Category-Specific Representations of Social and Nonsocial Knowledge in the Human Prefrontal Cortex

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Abstract

■ Complex social behavior and the relatively large size of the prefrontal cortex are arguably two of the characteristics that distinguish humans from other animals. Grafman presented a framework concerning how the prefrontal cortex (PFC) controls complex behavior using stored structured event complexes (SECs). We report behavioral and imaging data from a modified go/no-go paradigm in which subjects had to classify words (semantic) and phrases (SEC) according to category. In experimental trials, subjects classified items according to social or nonsocial activity; in control trials, they classified items according to font. Subjects were faster to classify social than nonsocial semantic items, with the reverse pattern evident for the social and nonsocial SEC items. In addition, the conditions were associated with different patterns of PFC activation. These results suggest that there are different psychological and neural substrates for social and nonsocial semantic and SEC representations. ■

INTRODUCTION

Complex social behavior and the relatively large size of the prefrontal cortex (PFC) are arguably two of the characteristics that distinguish humans from other animals. Although recent research has called into question this difference with respect to great apes (Semendeferi, Lu, Schenker, & Damasio, 2002), there is evidence that frontal area 10 is larger in humans than in other primates (Semendeferi, Armstrong, Schleicher, Zilles, & van Hoesen, 2001). Recent research and theory have begun to address how these characteristics may be related. One view proposes that structured event complexes (SECs) control social behavior (Grafman, 1995, 1999; Sirigu et al., 1998). According to this representational framework, SECs provide a general structure/organization in memory for particular behaviors over relatively long periods (e.g., from minutes to hours). SECs are stored representations of sequential event knowledge and represent sequences of activities that have been described elsewhere as "scripts" or "schemas" (Eldridge, Barnard, & Bekerian, 1994; Casson, 1983; Schank & Abelson, 1977). Grafman (1999) proposes that event features (an SEC subcomponent) are localized in the left PFC and that there is category specificity in terms of localization of these SEC representations within the PFC. More specifically, he has suggested that social and nonsocial SECs may be localized independently. In addition, SEC information is distinguishable from basic semantic information about words or objects, but these are temporally and associatively interconnected and may be bound together as an episode. The aim of the present experiment is to explore localization of social and nonsocial SEC and semantic representations in the human PFC using event-related functional magnetic resonance imaging (fMRI).

In a clinical study, Sirigu et al. (1995) explored the effects of lesions of the PFC on SEC knowledge. Relative to healthy controls and patients with posterior lesions, patients with PFC lesions made more errors in temporally ordering events, determining the end of an event sequence, and categorizing events. Although the patients included in these studies preclude the detailed neuroanatomical localization of this knowledge, these data suggest that the PFC is important for accessing event knowledge. There have been a few neuroimaging studies addressing the localization of SECs in the human brain. An fMRI study showed activation of bilateral frontal regions in processing of script sequence information—that is, the order of event components (Crozier et al., 1999). A PET study showed different patterns of PFC activation when subjects generated emotional and nonemotional plans (Partiot, Grafman, Sadato, Wachs, & Hallett, 1995). The nonemotional plans activated the right superior frontal gyrus and the bilateral middle and medial frontal gyri, whereas emotional plans activated the left anterior cingulate, bilateral medial frontal gyrus, and probably the amygdala. These studies support the suggestion that SEC knowledge may be localized to the PFC and Partiot et al.'s (1995) findings suggest that it is possible to

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demonstrate category-specific prefrontal networks for SECs using imaging techniques.

Basic semantic knowledge, on the other hand, concerns factual information about the world (e.g., knowledge that a dog is furry, has four legs, and barks). The PFC has also been implicated in semantic processing (Martin & Chao, 2001; Gabrieli, Poldrack, & Desmond, 1998). In particular, left frontal and temporal regions have been implicated across studies (see Table 1). With respect to the PFC, left inferior PFC regions have been most consistently reported, although it is unclear in some studies whether the activation is associated with semantic representations or retrieval strategies—it has been suggested that this region is associated with the selection of semantic information from competing alternatives (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). While there has been some consistency across studies, not all studies of semantic processing or representations have demonstrated involvement of the same regions.

The imaging studies discussed above are consistent with SEC/script and semantic imaging tasks resulting in some common areas of activation, although there appears to be representation-specific regions. Do semantic and SECs representations differ? There is evidence from patients with PFC lesions that semantic and SEC knowledge may be selectively impaired—such patients show impaired performance on script tasks, but normal performance on tests of semantic knowledge related to the script activities (Sirigu et al., 1996, 1998). In addition, there is some evidence to suggest that SEC and sentence processing can be dissociated (Sirigu et al., 1998). As such, it seems reasonable to suggest that semantic and script information may be localized in different areas of the brain.

The aim of the present experiment is to address the question of whether social and nonsocial semantic and SEC representations are localized differently in the human PFC. The term ''social'' is used to describe activities that are usually performed by a group of people together, whereas ''nonsocial'' was used to describe activities that are usually performed by one person alone—alternatively, social activities can be conceptualized as interpersonal and nonsocial as solitary activities. Although ''social-ness'' may be a continuum along which activity components can vary, the present study selected activities to be at the ends of any such continuum; selected social activities were ''going out to dinner'' and ''putting a child to bed'' and selected nonsocial activities were ''getting ready for work'' and ''doing the laundry.''

In the present study, single words were used to access the semantic component of the task and phrases (describing an action/event) were used to access the SEC component of the tasks. Categorization of single words has been used to explore semantic processing in previous studies (e.g., Tyler, Russell, Fadili, & Moss, 2001; Dalla Barba, Parlato, Jobert, Samson, & Pappata, 1998). The phrases were taken from a previous study in which participants generated events that were components of certain activities (Rosen, Caplan, Sheesley, Rodriguez, & Grafman, in press). The categorization of these same phrases was expected to access the same SEC representations as Rosen et al.'s study.

The paradigm we used in our study was a modified go/no-go task in which words and phrases were classified as belonging to particular categories. The go/no-go paradigm was selected as patients with PFC lesions show deficits in inhibition (Fuster, 1997; Grafman, Holyoak, & Boller, 1995; Sirigu et al., 1995); therefore, the use of this paradigm was appropriate to assess the role of the PFC in storage of knowledge representations of complex behavior. There were three experiments in the present study—Cognitive 1, Cognitive 2, and efMRI. The Cognitive 1 experiment has a standard self-paced cognitive design with stimuli being presented for 2 sec or until the subject responded; the Cognitive 2 and efMRI experiments had a fixed-paced design with stimuli being presented for 3, 5, or 7 sec; the Cognitive 2 experiment was carried out in a normal behavioral testing environment, whereas the efMRI experiment was carried out in a scanner. Event-related fMRI places certain constraints on experimental design and the inclusion of three experiments enabled the behavioral profiles of the designs to be compared; it also allowed us to determine whether subjects performed differently in and out of the scanner.

With respect to the social and nonsocial semantic and SEC conditions, there were experimental and control trials. In the experimental trials, subjects decided whether words and phrases were related to a particular activity. Decisions about single words were based on the category–word meaning association (semantic condition); decisions about phrases were based on the category–action association (SEC condition). In the control trials, subjects had to decide whether the words and phrases were typed in the same font. Phrases and words in the social conditions were related to social activities, whereas those in the nonsocial conditions were related to nonsocial activities. The go and no-go trials occurred with equal frequency and were evenly distributed between the conditions—the response inhibition component of the task is not reported, as it is not of interest to the present discussion. On completion of the task, subjects rated the conditions in terms of difficulty and rated the stimuli in terms of emotional valence and ''social-ness.''

The aim of the present study is to address the question of whether social and nonsocial semantic and SEC representations are localized differently in the human PFC. Based on previous research, the SEC conditions were expected to activate a network of regions involving bilateral PFC areas. Orbito-frontal cortex may be associated with representation of social

Table 1. Regions Reported in Neuroimaging Studies of Semantic Localization

	Left						*Right*		
	SFG	*MFG*	*IFG*	*STG*	*MTG*	*ITG*	*IFG*	*STG*	*Other Regions*
PET studies									
Associative knowledge–letter detection (Cappa, Perani, Schnur, Tettamanti, & Fazio, 1998)	✓	✓	✓		✓	✓	✓		left precentral gyrus; right parieto-occipital junction
Semantic categorization and episodic recognition (Dalla Barba et al., 1998)			✓	✓				✓	left precentral gyrus
Semantic, phoneme, and tone monitoring (Demonet et al., 1992)	✓		✓	✓	✓	✓			left posterior cingulate; left fusiform gyrus; left precuneus; left supramarginal and angular gyrus
Word and picture matching (Perani et al., 1999)			✓	✓					bilateral anterior cingulate; left superior parietal lobule; right inferior parietal lobule; bilateral lingual gyrus; right cerebellum
Semantic–nonsemantic judgments (Vandenburghe et al., 1996)			✓		✓	✓			right ITG; left parieto-temporal junction; left fusiform gyrus; left superior occipital gyrus; left hippocampus; left cerebellum
Semantic matching (Wise et al., 1991)				✓				✓	bilateral Heschl's gyrus
fMRI studies									
Semantic–nonsemantic encoding (Demb et al., 1995)	✓		✓						
Semantic–syntactic judgments (Friedrici, Opitz, & von Cramon, 2000)			✓	✓	✓		✓		left postcentral sulcus; left parietal operculum; bilateral precuneus; bilateral thalamus
Semantic–phonological judgments (Poldrack et al., 1999)	✓	✓	✓				✓		
Lexical decision semantic priming task (Rossell, Bullmore, Williams, & David, 2001)								✓	bilateral anterior cingulate; left posterior cingulate; right insula
Picture naming (Spitzer, Kwong, Kennedy, Rosen, & Belliveau, 1995)		fronto-lateral region		✓	✓				

Regions indicated are those that demonstrated greater activation for the semantic than control task. SFG = superior frontal gyrus; MFG = medial frontal gyrus; IFG = inferior frontal gyrus; STG = superior temporal gyrus; MTG = middle temporal gyrus; ITG = inferior temporal gyrus.

Table 2. Regions of Activation for Each Condition (Cluster Threshold of 20 Voxels)

	Region Size	*Anatomical Localization of Maximum Voxel*	*Brodmann's Area*	*Talairach Coordinates*			
				x	*y*	*z*	
Social SECs	287	L superior frontal gyrus	9	−12	41	42	*
		L superior frontal gyrus	9	−8	48	31	*
		L superior frontal gyrus	8	−16	30	50	*
Nonsocial SECs	161	B anterior cingulate	25	0	11	−11	*
	64	L medial frontal gyrus	6	−8	−24	68	
	63	R superior frontal gyrus	8	16	30	50	*
Social semantics	105	L superior frontal gyrus	8	−12	34	50	*
		L medial frontal gyrus	8	−4	45	38	
	93	L inferior frontal gyrus	47	−48	27	−8	*
		L middle frontal gyrus	11	−28	34	−15	
	77	B medial frontal gyrus	6	0	−21	49	
		R medial frontal gyrus	6	4	−20	64	
Nonsocial semantics	32	L inferior frontal gyrus	45	−55	20	6	
		L inferior frontal gyrus	47	−48	27	−5	

L = left; R = right; B = bilateral.

*Uncorrected $p < .005$.

SECs, as this region has been implicated in social cognition (Damasio, 1995, 1998; for recent reviews, see Davidson & Irwin, 2000; Schulkin, 2000). Based on previous research, the semantic conditions were anticipated to activate a network of areas involving the left inferior and superior PFC.

RESULTS

Imaging Data

Details of how the imaging data were preprocessed and modeled are reported in the Methods section. Contrasts were performed to subtract activation associated with the control (font classification) task from that associated with the experimental (category classification) condition to show those regions activated by the experimental task alone—due to analytical power, the data from the go and no-go trials were combined and were not considered separately. The resulting contrast images were entered into random effects analyses. The coordinates reported in Table 2 are the coordinates after transformation into Talairach stereotactic space.

SEC conditions activated networks of frontal regions—this was broadly consistent with expectations (see Figure 1 and Table 2). However, social and nonsocial SECs were associated with activation in different regions. Frontal activation for social SECs was restricted to the left superior frontal gyrus. Frontal activation for nonsocial SECs was restricted to the right superior frontal gyrus, left medial frontal gyrus, and the bilateral anterior cingulate. Thus, the social and nonsocial SECs activated different networks of areas. Correlational analyses (using Spearman's rank–order correlations) were carried out to determine whether the mean level of brain activation in the frontal areas in the social and nonsocial conditions were related to the mean social relatedness ratings of stimulus items presented in those blocks. The measures were not significantly correlated.

As predicted, both semantic conditions activated the left inferior frontal gyrus. However, the social and nonsocial semantic conditions were associated with different activation patterns. The nonsocial semantic condition activated Brodmann's area 45 (BA 45) in the left inferior frontal gyrus. The activation associated with the social semantic condition was more widespread than that for the nonsocial semantic condition. For social semantics, there were clusters of activation in the left superior and medial frontal gyri, left inferior and middle frontal gyri, and right medial frontal gyrus. Visual inspection of the functional images suggested that the absence of activation of orbito-frontal regions was due to signal dropout (see Figure 2), this was most likely due to susceptibility artifact from the nasal sinuses (Cordes, Turski, & Sorenson, 2000).

We were primarily interested in the prefrontal regions implicated in this task. However, for sake of

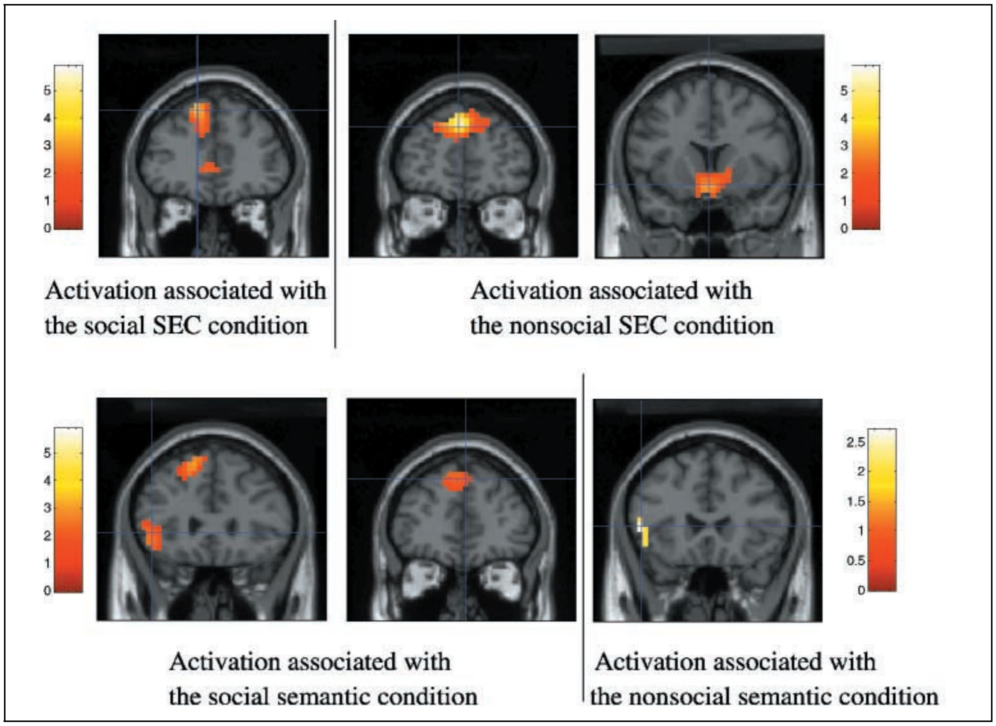

Figure 1. Frontal regions activated in each condition (coronal sections).

completeness, the whole-brain analysis showed significant activation of the left middle temporal gyrus for the social SEC (BA 39), nonsocial SEC (BA 19, 37), and social semantic (BA 21) conditions. No other brain regions were significantly activated.

Behavioral Data

Analysis of Response Latencies to Classify Stimuli

Median RTs to respond in the go trials were used in order to minimize the effects of skew in the data. There was a main effect of Design, $F(2,48) = 23.48, p < .001$. A main effect of Representation Type and a Task × Category interaction were qualified by a Task (category, font classification) × Category (social, nonsocial) × Representation Type (semantic, SEC) interaction, $F(1,48) = 11.16, p = .002$.

Subjects responded faster to items in the Cognitive 1 experiment (mean = 793 msec) than in either the Cognitive 2 study (mean = 1092 msec), $t(30) = 5.42$, $p < .001$, or the efMRI experiment (mean = 1174 msec), $t(34) = 6.86, p < .001$. Responses to the Cognitive 2 and efMRI experiment did not significantly differ, $t(34) = 1.35$, *ns*. There were no significant interactions involving Design suggesting that the Cognitive 1 design was simply easier, most likely due to the predictability of trial presentation.

Separate Category × Representation Type ANOVAs were performed on the data from each task to explore the Task × Category × Representation Type interaction. Analysis of the category classification data showed a main effect of Representation Type, which was qualified by a Category × Representation Type interaction, $F(1,50) = 25.92, p < .001$ (see Figure 3). Paired *t* tests

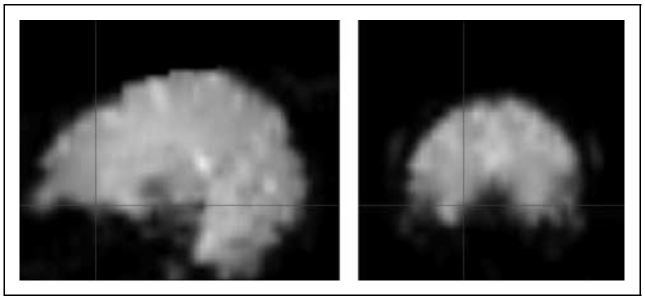

Figure 2. Functional image to illustrate signal dropout in orbitofrontal regions (sagittal and coronal sections).

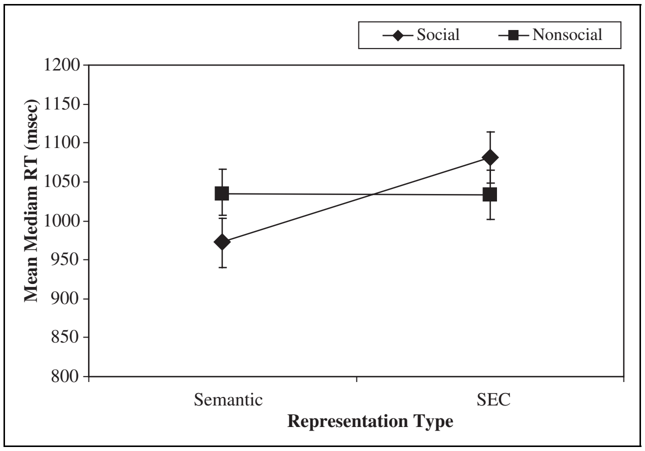

Figure 3. Category × Representation Type interaction in the category classification data (standard error bars shown).

showed that social items were categorized faster than nonsocial items in the semantic condition, $t(50) = 4.68$, $p < .001$; with the opposite pattern in the SEC condition, $t(51) = 2.57$, $p = .013$.

Analysis of the font classification data demonstrated main effects of Category, $F(1,50) = 6.17$, $p = .016$, and Representation Type, $F(1,50) = 7.29$, $p = .009$. These factors did not interact, $F(1,50) = .88$, *ns*. Subjects responded faster to nonsocial than to social items (means = 1011 and 1054 msec) and responded faster to semantic items than to SEC items (means = 994 and 1058 msec).

Error Rates

Subjects made too few errors to allow meaningful comparison of conditions—2.46% commission errors (responses to no-go trials) and 5.07% omission errors (no responses to go trials); 5.19% of go trials were incorrectly classified, with similar error rates for the category and font classification tasks (4.35% and 6.03%). There was a significant difference in error rate across the experiments (false negatives and false positives combined), $F(2,49) = 6.75$, $p = .003$. Subjects in the Cognitive 1 study made fewer errors (mean = 2.06 errors) than those in the Cognitive 2 study (mean = 8.88 errors), $t(30) = 3.48$, $p = .002$, or the efMRI experiment (mean = 5.35 errors), $t(34) = 2.63$, $p = .013$. The Cognitive 2 and efMRI experiment groups did not significantly differ, $t(34) = 1.70$, *ns*.

Postexperiment Ratings

Subjects reported no significant differences in difficulty between the conditions for the category or font classification task, F's$(2,49) = 2.39$ and .17, *ns*. Subjects rated social items as more positive than nonsocial items (means = 6.24 and 5.18), $F(1,140) = 40.13$, $p < .001$. Analysis of social relatedness ratings revealed a Category × Stimulus Type interaction, $F(1,140) = 11.17$, $p = .011$. Subjects rated nonsocial phrases as less social than the nonsocial words (means = 2.67 and 3.27), $t(70) = 2.67$, $p = .009$, with no significant difference for social stimuli (means = 5.11 and 4.59), $t(70) = 1.40$, *ns*. The distribution of the social ratings was consistent with a continuum of "social-ness" rather than a bimodal grouping of social and nonsocial stimuli. Social relatedness and emotionality ratings were significantly correlated, $r(144) = .59$, $p < .001$.

The behavioral profiles of data for each experiment did not differ, as indexed by the absence of any interactions with Design; the Cognitive 1 design was simply easier—probably due to the predictability of the onset of each trial. In the category classification task, subjects classified social faster than nonsocial semantic items, with the reverse pattern evident for the SEC items. In the font classification task, subjects responded faster to nonsocial than social items (irrespective of representation type) and responded faster to semantic than SEC items. Subjects' ratings of the stimuli confirmed that social items were "more social" than nonsocial items, although the social items were also rated as more positive than nonsocial items. There was a positive correlation between the social and emotional ratings of the stimuli.

DISCUSSION

The aim of the present experiment was to address the question of whether social and nonsocial semantic and SEC representations are localized differently in the PFC. The behavioral data are consistent with category-specific differences between these representations. This suggestion is consistent with findings of category-specific localization of representations in the imaging data. Importantly, the SEC and semantic conditions did not result in similar patterns of activation, suggesting that the SEC conditions were not simply utilizing basic semantic information in the task. The analyses of the semantic and SEC conditions of the imaging data involved subtraction of the control task (font classification) from the experimental task (category classification). Thus, the areas of activation for these conditions discussed below reflect the brain regions that are present only in the experimental conditions. Any activation that is due to low-level processing, for example, of stimulus features, should be common to both the experimental and control conditions and would be eliminated in the subtractions.

Semantic Representations

The behavioral data of the go trials of the category-specific task provide an indication of access to stimulus representations. In the category classification task, subjects were faster to classify the social than nonsocial items in the semantic condition. This pattern is consistent with social semantic representations being more accessible than nonsocial representations—this may be due to more and/or stronger connections between social semantic representations. Activation of a social semantic representation leads to activation of other social representations, leading to a higher activation state and hence priming of multiple social semantic representations. This leads to facilitation for social stimuli when the task demands require access to social semantic meanings and interference when these need to be ignored (e.g., the font classification task). This is analogous to the emotional Stroop effect reported for anxious individuals—anxious individuals' are slower to name colors of threat-related, relative to neutral, words (e.g., for reviews, see Williams, Watts, MacLeod, & Mathews, 1997; MacLeod, 1991).

Previous neuroimaging research has not addressed the question of category-specificity with respect to social–nonsocial distinctions. The suggestion of category-specificity in semantic representations is supported by the present imaging data. Activation of the left inferior prefrontal gyrus in both semantic conditions replicated previous research (Martin & Chao, 2001; Poldrack et al., 1999; Vandenburghe, Price, Wise, Josephs, & Frackowiak, 1996) and may represent a common region for some aspect of the processing of semantic representations. For example, it has been suggested that this region may be important in the selection of a single meaning from competing alternative candidates, which should require context (Martin & Chao, 2001; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Interestingly, the activation for the social semantic condition was more extensive than that for the nonsocial semantic condition. The more extensive activation evident in the social semantic condition is suggestive of a larger and more interrelated network for social semantic information. This is consistent with the interpretation of the behavioral data discussed above, with presentation of social semantic items resulting in activation of other social semantic representations.

The frontal activation incorporated the left inferior frontal gyrus and extended to the left middle frontal gyrus as well as the left superior and medial frontal gyri and the medial frontal gyrus bilaterally. The activation of the left frontal gyri has been reported in other neuroimaging studies of semantics (see Table 1). This might suggest that these regions are not specific to a social semantic network; however, the nonsocial semantic condition did not show a similar pattern of activation. It is possible that the stimuli used in previous studies may have been interpreted as social, but simply not classified by the experimenter in that way. Activation of the premotor cortex (BA 6) has been reported in studies of semantic processing (Fernandez et al., 2001; Crosson, 1999), particularly in semantic processing of tools or other manmade objects (Gerlach, Law, Gade, & Paulson, 2000; Grafton, Fadiga, Arbib, & Rizzolatti, 1997). However, the present stimuli were social and did not comprise tools. Although these stimuli contained action-related words, the number and ratings of action-related words were equated across the social and nonsocial conditions. Taken together, these findings suggest that the role of the premotor cortex in semantic representation or processing may not be limited simply to tool and action-related words.

In summary, the present data are consistent with the storage of basic social and nonsocial semantic representations in dissociable networks, of which the social semantic network is more extensive. The extent of the social semantic network and the closer relationship between representations may reflect the importance of social information in both our everyday lives and in our evolutionary development (Duchaine, Cosmides, & Tooby, 2001; Povinelli & Preuss, 1995).

SEC Representations

In our discussion of semantic representations, we proposed that social information is more readily accessible than nonsocial information and, therefore, social SECs should be associated with faster responses than the nonsocial SECs. However, the converse pattern was evident. Why might that be the case? Although speculative, we propose that semantic and SEC representations are different and that while semantic representations may be context independent, this is not the case for episodic SECs. By context independent, we suggest that a particular semantic representation is activated irrespective of the situational context in which it is encountered. A representation of an SEC contains several components that may have different versions (e.g., in an SEC of going out to dinner, there may be several ways to make a reservation or to choose a restaurant). Such instances are stored in distinct but overlapping representations. We propose that social SECs contain more of these than do nonsocial SECs. There are sufficient contextual constraints when performing the activity to enable the retrieval of only the relevant version. For social activities in experimental tasks like the one we administered, however, the context is insufficiently specified, leading to activation of several competing representations, resulting in a slower response relative to trials in which only one representation is activated (i.e., for nonsocial activities). As such, social SECs may be considered more complex than nonsocial SECs. By complex, we mean that social SECs have overlapping representations whereas nonsocial SECs do not. It is possible that this property of complexity may define the difference between social and nonsocial SECs, although this prospect will need to be addressed in future research.

We had predicted that the SECs would be associated with bilateral dorsolateral PFC and orbito-frontal regions (Partiot et al., 1995). Based on the possibility of differences in emotionality between the social and nonsocial activities, we had also predicted that the social SECs might be associated with activation of the left anterior cingulate. These predictions were partially upheld by the findings of dorsolateral PFC activation that was lateralized to the left for social SECs and to the right for nonsocial SECs. The difference in findings with the Partiot et al. (1995) study may be because they explored localization differences between generation of imagined *emotional* and *nonemotional* social plans, whereas the verbal classification categories in the present experiment were social and nonsocial activities. Given the present findings, it seems likely that social and nonsocial categories do not map *directly* to emotional and nonemotional categories. The mean activation and mean social relatedness ratings were not significantly correlated; however, activation and ratings of individual trials may have been correlated. Orbito-frontal activation was expected for the social SECs, but was not evident in the present study. Visual inspection of the functional images showed signal dropout in the orbito-frontal region and, therefore, the present data cannot address the question of whether this region is implicated in the storage of representations of social knowledge. Lesion data, however, strongly support this viewpoint (Milne & Grafman, 2001; Fuster, 1997).

We speculate that superior frontal gyrus activation may reflect the SEC representation of the meaning and features of the event. This includes the sequential dependencies between events. Therefore, the SEC representations' meaning and features are localized in dissociable regions in the PFC, with social SECs being localized to the left superior frontal gyrus and nonsocial SECs to the right. Although the superior frontal gyrus activation could reflect differences in processing effort, it is unclear why this would be lateralized differently for social and nonsocial SECs. Furthermore, the suggestion that representations of event knowledge may be stored in PFC regions is consistent with both theory (e.g., Grafman, 1995, 1999; Fuster, 1997; Burnod, 1991) and previous research (e.g., Ruby, Sirigu, & Decety, 2002; Partiot et al., 1995; Sirigu et al., 1995, 1996).

Activation of anterior cingulate has been associated with storage of overlearned procedures or schemas (Jueptner, Stephan, Frith, Brooks, & Frackowiak, 1997). It is possible that these procedures may include frequently used event sequences such as those comprising SECs—anterior cingulate activation was evident for the nonsocial SECs. Overlearned schemas are likely to have strong relations to motor regions and this may be reflected in the premotor activation that was also evident for the nonsocial SECs. Therefore, we speculate that the anterior cingulate and premotor activation reflects strong associations between nonsocial SECs and their related motor programs. Finally, the left middle temporal gyrus activation observed with both conditions may reflect activation of lower level representations by their association with the SECs—these may be semantic representations that are related to the SEC information (Whatmough, Chertkow, Murtha, & Hanratty, 2002; Castillo et al., 2001; Martin, Wiggs, Ungerleider, & Haxby, 1996; Vandenburghe et al., 1996).

The aim of the present article was to understand the role of the PFC in the storage of knowledge representations. Grafman's (1995, 1999) proposal that event features are localized in the left PFC appears to be partially upheld with both types of SEC demonstrating left PFC involvement. Social SECs were associated with left superior frontal gyrus activation, whereas nonsocial SECs were associated with activation of the left medial frontal gyrus, bilateral anterior cingulate, and right superior frontal gyrus. The differing patterns of activation provide support for the suggestion that there is category-specificity in the localization of knowledge in the PFC, with the social–nonsocial dimension forming the basis of one category distinction.

The behavioral data are consistent with social SECs being more complex than nonsocial SECs. The imaging data suggest that social SECs are localized in the left PFC, whereas nonsocial SECs are bilaterally localized. It is important to note the PFC regions implicated in the semantic conditions differ from those in the SEC conditions. This is consistent with the suggestion that SEC and semantic information are associated with representations that may be topographically differentiated in the PFC. Although the hypothesis regarding orbito-frontal involvement in the tasks we presented here could not be adequately tested due to signal dropout, there is evidence from clinical studies that this region is implicated in representation of social SECs. In summary, the imaging data are consistent with category-specific localization of social and nonsocial SEC representations in the human brain.

Summary and Conclusions

The present experiment demonstrated category-specific effects in the behavioral data that were consistent with social and nonsocial semantic and SEC representations having different properties. One suggested difference is in the context-dependence of the representations, with SECs having different versions whose activation is dependent on the situational context. The behavioral data are suggestive of social semantic representations being more closely interconnected than nonsocial semantic information and of social SEC representations being more complex than nonsocial SEC representations. Grafman (1999) suggested that SEC localization might be influenced by category membership, emotional valence, and frequency of expression. He proposed that there might be other properties that are important in determining localization and the present data support this viewpoint. The imaging data are consistent with our suggestion that separable networks of activation in the human brain support semantic and SEC representations and that there are category-specific differences in the behavioral and imaging data within each representation type. In addition, the present findings are broadly supportive of Grafman's (1995, 1999) proposal that the PFC stores representation of event knowledge with category–specific localization of these representations. The present research extends previous findings of emotional–nonemotional differences in plan generation (Partiot et al., 1995) and presents behavioral data consistent with social–nonsocial differences in the properties of knowledge representations and imaging data consistent with localization differences.

METHODS

Basic Experimental Design

There were three within subject factors: task (category, font), representation type (semantic [single words], SEC [phrases]), and category (social, nonsocial). Each run of trials presented the experimental (category classification) and control (font classification) trials of one representation type leading to four runs: semantic–social, semantic–nonsocial, SEC–social, SEC–nonsocial. Within each run, there were three blocks of experimental trials and three blocks of control trials. Subjects had to decide whether each stimulus was related to a specified activity (experimental trials) or presented in a specified font (control trials); for example, they might have responded "yes" if it was related to "going out to dinner" and "no" if it was related to "putting a child to bed." Within a particular block, a stimulus belonged to one of two classifications (e.g., "going out to dinner" or "putting a child to bed") and was colored either blue or red. Subjects responded to blue stimuli and did not respond to red stimuli.

Subjects

Subjects were right-handed native English speakers, aged 19–35 years old, and were not red/green color blind. They reported no history of neurological or psychiatric problems. Subjects in the efMRI study were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971) and were determined to have had a normal neurological examination by an NINDS neurologist during the previous 12 months. All subjects gave informed consent to a protocol that had been approved by the Institutional Review Board. Sixteen subjects participated in the Cognitive 1 (6 men, 10 women, mean age 28.17 years), 16 in the Cognitive 2 (8 men, 8 women, mean age 28.31 years), and 20 in the efMRI study (11 men, 9 women, mean age 27.05 years). Subjects' ages did not differ significantly between the experiments, $F(2,49) = 1.58$, *ns*. One additional individual was excluded from Cognitive 1 and 2 experiments due to failure to follow instructions and two additional subjects were excluded from the efMRI study due to head movement during the scan (3 mm or 3° in any plane). In the efMRI study, the behavioral data of one condition for one participant were unavailable for analysis due to equipment failure.

Stimuli

The stimuli in the SEC conditions were components of activities that were chosen from script norms (Rosen et al., in press) according to the constraints that they were high frequency and did not share component actions. The stimuli were matched across category conditions (social, nonsocial) for frequency: For the semantic conditions, frequency was assessed using established word frequency norms (MRC Psycholinguistic Database; Coltheart, 1981), and for the SEC conditions, frequency was assessed using established norms of daily activities (Rosen et al., in press). Due to the differences in nature between the word and activity frequency measures, matching of frequency across representation type (semantic, SEC) was not possible. Instead, the words were matched to the activity frequencies and were derived from the SEC stimuli (e.g., if an SEC stimulus was "read the menu," the derived semantic equivalent would be "menu"). There were similar numbers of nouns and verbs in each condition. There were no significant differences between the frequencies of the stimuli of each activity within each representation type, t's <1.3, *ns*.

Each run of trials presented the experimental (category classification) and control (font classification) trials of one representation type leading to four runs in total: semantic–social, semantic–nonsocial, SEC–social, SEC–nonsocial. Each run contained three blocks of experimental trials and three blocks of control trials. The experimental trials contained 18 items related to each category, giving 36 items in total. The items in each category were randomly assigned to the "go" (blue) or "no-go" (red) condition with the constraint that there were equal numbers of go and no-go trials for each category. In addition, stimuli were randomly assigned to a font (44-point Helvetica or 46-point Palatino), with the constraint that half of the "go" items were of one font and the remaining items were of the other font; the same applied to the "no-go" items. The fonts were chosen in order to make the discrimination difficult in order to minimize differences in the level of difficulty between conditions.

On experimental trials, subjects decided whether a stimulus item was related to the category specified in the preceding caption. The same stimuli were presented in the control trials; however, subjects instead decided whether the stimulus' font matched that of the preceding caption. The trials were randomly assigned to three blocks and were presented twice, once with each task instruction. Each block was preceded by a caption that instructed the participant whether the task concerned the category or the font and which category or font was associated with a "yes" response. The order of presentation of the conditions was counterbalanced between subjects. The semantic and SEC conditions had their own control conditions and the patterns of activation were compared in terms of the localization of the activation, that is, were the same areas activated? Therefore, the semantic and SEC conditions did not need to be equated for visual angle and resultant eye movement.

On completion of the experiment, subjects completed scales to rate all of the stimuli in terms of emotionality and in terms of social relatedness. Each was a 1–9 scale that was based on the Self-Assessment Manikin (Bradley & Lang, 1994). The emotional scale was anchored at *extremely unhappy* (1) and *extremely happy* (9); the social relatedness scale was anchored at *stimuli related to activities that someone would always do on their own* (1) and *stimuli related to activities that groups of people would always do together* (9).

Presentation Conditions

Each run consisted of six blocks—three experimental and three control blocks. At the beginning of each block, a caption printed in black was presented that informed the participant which activity or font was relevant to the task; for example, on an experimental run in which the target activity (''yes'' responses) was ''going out to dinner'' and the distracter activity (''no'' responses) was ''giving a party,'' then the initial caption read ''CATEGORY—GOING OUT TO DINNER.'' On the corresponding control run, the caption read ''FONT—GOING OUT TO DINNER.'' Words (semantic condition) or phrases (SEC condition) were then presented to the participant in blocks, as described above. The caption was presented for 3 sec followed by an interval of 3 sec. Twelve trials of one type (experimental or control) were then presented. After completion of the block, a new caption was presented followed by 12 more trials of the other type. The presentation order of the trials was randomized within each block.

Subjects responded ''yes'' to targets and ''no'' to foils. As described above, the stimuli in each run belonged to two activity types. For half of the subjects, Activity A items (e.g., ''going out to dinner'' or those in the Palatino font) were targets and Activity B items (e.g., ''putting a child to bed'' or those in the Helvetica font) were foils. For the remaining subjects, Activity B items were targets and Activity A items were foils. Subjects were instructed to respond (''yes'' or ''no'') to stimuli that were colored blue and not to respond to stimuli that were colored red.

There were three experimental designs that were incorporated into the present experiment—Cognitive 1, Cognitive 2, and efMRI experiments. The experiments all had the same basic design structure, as described above. The cognitive design was self-paced with each stimulus being presented for 2 sec or until the participant responded. The use of the self-paced cognitive design enabled the normal behavioral profile of the task to be established. The Cognitive 2 and efMRI experiments were not self-paced and each stimulus was presented for 2 sec, followed by an ISI of 1, 3, or 5 sec (Dale & Buckner, 1997). The event-related fMRI (efMRI) design allowed randomization of trial presentation. The ISIs were selected as short ISIs have been effectively used in efMRI designs providing the interval was jittered—the ISI is varied around a mean interval (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000; Dale, 1999; Dale & Buckner, 1997) This increases the number of time-points over which the hemodynamic response is sampled and ensures that there are enough sampling points to enable estimation of the shape and duration of the hemodynamic response (Miezin et al., 2000). Furthermore, Dale (1999) has demonstrated that using a short (1–8 sec), jittered ISI provides greater statistical efficiency than using a long ISI. Jittering also decreases the predictability of stimulus presentation, thus reducing some effects of anticipation and response preparation.

Procedures and fMRI Parameters

Subjects signed consent forms and practiced the task using a set of stimuli that were not presented in the experimental task. Presentation of stimuli was carried out using SuperLab Pro software (Abboud, 1989–1997) on a Macintosh computer. For all experiments, responses were made by pressing buttons on a response box that was held in the participant's right hand. For the Cognitive 1 and 2 experiments, subjects were then seated in front of a computer and presented the four runs as described above. The presentation order of these runs was counterbalanced across subjects.

The efMRI experiment was performed on a 3-T GE scanner. High-resolution anatomical images were acquired using a 3-D SPGR sequence to obtain 124 contiguous slices (slice thickness = 1.5 mm, in-plane resolution = $.9375 \times .9375\ \text{mm}^2$). The functional images were acquired using a 2-D gradient-echo echo-planar imaging sequence to obtain 22 contiguous slices (TR = 3 sec, TE = 40 msec, flip angle = 90°, FOV = 24 cm, slice thickness = 6 mm, in-plane resolution = $3.75 \times 3.75\ \text{mm}^2$). Head motion was restricted using foam pads placed around the participant's head. Visual stimuli were back-projected onto a screen, which was viewed in a mirror that was attached to the head coil.

Data Analysis

Behavioral data analysis was carried out using SPSS (1989–2000). fMRI data processing was carried out using SPM99 (Wellcome Department of Cognitive Neurology, 1999) running in Matlab5 (MathWorks, 1984–1998). Functional images were corrected for differences in slice timing acquisition by resampling of all slices to match the middle slice. The images were then realigned to the first image acquired and a mean functional image created (Friston, Ashburner, et al., 1995). Two subjects were eliminated from subsequent analysis due to head movement. The mean functional images from the remaining 20 individuals were normalized to the Montreal Neurological Institute (MNI) brain template and the resulting transformation matrix applied to the functional images. The functional images were resampled into 4-mm cubic voxels during the normalization process. Finally, data were smoothed with a 12-mm FWHM isotropic Gaussian kernel (Friston, Holmes, et al., 1995).

Statistical analyses were performed using the general linear model in SPM99. The trials for each condition and participant were modeled using a canonical hemodynamic response function with temporal derivative. This model was selected to provide optimal sensitivity in the analysis (Hopfinger, Buchel, Holmes, & Friston, 2000). Data were globally scaled at the individual subject level of analysis to allow comparison of images from different individuals at the group level of analysis. In addition, the data were temporally smoothed using an HRF filter to remove effects due to physiological noise. Linear statistical contrasts for each comparison of interest were used to estimate effect sizes for each participant. These estimates were entered into second-level random effects analyses. Random effects analyses take intersubject variability into account and eliminate the possibility of one participant skewing the results. These analyses also allow inferences to be made regarding the population in general rather than the specific subjects in the experiment (Friston, Holmes, & Worsley, 1999). One-sample t tests were used to determine the voxelwise t statistics for each condition.

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 for the PFC activation was carried out using an uncorrected p value of .02 and a cluster size threshold of 20—this corresponds to a per-voxel false-positive probability of less than .000001 (Forman et al., 1995). This method of dealing with multiple comparisons has been reported by other researchers (Wagner et al., 2001; Poldrack et al., 1999; Konishi, Nakajima, Uchida, Sekihara, & Miyashita, 1998; Konishi et al., 1999). For the whole-brain analysis, corrected p values were used to assess significance.

Approximate Brodmann's areas of the resulting activations were determined after transformation of the MNI coordinates into Talairach stereotactic space (Talairach & Tournoux, 1988)—this transformation takes into account differences between the MNI and Talairach brains (Duncan et al., 2000) (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html).

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The data reported in this experiment have been deposited in The fMRI Data Center (http://www.fmridc.org). The accession number is 2-2002-1139Y.

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