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Neural Processing of Threat Cues in Social Environments

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Abstract: Previous research showed that the processing of overt threat cues formed by evolutionary experience such as snake or angry face induced automatic increased responses of the emotion-related system consisting of the amygdala, the anterior cingulate, and the orbitofrontal cortex. The present study used functional magnetic resonance imaging (fMRI) to investigate brain circuits involved in perception of threat cues that lack obvious emotion contents but are potentially dangerous in a particular social situation. Subjects were scanned while watching images showing a person in either a safe or a potentially dangerous situation and being asked to detect threat signals or to evaluate the degree of threat. We found that, in contrast with gender identification, threat detection and evaluation were underpinned by a neural network, shared by both male and female subjects, consisting of the medial and lateral frontal cortex, superior parietal lobes, posterior middle temporal cortex, and cerebellum. In addition, detection of threat cues was associated with stronger posterior parietal activation for males than females. Our findings suggest that neural processing of evolutionary unprepared threat cues in social environments does not necessarily involve the emotion-related neural system and is influence by evolutionary pressure on sex differences. *Hum Brain Mapp 29:945–957, 2008.* © 2007 Wiley-Liss, Inc.

Key words: threat cue; emotion; fMRI; gender

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INTRODUCTION

The perception of danger is a primitive cognitive ability that is crucial for humans to survive in both natural and social environments. It is also an ability that may differ across males and females. Evolutionary pressure biases men toward hunting and women toward gathering [Ardrey, 1976; Dahlberg, 1981]. Hunters are more likely to be confronted with dangerous situations than gatherers, and this may lead to disparities in the processing of threat signals in males and females. Indeed, relative to males, females have a lower threshold for fear when faced with the same level of objective physical danger [Campbell et al., 2001] and show greater perceived risks when faced with a potential dangerous social situation [Harris and Miller, 2000] or when assessing physical risks to health [Weber et al., 2002]. These differences may partially reflect the lesser physical strength of females [Hines and Fry, 1994; Thompson et al., 1992], along with an evolutionary bias for females to behave in a more cautious and less aggressive fashion [Campbell, 1999; Hines and Fry, 1994].

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However, despite the importance of understanding responses to threat, and gender differences in this ability, there has been minimal study of the underlying neural substrates. The present article sets out to rectify this.

Previous research has examined specific physiological responses to the perception of images containing overt threat cues formed by evolutionary experience. For instance, images of snakes or spiders produce enhanced skin conductance responses [Globisch et al., 1999; Öhman and Soares, 1993] and associated increased activity in the amygdala, the anterior cingulate, and ventromedial prefrontal cortex [Carlsson et al., 2004; Carretie et al., 2005]. These responses are most pronounced in snake- or spider-fearful subjects. Angry or fearful faces also elicit increased activity in the amygdala and anterior cingulate [Morris et al., 1996; Pissiota et al., 2003]. In addition, males and females appear to show differential neural activity to images associated with potential danger, though the direction of these effects do not necessarily fit with the idea that females are more sensitive to threat signals. For example, pictures of attacks by humans or animals have been shown to induce greater activation in the amygdala in males than females [Schienle et al., 2005]. In contrast, fearful or angry faces elicited a more persistent or stronger response in the amygdala for females than males [McClure et al., 2004; Williams et al., 2005].

All these studies used threat cues such as snake or angry faces that induced automatic increased responses of the emotion-related system (i.e., the amygdala, the anterior cingulate, and the orbitofrontal cortex showed increased activation to dangerous signals even when no explicit tasks were assigned to the dangerous stimuli). It has been suggested that these threat cues are evolutionary-prepared because of the requirement for predatory defense, and fear is most likely to occur to these threats that are dangerous to pretechnological man and induces a specific fear neural system in the brain [Mineka and Öhman, 2002; Öhman and Mineka, 2001]. However, people are often confronted with threat cues in contemporary social environments that lack obvious emotion contents but are potentially dangerous in a particular social situation. For example, a car or a gun may produce injury on people when these objects are related to people in a particular way. Deliberative cognitive processes are possibly required for detection and evaluation of such threat signals. To date, we have known little about the neural substrates underlying the cognitive processes of these "evolutionary unprepared" threat cues.

The current work first examined if there exists a neural network supporting the processing of evolutionary unprepared threat cues that is independent of the fear or emotion-related system. We used stimulus displays that consisted of a person with a neutral facial expression in either a safe situation (e.g., walking besides a stationary car) or a potentially dangerous situation (e.g., walking in front of a moving car, Fig. 1). These stimulus displays did not include any overt threat cues such as angry faces or snakes and spiders that induce automatic emotional responses. Participants were asked either to judge whether the person in the situation was in potential danger (Experiment 1) or to evaluate the degree of danger the person in the situation was in (mild vs. severe, Experiment 2). These tasks were contrasted with a baseline condition of judging the gender of the person in the stimuli, to control for low-level visual feature processing, any automatic emotional responses elicited by the attended stimuli, and the processing of threat irrelevant social information such as people's gender. Experiment 2 complemented Experiment 1 in two aspects. First, in Experiment 1, the contrast between the threat detection task and the controlled condition revealed neural substrates of initial threat processing (i.e., detection of the presence of threat cues). Experiment 2 asked sub-

nately. Subjects pressed one of two buttons with the left or right index finger (counterbalanced across subjects) to respond to each stimulus according to the instructions. The order of the tasks (threat detection and threat evaluation) was counterbalanced across subjects. Anatomical images were obtained from each subject after the functional scanning. Two-sample *t*-tests were conducted to compare the difference in behavioral performance between males and females.

fMRI Measurement

Scanning was performed on a 3 T Siemens Trio system using a standard head coil at Beijing MRI Center for Brain

RESULTS

Behavioral Performance

In Experiment 1, response accuracy for threat detection did not differ between females (89.8% ± 5.1%) and males (85.5% ± 7.7%) ($t = 1.587$, $P < 0.127$). However, females (836 ± 97 ms) responded faster than males (954 ± 160 ms) when asked to identify if the person in the situation was in danger ($t = 2.170$, $P < 0.041$). Responses to gender identification did not differ between females (95.6% ± 3.2%, 707 ± 111 ms) and males (95.1% ± 4.8%, 783 ± 164 ms, $t = 0.351$ and 1.324, both $P < 0.199$), but were faster to those to threat detection (females: $t = 5.053$, $P < 0.001$; males: $t = 6.916$, $P < 0.001$).

In Experiment 2, females and males did not differ in the number of stimuli judged as extremely dangerous (52.8% ± 14.3% vs. 47.7% ± 12.7%, $t = 0.918$, $P < 0.369$), or the time taken to make this judgment (872 ± 155 vs. 883 ± 108 ms, $t = 0.186$, $P < 0.855$). Performance of gender identification did not differ between males (703 ± 146 ms,

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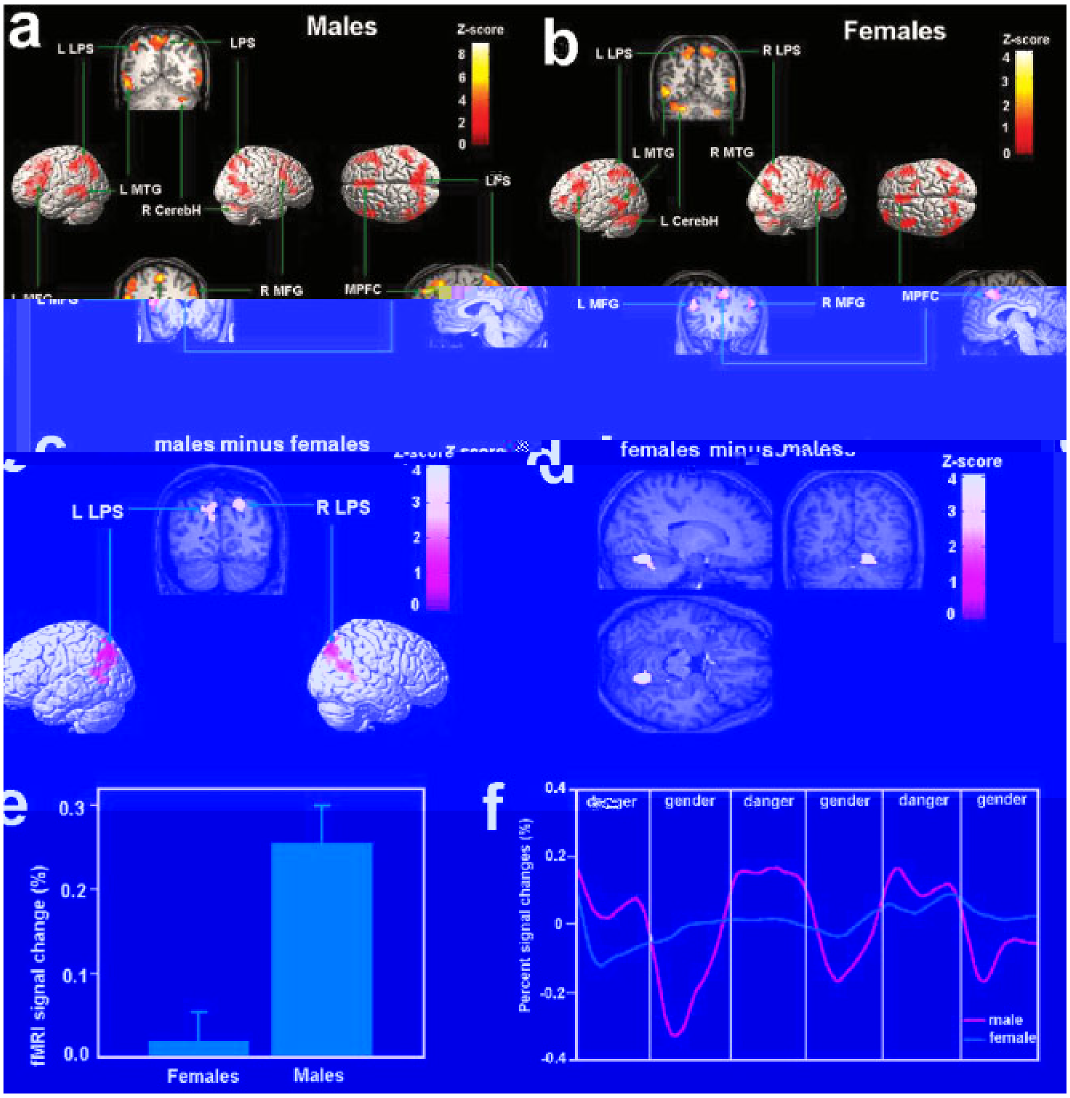

Figure 2.

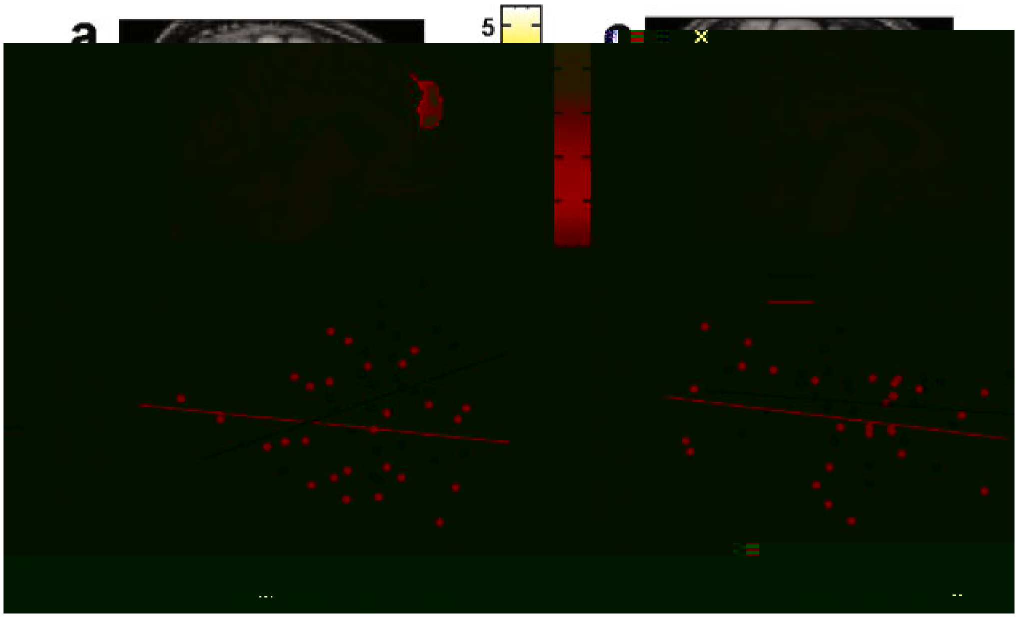

Figure 3.

TABLE I. Brain areas showing increased activity in danger detection relative to gender identification in Experiment 1

Region	Voxel no.	BA	*X*	*Y*	*Z*	*Z* value	*P* value
Males							
Medial/left superior parietal cortex	1,453	7	−10	−57	54	4.76	0.01
Right superior parietal cortex	89	7	38	−66	40	4.05	0.05
Left inferior parietal cortex	251	40	−48	−41	43	4.54	0.01
Dorsal medial prefrontal cortex	477	8	0	16	49	4.63	0.01
Left inferior frontal gyrus	234	46	−44	39	5	4.51	0.01
Left superior/middle frontal gyrus	482	6/44	−38	6	40	4.37	0.01
Right middle/inferior frontal gyrus	612	9/45	42	24	14	4.10	0.01
Left posterior middle/inferior temporal gyrus	161	21/37	−52	−62	3	3.98	0.01
Cerebellum	545		34	−70	−20	3.80	0.01
Females							
Right superior parietal gyrus	433	7	22	−64	51	4.44	0.01
Left superior parietal gyrus	327	7	−16	−62	51	3.39	0.01
Dorsal medial prefrontal cortex	451	8	6	33	44	3.91	0.01
Left middle/inferior frontal gyrus	584	9/46	−44	27	26	4.03	0.01
Right middle/inferior frontal gyrus	721	9/46	50	30	26	3.53	0.01
Left posterior middle/inferior temporal gyrus	490	21	−53	−52	3	3.89	0.01
Right posterior middle/inferior temporal gyrus	857	21/39	55	−65	16	3.85	0.01
Cerebellum	1,277		−24	−61	−24	4.05	0.01

Voxel no. = number of voxels in a cluster; BA = Brodmann area.
The *P*-values at the cluster-level were corrected for multiple comparison.

gyrus, and the temporal-occipital junction. Increased activation was also found in both the right and left hemispheres of the cerebellum.

Females similarly showed activation increases in bilateral superior parietal cortex (Fig. 4 and Table II), the left middle and inferior frontal gyrus, the right superior and middle frontal gyrus, the superior medial prefrontal cortex, bilateral posterior middle temporal gyrus, and the temporal-occipital junction. Females also showed increased activation in both hemispheres of the cerebellum.

Two-sample *t*-tests were also conducted to examine gender differences in neural activity related to threat evaluation. However, no differential activity in any brain areas was observed between males and females.

Figure 2.

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Figure 3.

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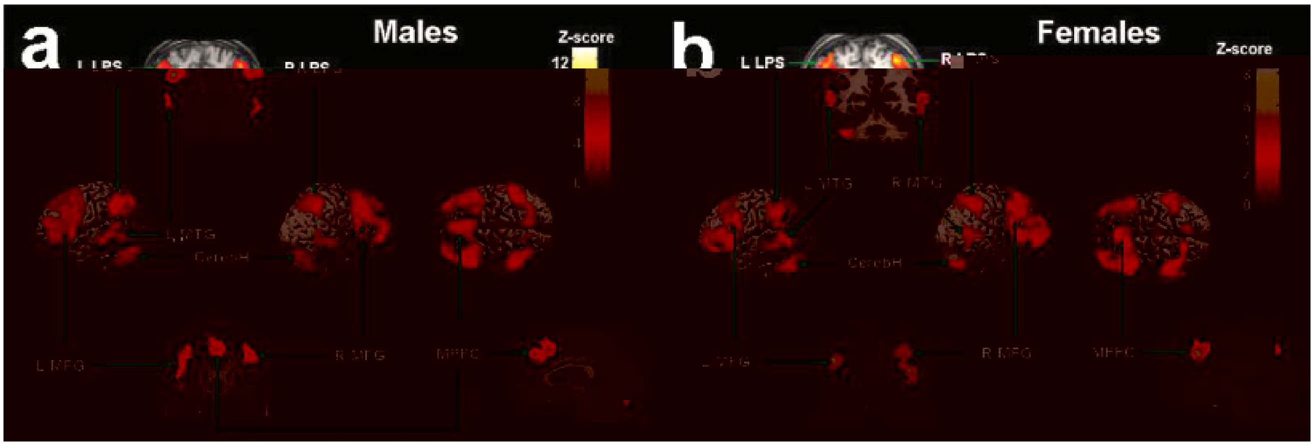

Figure 4.
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Comparison across experiments 1 and 2

The conjunction analysis identified brain activations common for both threat detection (Experiment 1) and threat evaluation (Experiment 2). For male subjects, the conjunction analysis showed activations in the superior parietal lobe (−12/−72/46, $Z = 4.15$), left prefrontal cortex (−52/26/15, $Z = 4.03$), right posterior temporal cortex (53/−45/−8, $Z = 3.92$), medial prefrontal cortex (−2/44/35, $Z = 3.82$), right prefrontal cortex (57/20/21, $Z = 3.59$), right posterior temporal cortex (−55/−55/−2, $Z = 3.78$), and the cerebellum (30/−61/−23, $Z = 3.95$). For female subjects, the conjunction analysis showed activations in the right posterior temporal cortex (60/−58/6, $Z = 4.25$), superior parietal lobe (22/−62/56, $Z = 4.16$), left posterior temporal cortex (−53/−62/3, $Z = 4.12$); left prefrontal cortex (−46/26/26, $Z = 3.72$), medial prefrontal cortex (4/31/43, $Z = 3.64$), right prefrontal cortex (46/10/42, $Z = 3.58$), and the cerebellum (−24/−64/−24, $Z = 4.52$).

To compare the magnitudes of the activation increases related to threat detection and evaluation, paired t-tests were conducted by contrasting brain activation associated with threat evaluation (Experiment 2) and threat detection (Experiment 1) for males and females, respectively. For males, threat evaluation elicited stronger activity in the superior parietal cortex bilaterally, the superior and inferior frontal cortex bilaterally, and the medial prefrontal cortex (Table III). For females, threat evaluation showed increased activity in the right superior parietal cortex and the right superior/middle/inferior frontal cortex as compared with threat detection. The reverse contrast did not show any increased activity in the network associated with threat detection compared with threat evaluation.

DISCUSSION

The current study provides evidence that a neural network that is independent of the emotion-related fear system in the human brain can mediate detection and evaluation of evolutionary unprepared threat cues. To investigate the processing of evolutionary unprepared threat cues in social environments, we presented displays showing people in safe or potentially dangerous situations that did not contain evolutionary prepared threats (e.g., sakes) and overt emotional contents (e.g., angry faces). We assessed the neural activity when subjects either detected the presence of potential danger or evaluated degree of danger to a subject in a display by comparing threat detection and evaluation tasks with a gender identification task that controlled for the processing of low-level visual features and threat irrelevant social information. Because the stimuli and motor responses in Experiment 1 were identical for these comparisons, any differential activity caused by automatic emotional responses to stimuli should be eliminated. Even the contrast between potentially dangerous and safe situations in Experiment 2 did not show any activation increase in the neural system usually associated with emotional responses (e.g., the amygdala, anterior cingulate cortex, and orbitalfrontal cortex) [Carlsson et al., 2004; Carretie et al., 2005; Morris et al., 1996; Pissiota et al., 2003]. Thus, our findings indicate that detection and evaluation of evolutionary unprepared threats in social situations do not necessarily involve the emotion-related neural system and that the processing of threat signals can be independent of the affective network in the absence of overt threat cues (such as fearful faces or snakes). The lack of increased activity of the emotion-related neural system was evident

TABLE II. Brain areas showing increased activity in danger evaluation relative to gender identification in Experiment 2

Region	Voxel no.	BA	*X*	*Y*	*Z*	*Z* value	*P* value
		Males					
Right superior parietal gyrus	845	7/40	51	−40	50	4.47	0.01
Left inferior parietal gyrus	1022	40	−55	−43	38	5.47	0.01
Dorsal medial prefrontal cortex	1231	8	−8	32	55	4.86	0.01
Left middle/inferior frontal gyrus	2484	9/44	−48	17	21	5.14	0.01
Right middle/superior frontal gyrus	1214	8/9	38	18	40	4.69	0.01
Right inferior frontal gyrus	442	9/10	38	53	15	4.96	0.01
Left posterior middle/inferior temporal gyrus	196	21/37	−59	−54	6	3.90	0.01
Cerebellum	703		−16	−78	−30	4.64	0.01
	75		26	−71	−18	3.82	0.01
		Females					
Right superior parietal gyrus	530	7	40	−50	52	4.03	0.01
Left superior parietal gyrus	230	7/40	−53	−41	41	3.74	0.01
Dorsal medial prefrontal cortex	340	8	−8	31	37	4.08	0.01
Left inferior frontal gyrus	644	9/46	−48	32	11	4.25	0.01
Left middle frontal gyrus	213	8/9	−51	13	32	4.02	0.01
Right superior frontal gyrus	1196	8/9	42	10	38	4.13	0.01
Right inferior frontal gyrus	1409	45/46	40	33	4	4.58	0.01
Left posterior middle/inferior temporal gyrus	203	21/37	−51	−60	3	4.08	0.05
Right posterior middle/inferior temporal gyrus	149	21/37	60	−60	5	3.98	0.05
Cerebellum	427		−28	−63	−25	4.45	0.01
	267		38	−68	−32	4.24	0.05

Voxel no. = number of voxels in a cluster; BA = Brodmann area.
The *P*-values at the cluster-level were corrected for multiple comparison.

even when explicit tasks were assigned to the evolutionary unprepared threat cues in the stimuli, suggesting that the processing of such threat cues is significantly different from that of overt threat cues that automatically activated the emotion-related neural system. One account for the absence of the activity of the affective network was that our stimuli did not activate the emotion-related system because the stimuli had no overt emotion contents such as angry face or snakes. Alternatively, the activity of other brain areas related to the detection or evaluation tasks might dampen the activity to the evolutionary unprepared threat cues in brain structures such as amygdala. Such modulation of the amygdala activity has been observed in the previous research that found increased frontal activity

TABLE III. Brain areas showing stronger activity in danger evaluation (Experiment 2) relative to danger detection (Experiment 1)

Region	Voxel no.	BA	*X*	*Y*	*Z*	*Z* value	*P* value
		Males					
Right superior parietal gyrus	749	7/40	48	−47	41	4.71	0.01
Left superior parietal gyrus	592	7/40	−48	−56	52	5.65	0.01
Dorsal medial prefrontal cortex	588	8	2	29	39	4.31	0.01
Left superior frontal gyrus	97	9	−36	26	36	3.97	0.05
Left middle frontal gyrus	411	46	−30	45	14	4.58	0.01
Left inferior frontal gyrus	111	47	−46	15	−2	4.03	0.05
Right superior frontal gyrus	646	8	42	25	44	4.54	0.01
Right inferior frontal gyrus	191	10	44	52	−4	4.60	0.01
		Females					
Right superior parietal gyrus	445	7/40	57	−46	43	3.37	0.05
Right superior frontal gyrus	352	8	28	19	34	4.49	0.05
Right middle frontal gyrus	363	9/46	40	46	23	3.76	0.05
Right inferior frontal gyrus	917	45	42	31	2	4.07	0.01

Voxel no. = number of voxels in a cluster; BA = Brodmann area.
The *P*-values at the cluster-level were corrected for multiple comparison.

and decreased activity in the amygdala associated with determining whether affect pictures goes with the word "angry" or "afraid" [Hariri et al., 2000, 2003].

Across both male and female subjects, we found evidence for a shared neural network engaged in detection and evaluation of evolutionary unprepared threat cues. This network includes the medial and lateral frontal lobes, superior parietal lobes, posterior middle temporal cortex, and the cerebellum. Parietal activity associated with the processing of these threat cues was evident in the superior parietal cortex and the intraparietal sulcus (BA 7/40) in both hemispheres. Previous studies have shown evidence that these brain areas in the dorsal pathway play an important role in the processing of spatial information [Colby and Goldberg, 1999]. Particularly, the posterior superior and inferior parietal cortices mediate the formation of spatial representations of body locations with respect to the subject's environment [the intraparietal sulcus, Their and Andersen, 1996] and visual-spatial judgments [BA7/40, Fink et al., 2000], while the mesial superior parietal cortex (BA7) is linked to representing location information from a third person's perspective [Vogeley et al., 2004]. Applying the prior results on spatial-cognition in the parietal cortex, we suggest that the functional role of the parietal activation in our study was to analyze the spatial information in the stimulus displays for identification of the evolutionary unprepared threat cues. For instance, the spatial relationship between the person and the car (i.e., whether the person is in front of or besides the car and the distance between the person and the car) is pivotal for judging if the person in Figure 1 is in danger. Interestingly, recent monkey studies showed that both stimulation of the intraparietal sulcus and air pruff simulating noxious threats evokes facial or shoulder movement specific for a defense reaction [Cooke and Graziano, 2003], suggesting that the intraparietal sulcus plays a role in visuospatial encoding of noxious threats. Our fMRI results reinforce this by showing that this brain area is also involved in perception of threat cues in social environments.

Detection and evaluation of these threat cues were also linked to the lateral prefrontal lobes in both hemispheres, the posterior middle/inferior temporal gyrus (in the left hemisphere for males and bilaterally for females), and the cerebellum. Numerous imaging studies have demonstrated that these brain regions are involved in memory retrieval. Particularly, the retrieval of semantic knowledge is linked to the left frontal and temporal gyrus [Martin et al., 1995; Thompson-Schill et al., 1997; Tulving et al., 1994; Wiggs et al., 1999] and the retrieval of information from episodic memory is associated with the right frontal gyrus and the cerebellum [Donohue et al., 2005; Henson et al., 1999; Wiggs et al. 1999]. These results support a hemispheric encoding retrieval asymmetry model that differentiates the functions of the left and right hemispheres in memory retrieval [Tulving et al., 1994]. Retrieval of information from both semantic knowledge and episodic memory is critical for threat detection and evaluation. To decide that a person walking in front of a moving car is in potential danger requires semantic knowledge that people can be hit when they walk in this position and recall of traffic accidents observed in media or movies. The posterior parietal lobes may also contribute to episodic memory retrieval when processing threat signals by guiding attention to the appropriate internal representation in memory [Wagner et al., 2005].

One further region engaged in processing threat signals was the medial prefrontal cortex (BA 8). Activation of these brain regions has been observed when people make judgments about humans relative to objects [Mitchell et al., 2002] or animals [Mason et al., 2004] and when people perceive humans but not animals [Han et al., 2005]. These results indicate a key role of this area in the processing of person knowledge. In addition, the medial prefrontal cortex has been associated with drawing inductive reasoning based on others' knowledge states [Goel et al., 1995] and deductive reasoning about contexts within a social content [Canessa et al., 2005]. Since subjects in our study were asked to make judgments about people in particular social contexts, the medial prefrontal cortex could be recruited to represent person knowledge. Detection of these threat cues required more inspection of social contexts (and took longer time) than judging a person's gender. The medial prefrontal cortex might also be involved in making inference about potential danger based on the analysis of the contexts, providing a third cognitive component in processing threat signals in addition to spatial analysis and memory retrieval.

While our fMRI results showed evidence for a shared neural network in males and females associated with threat detection and evaluation, we also found evidence for differential activity. Specifically, we found stronger activity in the posterior parietal cortex including the inferior parietal sulcus (BA 7), with an extension into the precuneus bilaterally, in males than in females. The ROI analysis showed that fMRI signal change in the right posterior parietal cortex varied systematically as a function of the task (threat detection vs. gender identification) for males but not for females. These differences were evident during detection (Experiment 1) but not evaluation (Experiment 2) of the threat cues. Cells in the posterior parietal cortex (BA7) receive input from areas (e.g. V3) that are implicated in spatial or motion analysis [Baizer et al., 1991] and play an important role in multimodal representation of space [Andersen et al., 1997]. The precuneus also acts in concert with the lateral posterior parietal cortex in elaborating spatial relations in egocentric and allocentric space for the control of body movement and other higher-order spatial processes, including attention shifts in space [Cavanna and Trimble, 2006]. Therefore, the increased posterior parietal activity observed in males relative to females is consistent with males having enhanced processing of spatial relationships between people and objects (e.g., car, gun) in the stimulus displays when asked to detect threat. This fMRI result also fits with the hunter-gatherer theory of spatial abilities [Silverman and Eals, 1992; Silverman et al., 2000], which posits that males should out-perform females in spatial skills (i.e., orienting oneself in relation to objects and places or assessing spatial relations between objects and places) that would facilitate successful hunting. Our results suggest that these enhanced spatial abilities may also be recruited when responding to the presence of threat signals. The spatial processing involved, however, appears to be different from the visuospatial navigation ability that is associated with stronger activity in right inferior parietal cortex (BA 40) in females than in males [Grön et al., 2000].

The precuneus also shows activation during tasks requiring memory retrieval. In particular, the increased activity of precuneus has been associated with retrieval of information from episodic memory [Cavanna and Trimble, 2006]. Given that males report being exposed to violence more than females [Barkin et al., 2001], it may be proposed that, when detecting the presence of threat signals in the stimuli, past experience of exposure played a stronger role for males relative to females. The additional spatial analysis and memory retrieval might take more time and result in longer reaction times to threat detection in males than females. Another interpretation, however, is that females were superior at responding to threat signals relative to males, and therefore had less need to recruit explicit memory retrieval and spatial processing in order to decide that a given situation was dangerous. This would fit with work showing that females are more cautious and sensitized to danger, relative to males [Campbell, 1999; Hines and Fry, 1994], and with the behavioral evidence for females having faster RTs to detect threat in Experiment 1 here. The one area that showed the opposite pattern across the genders, with more activation for females compared to males, was the cerebellum. However, the cerebellum activity was only observed with a relatively lax threshold, and this result needs to be confirmed in future work.

Interestingly, the increased posterior parietal activity in males relative to females was evident only when the task required discrimination between dangerous and safe situations, and no gender difference was observed when subjects were asked to evaluate the degree of danger in scenes already selected as being dangerous. This suggests that males and females differed in their responsiveness and the processes they brought to bear when they had to detect threat. However, having decided there was threat present, males and females engaged in similar explicit processes to judge the degree of danger. Hence, there was increased neural activity in both genders, in regions activated in detecting threat.

Finally, the PPI analysis showed stronger functional connectivity between the right parietal cortex and the medial prefrontal cortex during threat detection than gender identification. But this was evident in male but not female par-
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