pairs were presented in the center of a computer screen for 2400 ms; inter-trial interval was 100 ms; inter-block interval was 3 s. Each run was preceded by a 12-s T1-equilibration period. Run order was counterbalanced across subjects.

### 2.5. Procedures and fMRI parameters

Subjects gave informed consent and completed Phase 1. Stimuli were presented using SuperLab Pro software (Aboud, 1989–1997, Cedrus Corporation, Phoenix, AZ) on a Macintosh computer; subjects responded by pressing keyboard keys with their right hand. Phase 2 was administered within 3 days of Phase 1. The fMRI experiment (Phase 2) was performed on a 1.5 T GE scanner. High-resolution anatomical images were acquired (3D-SPGR sequence, 124 contiguous slices, slice thickness = 1.5 mm, in-plane resolution = 0.9375 mm × 0.9375 mm). During the acquisition of anatomical images, subjects practiced the task using stimuli not presented in the experiment. Functional images were acquired (2D-gradient echo EPI sequence, interleaved acquisition, 22 contiguous slices, TR = 3 s, TE = 40 ms, flip angle = 90, FOV = 24 cm, slice thickness = 6 mm, in-plane resolution = 3.75 mm × 3.75 mm). Head motion was restricted using foam pads and a head strap. On completion of the experimental tasks, subjects were debriefed and completed state and trait anxiety measures (Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1968) and a checklist of social disinhibition symptoms (e.g., acting impulsively without consideration of the consequences; adapted from the UCLA Neuropsychiatric Inventory (Cummings et al., 1994)).

### 2.6. Data analysis

Behavioral data analyses were carried out using SPSS. Imaging data processing was carried out using SPM99

(Wellcome Department of Cognitive Neurology, London; <http://www.fil.ion.ucl.ac.uk/spm>) running in Matlab5 (Mathworks). Functional images were realigned to the first image acquired and a mean functional image created (Friston, Ashburner et al., 1995). Mean functional images were normalized to the Montreal Neurological Institute (MNI) brain template (Evans et al., 1993) and the resulting transformation matrices applied to the functional images. Functional images were resampled into 4 mm cubic voxels. Finally, the data were spatially smoothed with a 12-mm FWHM isotropic Gaussian kernel (Friston, Holmes et al. 1995b). Statistical analyses were performed using the general linear model. Contrasts were performed within-valence to eliminate activation due purely to differences in emotional valence. Activation was modeled using a boxcar model convolved with the hemodynamic response function. Data were temporally smoothed at the individual subject level of analysis using a 4-s Gaussian filter to remove effects due to physiological noise. Effect sizes were estimated using linear statistical contrasts and entered into random effects analyses. In addition, correlations were used to establish where relative brain activation correlated with behavioral measures.

The intention of imaging data analysis is to identify brain regions that exhibit true task-related activation. The nature of the data analysis results in the performance of multiple comparisons that must be taken into account when reporting and interpreting imaging data. In the present study, the correction for multiple comparisons was carried out using an uncorrected  $p$ -value of 0.02 and a cluster size threshold of 20—this corresponds to a per voxel false positive probability (Forman et al., 1995) of <.000001. This method of dealing with multiple comparisons has been reported elsewhere (Konishi et al., 1999; Konishi, Nakajima, Uchida, Sekihara, & Miyashita, 1998; Poldrack et al., 1999; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001; Wood, Romero, Makale, & Grafman, 2003). MNI coordinates were transformed into Talairach stereotactic space (Talairach & Tournoux, 1988) and approximate Brodmann areas determined (Duncan et al., 2000) (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>).

## 3. Results

### 3.1. Behavioral results

Analysis of median response times indicated a significant valence (positive and negative) × attitude condition (activation and inhibition) interaction,  $F(1, 22) = 7.16, p = 0.014$  (see Fig. 1; error rates were too low to permit meaningful analysis, 4.97%). Subjects responded faster to positive than negative attitude-objects in the activation condition,  $t(22) = 2.77, p = 0.011$ , but showed no difference in the inhibition condition,  $t(22) = 1.13$  ns. This suggests that positive attitudes are accessed more easily than negative attitudes, but are inhibited at similar speeds.

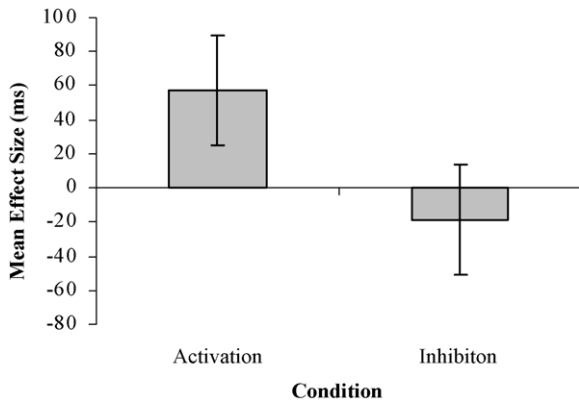


Fig. 1. Valence × attitude condition interaction with standard error bars shown; effect size = mean median RT to negative trials—mean median RT to positive trials.

3.2. fMRI results

Activation (relative to inhibition) of positive attitudes was associated with *left* ventrolateral PFC (BA 47), left premotor cortex (BA 6), bilateral parahippocampal gyrus (PHG; BAs 35, 28) and *left* hippocampus activation (see Table 1 and Fig. 2).

Activation (relative to inhibition) of negative attitudes was associated with *right* dorsolateral PFC (superior frontal gyrus, BA 10) and left premotor cortex (BA 6) activation

(see Table 1). The dorsolateral PFC activation was correlated with measures of state and trait anxiety, such that increased activation was associated with increased anxiety.

Inhibition (relative to activation) of positive attitudes was associated with activation of the right inferior frontal gyrus (BA 47), left premotor cortex (BA 6), and anterior cingulate bilaterally (BA 32; see Table 1 and Fig. 3). Activation of these regions has been reported with tasks involving response inhibition and suppression of interference. The inferior PFC activation was correlated with state, but not with trait, anxiety. In addition, left anterior cingulate activation was correlated with self-reported frequency of real-world disinhibited behavior.

Inhibition (relative to activation) of negative attitudes was associated with activation of left orbitofrontal cortex (BAs 10, 11 and 47), right amygdala, and bilateral PHG (BAs 28 and 35; see Table 1 and Fig. 4). Patients with damage to the orbitofrontal cortex often display behavioral disinhibition (Cummings, 1993; Fuster, 1997; Masterman & Cummings, 1997).

4. Discussion

The aim of the present study was to address directly hypotheses regarding the localization and inhibition of positive and negative attitudes. We predicted that the PFC and amyg-

Table 1  
Regions of PFC and limbic activation associated with each contrast

Cluster size	Anatomical localization of maximum voxel	BA	x	y	z
<b>Negative activation</b>					
1030	L middle frontal gyrus	6	-28	-1	52**
98	R superior frontal gyrus	10	28	47	1**
<b>Negative inhibition</b>					
68	L parahippocampal gyrus	35	-24	-21	-23**
59	R parahippocampal gyrus	28	20	-17	-23**
	R amygdala		28	-9	-26*
51	L inferior frontal gyrus	11	-20	34	-19**
	R medial frontal gyrus	47	-20	22	-18**
		10	8	38	-12*
<b>Positive activation</b>					
194	L parahippocampal gyrus	28	-20	-13	-23**
	L hippocampus		-28	-9	-20**
122	R parahippocampal gyrus	35	24	-17	-26**
		47	-55	23	-1*
49	L inferior frontal gyrus		-48	30	-15*
			-51	27	-8*
			-63	-10	26**
28	L precentral gyrus	4	-63	-10	26**
		6	-59	-3	26*
<b>Positive inhibition</b>					
510	B anterior cingulate	32	0	36	24**
	L medial frontal gyrus	6	-16	7	55*
65	R inferior frontal gyrus	47	40	19	-11**
			44	19	-4**
24	L middle frontal gyrus	6	-36	10	47*

Key: L, left; R, right; B, bilateral; p < 0.02, cluster size threshold = 20.

\* p ≤ 0.01.

\*\* p ≤ 0.001.

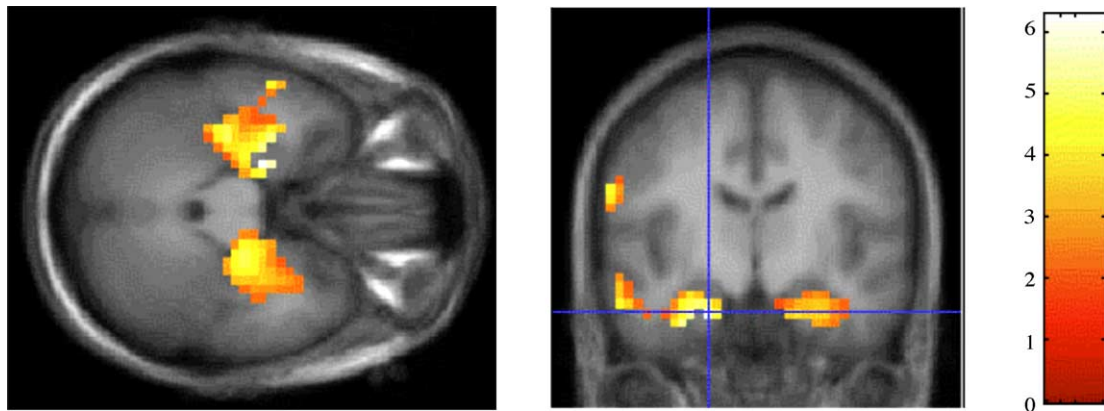


Fig. 2. Brain activation associated with positive attitudes in the attitude activation condition (after subtraction of that attitude inhibition condition). Crosshairs indicate activation of the left parahippocampal gyrus (right parahippocampal gyrus and left frontal regions also shown).

dala would be implicated in attitude representation and, consequently, we restricted fMRI data analysis to PFC and limbic brain regions. Further, we expected that inhibition of attitudes would implicate a network of regions including dorsolateral PFC, right inferior PFC and anterior cingulate.

#### 4.1. Activation of attitudes

Activation (relative to inhibition) of negative attitudes was associated with *right dorsolateral* PFC and left premotor cortex activation, whereas activation (relative to inhibition) of positive attitudes was associated with *left ventrolateral* PFC, left premotor cortex, bilateral PHG and *left* hippocampus activation. These regions differ from those reported in stereotype research (Hart et al., 2000; Milne & Grafman, 2001; Phelps et al., 2000) and upholds the assumed distinction between stereotypes and attitudes, in which stereotypes may be considered representations of categorical information about particular social groups and attitudes may be considered biases in the evaluation of stimuli (e.g., people, objects and places) (Ochsner & Lieberman, 2001). The degree of dorsolateral PFC activation for negative attitudes was correlated with trait and state anxiety measures. Subjects with greater dorsolateral

PFC activation also reported higher levels of state and trait anxiety. This suggests that anxiety may modulate dorsolateral PFC activation in the presence of negative attitude-objects. This finding is broadly consistent with neuropsychological findings of increased anxiety in patients with damage to the right PFC (Grafman, Vance, Weingartner, Salazar, & Amin, 1986).

The present data are consistent with dissociable networks for positive and negative attitude representations in PFC and limbic brain regions. Cerebral asymmetry for frontal and temporal regions has been reported in several studies of laterality of behavior, with left frontal regions being associated with approach behavior and right frontal regions with withdrawal behaviors (Davidson, 2001; Fox & Davidson, 1984; Kinsbourne, 1978; Kinsbourne & Bemporad, 1984). Developmental studies have also provided support for laterality differences (Davidson & Fox, 1989; Fox, Bell, & Jones, 1992; Henderson, Fox, & Rubin, 2001; Schmidt, Fox, Shulkin, & Gold, 1999). The present data are consistent with these findings with activation of left PFC for positive and right PFC for negative attitudes. Although the present data map nicely onto the general 'approach = left, withdrawal = right' framework, we are not suggesting that approach behavior is *simply*

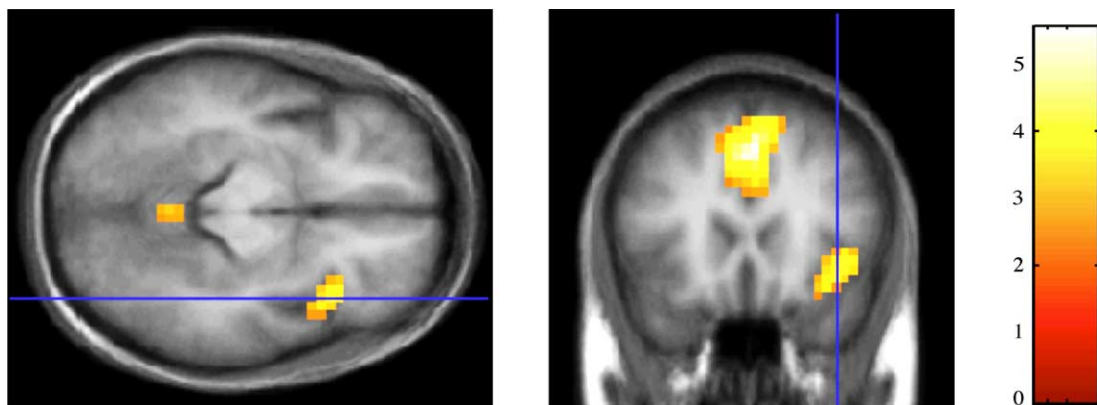


Fig. 3. Brain activation associated with positive attitudes in the attitude inhibition condition (after subtraction of that attitude activation condition). Crosshairs indicate activation of the right inferior frontal gyrus (bilateral anterior cingulate also shown).

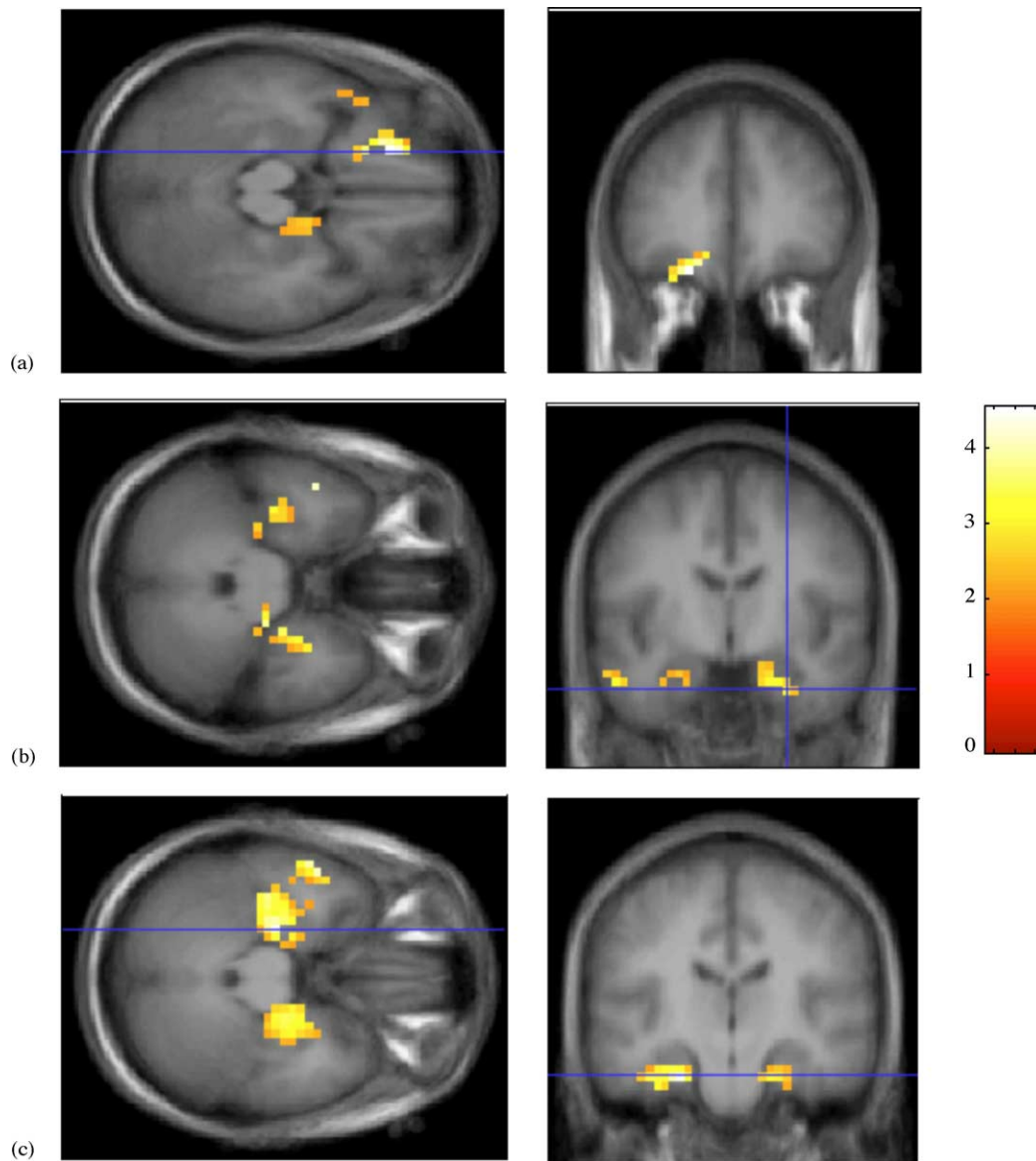


Fig. 4. Brain activation associated with negative attitudes in the attitude inhibition condition (after subtraction of that attitude activation condition). Crosshairs indicate activation of the (a) left orbitofrontal cortex (BA 11), (b) right amygdala and (c) left parahippocampal gyrus (right parahippocampal gyrus also shown).

due to positive attitudes and withdrawal behavior to negative attitudes. However, positive attitudes are more likely to be associated with approach behavior and negative attitudes with withdrawal behavior.

Left inferior PFC activation has been consistently reported in association with semantic tasks (Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998; Dalla Barba, Parlato, Jobert, Samson, & Pappata, 1998; Demb et al., 1995; Demonet et al., 1992; Friedrici, Opitz, & von Cramon, 2000; Martin & Chao, 2001; Poldrack et al., 1999; Vandenburghe, Price, Wise, Josephs, & Frackowiak, 1996) thus, its activation in the present task may reflect representation of the attitude-object component of the attitude and its semantic features. However, it is then unclear why the activation of negative attitudes is not also associated with activation of this region as

one might expect negative attitude-objects to have semantic features to a similar degree as positive attitude-objects. Alternatively, some authors have suggested that the left inferior PFC is involved in the selection of information from competing alternatives (Martin & Chao, 2001; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) and it may be the case that positive attitudes are less distinct (associated with more evaluations or behavioral responses) than negative attitudes.

Activation of negative attitudes was not associated with the predicted amygdala activation. Given the nature of imaging data analysis (subtraction of one condition from another), it is possible that the amygdala may have been activated in both negative conditions, but that it is simply more activated in the inhibition than activation condition (see the section below regarding negative attitude inhibition). Contrasts were

performed within-valence to eliminate activation purely due to differences in emotional valence, irrespective of attitude processing.

#### 4.2. Inhibition of attitudes

Based on previous research exploring brain regions implicated in response inhibition, set-shifting and Stroop interference, we expected that right inferior and dorsolateral PFC regions and anterior cingulate would be associated with the inhibition of attitudes (Casey et al., 2000; Collette et al., 2001; Garavan et al., 1999; Klingberg & Roland, 1997; MacDonald et al., 2000). It is important to note that the present study is agnostic to a distinction between response conflict and inhibition—both processes are likely to be involved in the inhibition condition due the nature of the task (subjects having to make responses that are incompatible with their own attitudes).

Inhibition (relative to activation) of positive attitudes was associated with activation of the right inferior frontal gyrus, left premotor cortex and anterior cingulate bilaterally. These data were consistent with our prediction and suggest that the inhibition of positive attitudes utilizes similar mechanisms to those reported for other inhibitory tasks. Right inferior PFC activation was correlated with the state anxiety measure—subjects with greater activation reported higher levels of state anxiety – but there was no correlation with the trait anxiety measure. Left anterior cingulate activation was correlated with the social disinhibition measure – this is a self-report measure of the frequency of real-world socially disinhibited behavior, e.g., acting impulsively without considering the consequences. Therefore, subjects with greater activation of the left anterior cingulate on this condition also reported more socially disinhibited behavior in real-world situations.

Inhibition (relative to activation) of negative attitudes was associated with activation of left orbitofrontal cortex, right amygdala and bilateral PHG. Patients with damage to the orbitofrontal cortex demonstrate disinhibited, socially inappropriate behavior (Cummings, 1995; Fuster, 1997; Masterman & Cummings, 1997). In addition, orbitofrontal cortex has been implicated in primate studies of inhibition (Jentsch et al., 2002; Wallis et al., 2001). The present data are consistent with these data and we speculate that neurological patients' disinhibited behavior may be partly due to an inability to inhibit behavior that is cued by attitudes. These data suggest that there are two different inhibitory networks, with positive and negative attitudes utilizing different networks of brain regions.

Previous studies have demonstrated amygdala activation in response to threat-related stimuli (Gur et al., 2002; Phan, Wager, Taylor, & Liberzon, 2002; Phelps et al., 2001; Whalen et al., 1998) and some have reported greater activation of right, relative to left, amygdala (Tabert et al., 2001). The negative attitude inhibition condition may have been more threatening than the negative attitude activation condition in-

sofar as the expression of a positive attitude towards a negative attitude-object is likely to be more threatening than the expression of a negative attitude towards the same attitude-object, e.g., someone who believes that 'murder is good' is likely to provide a greater threat than someone who believes that 'murder is bad'. The activation of the amygdala in the negative attitude inhibition condition is likely to be due to the greater threat evaluation of the stimuli, rather than the involvement of the amygdala in an inhibitory mechanism.

#### 4.3. Regions of activation common to attitude activation and inhibition

Parahippocampal gyrus (PHG) activation was evident in the activation of positive attitudes and inhibition of negative attitudes. Parahippocampal activation has been reported in studies of memory (Cabeza, Dolcos, Graham, & Nyberg, 2002; Leube, Erb, Grodd, Bartels, & Kircher, 2001; Spatt, 2002). Therefore, it is possible that the present PHG activation is due to a memory component of attitudes, possibly that positive activation and negative inhibition are more memorable than the other trial types. As discussed earlier, however, neuropsychological studies have shown that attitudes are independent of episodic memory that is subserved by the hippocampus and surrounding structures (Johnson et al., 1985; Lieberman et al., 2001). Thus, it seems unlikely that the PHG activation in the present study is due to episodic memory. Neuroimaging studies of emotional evaluation have also reported PHG activation (Lane et al., 1997; Tabert et al., 2001; Winston, Strange, O'Doherty, & Dolan, 2002). Further, the parahippocampal region has been implicated in animal studies of emotional learning, particularly with respect to object–context and emotion–context associations (Parker & Gaffan, 1998; Suzuki, 1996; Yaniv, Schafe, LeDoux, & Richter-Levin, 2000). Thus, it seems likely that PHG activation reflects an emotional component of attitude, with its involvement in the negative attitude inhibition condition arising for reasons similar to those outlined earlier for the amygdala, i.e., the greater emotional valence of the stimuli in the inhibition relative to activation condition. This argument implies that the positive attitude activation condition is more emotional (in this case more positive) than the positive attitude inhibition condition.

Premotor cortex activation was evident in all but the negative attitude inhibition condition. One explanation for premotor involvement is that as outlined in Section 1, activation of an attitude representation leads to activation of the associated behavioral response. This may involve priming of motor programs for that behavioral response, leading to the observed premotor activation. Although highly speculative, we suggest that the absence of premotor activation for the negative attitude inhibition condition may reflect the absence of motor programs for the behavioral responses appropriate to “abnormal” condition, e.g., behavior consistent with murder and rape being “good”.



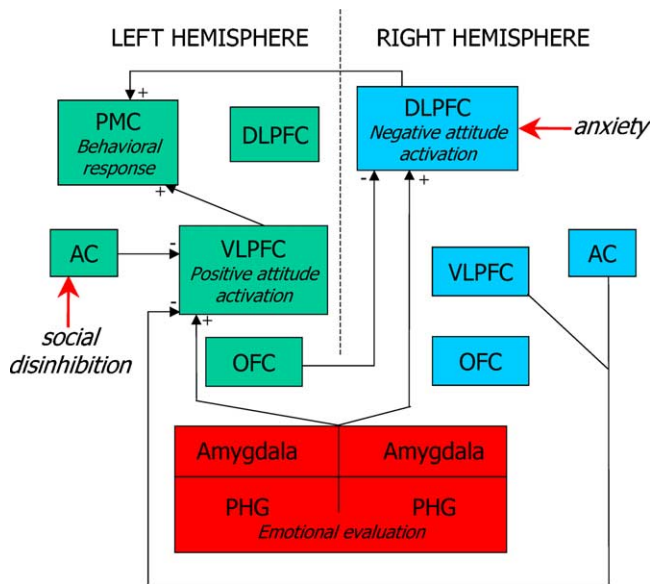


Fig. 5. Summary of brain regions implicated in the activation and inhibition of positive and negative attitudes.

#### 4.4. Summary and conclusions

In summary, right dorsolateral PFC mediates negative attitudes and left ventrolateral PFC mediates positive attitudes (see Fig. 5).

The amygdala and bilateral parahippocampal regions are implicated in the emotional evaluation of attitude-objects. Premotor cortex is implicated in the representation of attitude-related behavior, irrespective of the emotional valence of the attitude. Furthermore, right dorsolateral PFC activation may be modulated by state and trait anxiety levels. Positive and negative attitudes appear to be inhibited by distinguishable inhibitory networks. The network involved in inhibition of positive attitudes has been reported in many previous studies of cognitive inhibition (Casey et al., 2000; Collette et al., 2001; Garavan et al., 1999; Klingberg & Roland, 1997; MacDonald et al., 2000). The network involved in inhibition of negative attitudes implicates the orbitofrontal cortex. These data correspond both to real-world behavior reported by healthy subjects and to clinical observations of patients with damage to the orbitofrontal cortex. Such patients are described as “disinhibited” and these data suggest that their behavior may be due to inability to inhibit attitude-based behavior that may be socially inappropriate.

The present study extends previous cognitive neuroscientific research into stereotypes and attitude formation and change to the localization and inhibition of attitudes in the brain. The present data also suggest that some aspects of social cognition may map onto rather general cognitive functions (e.g., inhibition and emotional evaluation). With the rapidly increasing interest in the relationship between social cognition and the brain, researchers should be careful to ensure that each social concept is not considered a new type of process or representation, by evaluating its similarity to estab-

lished cognitive processes and representations. Finally, social cognition tasks, such as the one used in the present study, are increasingly being adapted for neuropsychological and neuroimaging studies (Gallagher et al., 2000; Goel & Dolan, 2001; Happe, Malhi, & Checkley, 2001; Phelps et al., 2000) and this approach is beginning to be applied to schizophrenia research. Patients with schizophrenia clearly have social cognitive deficits (Pinkham, Penn, Perkins, & Lieberman, 2003) and so the use of social cognitive paradigms along with other approaches (Haggard, Martin, Taylor-Clarke, Jeannerod, & Franck, 2003; Jeannerod, 2003; Slachevsky et al., 2003) may help to identify the nature of the social cognitive deficits in schizophrenia.

#### Acknowledgements

We thank Linda Mah, MD, for performing neurological examinations for this study. We are grateful to anonymous reviewers for their comments on an earlier version of this manuscript.

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