

Mind Your Left: Spatial Bias in Subcortical Fear Processing

Tali Siman-Tov^{1,2}, David Papo¹, Natan Gadoth^{3,4}, Tom Schonberg¹,
Avi Mendelsohn¹, Daniella Perry¹, and Talma Hendler^{1,3}

Abstract

■ Hemispheric lateralization of emotional processing has long been suggested, but its underlying neural mechanisms have not yet been defined. In this functional magnetic resonance imaging study, facial expressions were presented to 10 right-handed healthy adult females in an event-related visual half-field presentation paradigm. Differential activations to fearful versus neutral faces were observed in the amygdala, pulvinar, and superior colliculus only for faces presented in the left hemi-

field. Interestingly, the left hemifield advantage for fear processing was observed in both hemispheres. These results suggest a leftward bias in subcortical fear processing, consistent with the well-documented leftward bias of danger-associated behaviors in animals. The current finding highlights the importance of hemifield advantage in emotional lateralization, which might reflect the combination of hemispheric dominance and asymmetric interhemispheric information transfer. ■

INTRODUCTION

Functional hemispheric lateralization is considered crucial for brain efficiency; it enhances neural capacity by allowing separate, parallel, and specialized processing in the hemispheres (Vallortigara, 2006). Like motor, language, and memory functions, emotional processing has long been considered to be lateralized. A central role was ascribed to the right hemisphere (RH) in perception and processing of either emotions in general or negative emotions in particular (Demaree, Erik Everhart, Youngstrom, & Harrison, 2005). However, this lateralization pattern was suggested based on studies of cortical function while little is known about lateralization of emotional processing at the subcortical level.

The amygdala is considered a center for subcortical emotional processing, particularly of fear perception and fear conditioning (Calder, Lawrence, & Young, 2001). Despite evidence for significant differences in the function of the right and left amygdalae, no consistent lateralization pattern has been established (Baas, Aleman, & Kahn, 2004; Zald, 2003). Although animal studies tend to highlight the importance of the right amygdala in fear perception (Baker & Kim, 2004; Zald, 2003), neuroimaging studies of negative emotions frequently reported left amygdalar superiority (Baas et al., 2004).

Aside from the amygdala, two other subcortical structures have been implicated in a subcortical route for fear processing: the pulvinar and the superior colliculus (SC)

(Liddell et al., 2005; Morris, DeGelder, Weiskrantz, & Dolan, 2001; DeGelder, Vroomen, Pourtois, & Weiskrantz, 1999; Morris, Ohman, & Dolan, 1999; LeDoux, 1996). It was suggested that the collicular–pulvinar–amygdala pathway, which bypasses the striate cortex, allows unconscious processing of emotional stimuli and rapid orienting to sources of potential threat (Liddell et al., 2005; Vuilleumier, Armony, Driver, & Dolan, 2003). Key evidence for the existence of such a pathway comes from “blindsight” patients, individuals with striate cortical damage who show residual visual processing of stimuli presented in their blind visual field (Weiskrantz, 1996). It was shown that these individuals are able to discriminate between emotional expressions in their “blind” visual field (Hamm et al., 2003) and that their amygdala, pulvinar, and SC can be activated by fearful stimuli presented to the “blind” hemifield (Morris et al., 2001). However, it should be mentioned that the existence of a subcortical pathway for fear processing is still an area of debate. The anatomical basis for such a pathway in primates has not been established (Pessoa, 2005; Cowey, 2004; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002).

To the best of our knowledge, no direct evidence of emotional lateralization at the pulvinar or the SC level has been reported before. Behavioral studies of unconscious emotional processing, based on masked stimuli, have shown enhanced autonomic response to fearful faces presented to the left visual field (LVF) relative to fearful faces presented to the right visual field (RVF) or to neutral faces on both sides (Kimura, Yoshino, Takahashi, & Nomura, 2004). If contralaterality in brain activation is assumed, these results provide psychophysical support

¹Tel Aviv Sourasky Medical Center, Tel Aviv, Israel, ²University of Michigan, Ann Arbor, ³Tel Aviv University, Tel Aviv, Israel, ⁴Mayanei Hayeshua Medical Center, Bnei-Brak, Israel

for right lateralization of emotional processing at the subcortical level (for either emotions in general or negative emotions in particular). We are aware of only one neuroimaging study that proposed lateralization of the subcortical route: Morris et al. (1999) presented evidence for a subcortical route to the right amygdala for “unseen” fear; however, no explicit evidence for lateralization at the pulvinar or the SC was presented.

The current fMRI study, originally aimed at investigating the effect of unilateral amygdalar lesions on subcortical and cortical emotion-related activation, serendipitously revealed a clear lateralization pattern of subcortical fear processing in a control group of right-handed healthy adult females. Fearful expressions presented in the LVF differentially activated the amygdala, the pulvinar, and the SC in both hemispheres. In contrast, fearful expressions presented in the RVF did not induce any obvious differential activation (relative to neutral expressions) in these subcortical regions. These findings suggest a bihemispheric left spatial bias in subcortical processing of fear.

METHODS

Subjects

Ten right-handed healthy adult women [mean age = 28.1 years (range = 24–35); mean education = 17 years (range = 13–20)] participated in the fMRI study. They all had normal or corrected-to-normal vision, no past neurological or psychiatric history, no structural brain abnormality, and used no medication. In addition, eye monitoring was applied during the study of eight healthy female volunteers [mean age = 27.5 years (range = 23–36)] performing the same experiment outside the magnet. The study was approved by the local review board and all subjects signed an informed consent form.

Stimuli and Experimental Paradigm

Black-and-white pictures of facial expressions (fearful/happy/neutral) were taken from the following databases: *The Averaged Karolinska Directed Emotional Faces (KDEF)* database (Lundqvist, Flykt, & Öhman, 1998) and the *Pictures of Facial Affect* (Ekman & Friesen, 1976). Stimuli size was 3.7° (width) × 4.7° (height). Using Presentation 0.80 software (Neurobehavioral Systems, Albany, CA), a mixed-design paradigm was prepared, comprising epochs for visual field (LVF/RVF) and events of facial expressions (fearful/happy/neutral). Each study included four separate sessions, each of 116 repetitions (5.8 min). A single session was composed of eight blocks (4 LVF and 4 RVF) and each block contained 11 events (3 fearful, 3 happy, 3 neutral, and 2 blank), which were presented in a pseudorandom manner. The overall event duration was 3 sec and it included presentation of a red or green central fixation dot for 500 msec immediately followed by parafoveal presentation (5° angle) of a facial expression to the right or left of the fixation for 150 msec,

and then by a white fixation dot for the remaining time of the event (Figure 1).

To achieve visual field segregation, the participants were explicitly instructed to carefully maintain fixation throughout the experiment and to report on color change of the fixation dot. The color of the fixation dot (red/green) was randomly selected every 3 sec. Reports on color were done via a response box, using the right thumb for a red dot and the left thumb for a green dot, to prevent a potential bias in motor-related activations.

MRI Scanning

Imaging was performed on a 1.5-T GE Signa horizon echo speed LX MRI scanner (GE, Milwaukee, WI). All images were acquired using a standard head coil. The scanning session included conventional anatomical MR images (T1-WI, T2-WI, T2-FLAIR), 3-D spoiled gradient (SPGR) echo sequence (FOV = 240 mm, matrix size = 256 × 256, voxel size = 0.9375 × 0.9375 × 1.5) and functional T2*-weighted images (FOV = 240 mm, matrix size = 128 × 128, voxel size = 1.875 × 1.875 × 4, TR/TE/FA = 3000/55/90, 27 axial slices without gap).

fMRI Data Analysis

fMRI data were processed using Brain Voyager 4.9 software package (Brain Innovation, Maastricht, The Netherlands). Functional images were superimposed

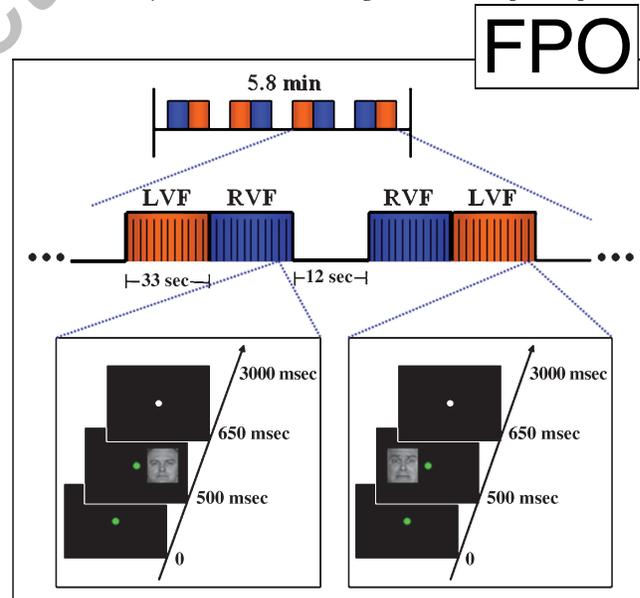


Figure 1. Experimental paradigm. Each study included four separate sessions, each with 116 repetitions (5.8 min). A single session was composed of eight blocks (4 LVF and 4 RVF). In each block, 11 events (3 fearful, 3 happy, 3 neutral, and 2 blank) were presented in a pseudorandom manner. The overall event duration was 3 sec and it included the following steps: presentation of a central fixation dot in red or green for 500 msec; parafoveal presentation (5° angle) of a facial expression to the right or left of the fixation for 150 msec; and fixation dot presentation in white for the remaining time of the event.

Table 1. Amygdala, Pulvinar, and SC ROI Parameters

	No. of Voxels	Average p Value	Average t Value	Talairach Coordinates		
				x	y	z
R Amygdala	730	$3.3 \cdot 10^{-2}$	3.40	22	-2	-12
L Amygdala	716	$3.1 \cdot 10^{-2}$	3.09	-20	-2	-13
R Pulvinar	1508	$2.1 \cdot 10^{-5}$	9.55	15	-25	7
L Pulvinar	1243	$2.7 \cdot 10^{-5}$	8.99	-11	-25	7
R SC	107	$2.0 \cdot 10^{-3}$	4.72	5	-29	-1
L SC	99	$4.2 \cdot 10^{-3}$	4.10	-2	-29	-2

ROI volume, average uncorrected p and t values, and Talairach coordinates of the central point are shown for each region (multisubject analysis, $n = 10$, random effects). R = right; L = left.

and incorporated into 3-D SPGR datasets through trilinear interpolation. The complete dataset was transformed into Talairach and Tournoux (1988) space. Preprocessing of functional scans included motion correction, sinc interpolation, temporal smoothing (high-pass filtering = 3 Hz), and spatial smoothing (FWHM = 6 mm), to minimize anatomical differences. Statistical maps were prepared for each subject using a general linear model (GLM) with six conditions (LVF/RVF \times fearful/happy/neutral), followed by a multisubject analysis computed with random effects.

For region-of-interest (ROI) analysis, the amygdala, the pulvinar, and the SC were outlined anatomically in each hemisphere (based on Talairach & Tournoux, 1988 stereotaxic atlas). Table 1 gives the Talairach coordinates of the central point of each ROI, the total number of voxels, and the average uncorrected p and t values. For ROI analysis of the primary visual cortex, the fusiform gyrus, and the intraparietal sulcus (IPS), the point of maximal activation in each region was defined on the multisubject statistical parametric map (all conditions vs. baseline). The Talairach coordinates were: pericalcarine cortex, R: 8, -80, -3, L: -13, -83, -6; fusiform gyrus, R: 31, -65, -15, L: -28, -62, -15; and IPS: R: 26, -56, 31, L: -34, -56, 30. Activations of all conditions within a 6-mm diameter around the peak activation were considered for a deconvolution analysis. Beta values for all conditions of each subject were extracted by the deconvolution analysis, and values surrounding peak activation (hemodynamic response time points 1–3) served for a three-way repeated measures ANOVA (factors: hemisphere, hemifield, valence [fearful/neutral]) performed by STATISTICA 6.0 software (Statsoft, Tulsa, OK).

Eye Movement Data Acquisition and Analysis

Right eye position was monitored in eight additional healthy female volunteers who performed the same experiment without scanning (ASL eye tracking system, Model R-LRO6, Bedford, MA). The acquisition rate was

60 Hz. Eye data were analyzed using Microsoft Excel (Redmond, WA) and Matlab 6.0 (MathWorks, Natick, MA) softwares. Eye data artifacts related to blinking were removed. Distribution of eye displacement along the horizontal axis was shown for LVF epochs compared to RVF epochs for each study. The ratio between standard deviations of displacement during LVF and RVF epochs (σ_L/σ_R) was indicated for each subject.

RESULTS

The averaged reaction times to fixation dot color change showed no significant difference between epochs of LVF and RVF presentation (514 msec and 521 msec, respectively), or between valence types (fearful, 522 msec; happy, 510 msec; and neutral, 505 msec). Due to the simplicity of the task, reaction times were relatively short and very close to the onset of the unilateral parafoveal stimuli (500 msec; see Figure 1).

Differential Activation of Both Amygdalae to Fear-associated Stimuli is Spatially Biased

Multisubject statistical brain maps resulting from the fearful versus neutral contrast showed bilateral activation in the amygdala for expressions presented to the LVF. Surprisingly, the same contrast for expressions presented to the RVF did not yield any significant activation within the amygdalae (Figure 2). When it emerged that happy faces were not associated with any significant lateralization pattern (happy vs. neutral and happy vs. fearful contrasts), responses to these expressions were discarded from subsequent analysis.

LVF Advantage for Fear Processing is Exemplified Bilaterally in the Amygdala, the Pulvinar, and the Superior Colliculus

To corroborate the finding of the whole-brain analysis, an ROI analysis was conducted on the amygdalae. Three-way

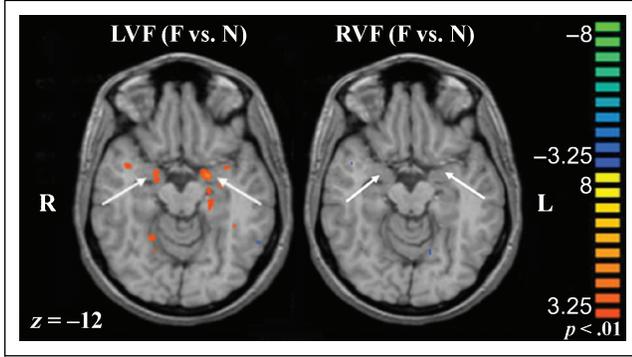


Figure 2. Bilateral LVF advantage of fear-related activation in the amygdala. Multisubject statistical brain maps of the fearful versus neutral contrast are presented separately for LVF and RVF epochs ($n = 10$, random effects, $p < .01$). Red and blue colors indicate enhanced activation by fearful and neutral stimuli, respectively. Significant activations to fearful versus neutral stimuli can be observed within the amygdalae only for LVF stimuli.

repeated measures ANOVA (factors: hemisphere, hemifield, valence) revealed a significant interaction between hemifield and valence type [$F(1, 9) = 11.17, p < .0086$]: Fearful faces induced more robust activation relative to neutral faces, but only when presented to the LVF [post hoc analysis, LVF (fearful > neutral): $p < .004$] (Figure 3A). There was also a main effect for valence [$F(1, 9) = 5.70, p < .04$], but there was neither a main effect nor an interaction for the hemisphere factor. Thus, fear-induced differential activation within the amygdala was affected by hemifield more than by hemisphere.

When a similar ROI analysis was conducted on the pulvinar and the SC (Figure 3B and C), the same pattern of a Hemifield \times Valence interaction emerged [pulvinar, $F(1, 9) = 7.61, p < .02$; SC, $F(1, 9) = 10.09, p < .01$]. Fearful faces induced more robust activations relative to neutral faces only when presented to the LVF [post hoc analysis: pulvinar, LVF (fearful > neutral): $p < .05$; SC, LVF (fearful > neutral): $p < .01$]. In addition, a modest LVF main effect was found in the pulvinar [$F(1, 9) = 5.24, p < .05$], whereas no main effect was noted in the SC for either hemifield or hemisphere [$F(1, 9) = 1.25, p < .29$ and $F(1, 9) = 1.58, p < .24$, respectively].

The LVF Advantage for Fear Processing is Not Exemplified in Visual- and Attention-related Cortical Regions

Contrary to the results in subcortical regions, a significant Hemifield \times Valence interaction could not be demonstrated in cortical visual areas (pericalcarine region and fusiform gyrus) or in the IPS (Figure 4). However, a weak trend for such an interaction was noted for the pericalcarine region and the fusiform gyrus [$F(1, 9) = 1.87, p < .20$ and $F(1, 9) = 3.21, p < .11$, respectively] (Figure 4A and B). A significant Hemisphere \times Hemifield

interaction was shown for activations of the pericalcarine region, as expected [$F(1, 9) = 54.14, p < .00004$] (Figure 4A). The fusiform gyrus showed a similar interaction, albeit with smaller magnitude [$F(1, 9) = 9.45, p < .01$] (Figure 4B). An LVF main effect was found within the IPS [$F(1, 9) = 4.98, p < .05$], with no significant interactions (Figure 4C). Multisubject statistical brain maps of the LVF versus RVF contrast clearly demonstrated segregation of visual input in low-level visual

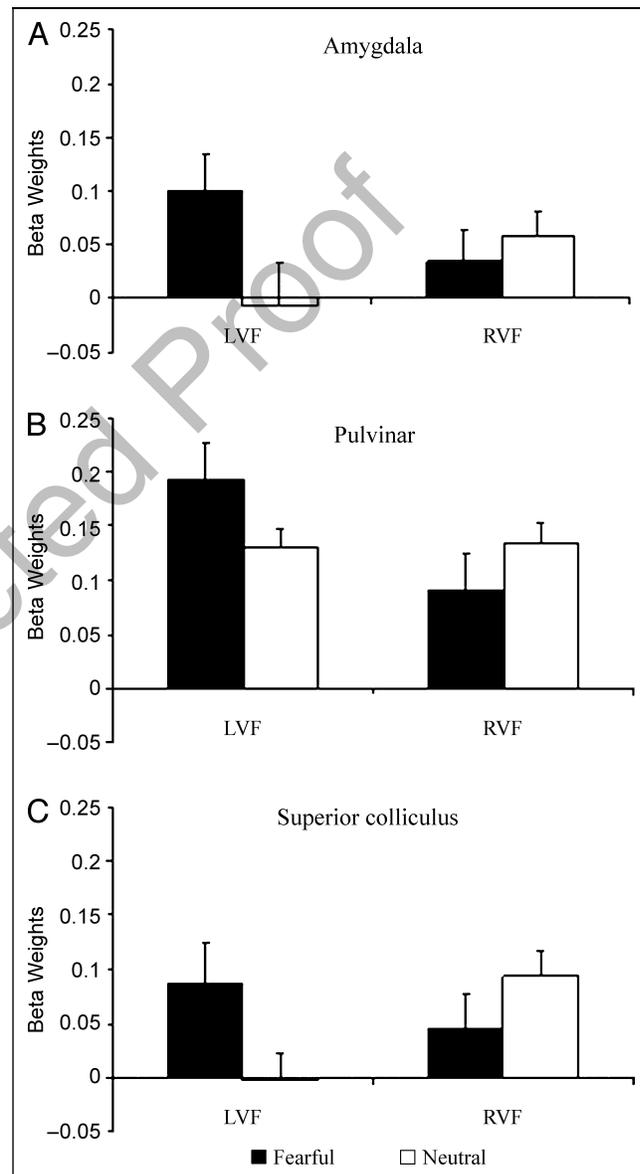


Figure 3. ROI analysis of the bilateral amygdala, the pulvinar, and the SC ($n = 10$). Three-way repeated measures ANOVA (factors: hemisphere, hemifield, valence) disclosed a significant interaction between hemifield and valence. Fearful faces induced much more robust activation relative to neutral faces only when presented to the LVF [amygdala: $F(1, 9) = 11.17, p < .0086$; pulvinar: $F(1, 9) = 7.61, p < .02$; and SC: $F(1, 9) = 10.09, p < .01$]. In addition, a valence main effect was noted in the amygdala [$F(1, 9) = 5.70, p < .04$] and an LVF main effect was noted in the pulvinar [$F(1, 9) = 5.24, p < .05$]. Error bars indicate $\pm SE$ of the mean (see Table 1 for ROI details).

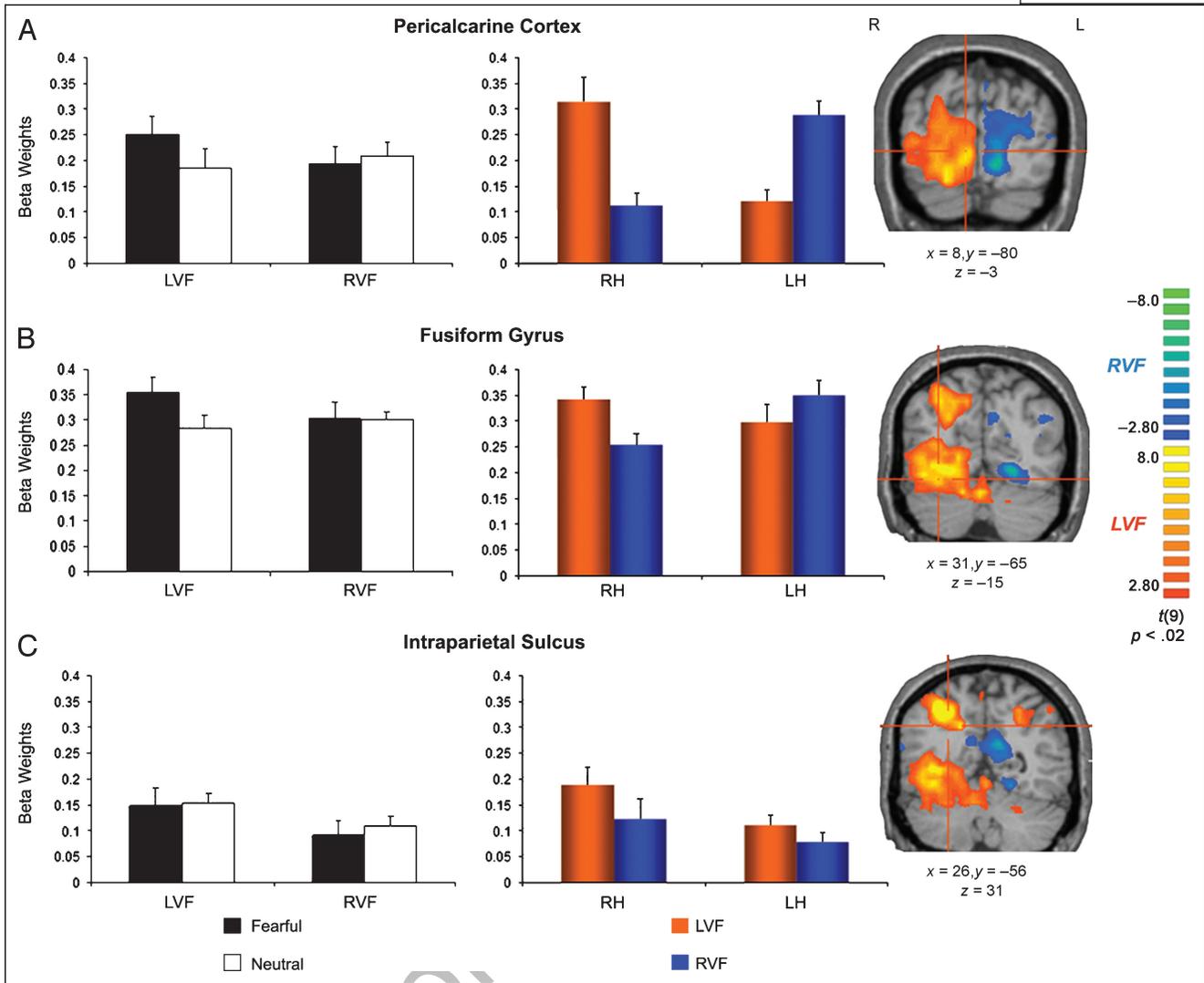


Figure 4. ROI analysis of bilateral pericalcarine region, fusiform gyrus and IPS ($n = 10$). Three-way repeated measures ANOVA (factors: hemisphere, hemifield, valence) disclosed no significant interaction between hemifield and valence. A weak trend towards interaction was noted for the pericalcarine region and the fusiform gyrus ($p < .20$ and $p < .11$, respectively) (left column). In addition, a hemisphere \times hemifield interaction was shown for activations of the pericalcarine region ($F(1, 9) = 54.14, p < .00004$) and the fusiform gyrus ($F(1, 9) = 9.45, p < .01$). A LVF main effect was noted in the IPS ($F(1, 9) = 4.98, p < .05$) (middle column). Multisubject statistical brain maps of the LVF vs. RVF contrast clearly demonstrated the segregation of visual input in cortical visual areas and the bilateral LVF advantage in the IPS (right column).

areas (Figure 4A), in contrast to the bihemispheric LVF advantage within the IPS region (Figure 4C).

Segregation of visual input in low-level visual cortical areas suggested maintenance of fixation by subjects during the experiments. In addition, the monitoring of eye movement that was conducted on eight additional female volunteers showed no significant difference in horizontal eye displacement between epochs of LVF and RVF presentation (Supplementary Figure 1).

DISCUSSION

The results of our current study show that activations to fearful faces in the amygdala, the pulvinar, and the SC are enhanced when presented in the left visual hemifield. Assuming contralaterality in brain activation, this

finding is consistent with previous models for emotional lateralization suggesting RH dominance for the processing of either emotions in general or negative emotions in particular (Demaree et al., 2005). LVF superiority does not seem to reflect an RH advantage for face stimuli (Yovel, Levy, Grabowecky, & Paller, 2003) because there was no such effect for neutral faces (Figure 3). Yet, an RH advantage in discriminating perceptual cues associated with different facial expressions cannot be ruled out. In the present study, no significant emotion-related spatial bias could be demonstrated for cortical visual areas or the IPS. Taken together, these results suggest a left hemifield bias in subcortical fear processing.

To the best of our knowledge, only one previous split-field neuroimaging study reported a distinct LVF advantage in emotional processing. Noesselt, Driver, Heinze,

and Dolan (2005) recently demonstrated differential activation of right visual areas and the amygdala to fearful versus neutral faces presented in the left hemifield, and reported that there had been no analogous activation for fearful faces presented in the right hemifield. Moreover, they reported that LVF presentation of fearful faces improved the performance of a behavioral task in this hemifield (Noesselt et al., 2005). The described fear-related LVF advantage applied to both cortical regions and the amygdala, but no activations within the pulvinar or the SC were mentioned.

The absence of differential activation to fearful expressions within cortical visual areas in the present study may reflect lack of statistical power (small sample size, $n = 10$), or may be secondary to the specific experimental design (task-irrelevant emotional stimuli). The use of bilateral simultaneous stimulation in the study by Noesselt et al. (2005), in contrast to unilateral stimulation in our study, may also have contributed to the different results. The small trend toward lateralization in the pericalcarine region and the fusiform gyrus in our study (Figure 4A and B) may represent a secondary effect of inputs from subcortical structures (Vuilleumier & Driver, 2007; Ward, Calder, Parker, & Arend, 2007; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). In any case, the clear evidence for a leftward bias in subcortical activations during fear processing suggests an ancient phylogenetic origin for this trait. Functional cerebral asymmetries are now accepted as a general principle of brain organization in vertebrates and even in some invertebrate species (Halpern, Gunturkun, Hopkins, & Rogers, 2005; Vallortigara & Rogers, 2005). A left hemifield visuospatial bias was recently observed in birds during pecking activity (Diekamp, Regolin, Gunturkun, & Vallortigara, 2005). This bias may correlate with a well-documented leftward attentional bias in humans, named “pseudoneglect” (Orr & Nicholls, 2005), but is there any evidence in nonhumans of an LVF advantage for fear or danger processing?

In fact, there is ample evidence for a spatial bias in animal behavior in response to fearful stimuli. Toads, chickens, and fish have been reported to react faster when a predator approaches from the left (Vallortigara, 2006). In toads, heightened responsiveness to predator stimuli and increased attack rate of conspecifics were associated with the LVF, whereas prey catching was associated with the RVF (Robins, Lippolis, Bisazza, Vallortigara, & Rogers, 1998; Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998). Similar behaviors have been reported in birds, reptiles, and mammals (Lippolis, Wendy, Bronwyn, & Rogers, 2005; Robins, Chen, Beazley, & Dunlop, 2005; Rogers, 2000). For example, gelada baboons use their LVF significantly more frequently than their RVF during fights, threats, and approaches of conspecifics (Casperd & Dunbar, 1996). These findings suggest that predator-escape and associated fear responses are more prominently induced by left hemifield stimuli

and that aggressive behaviors are more frequently expressed toward the left.

The LVF advantage for fear processing was demonstrated in the current study not only in the RH, as previously reported by others (Noesselt et al., 2005; Morris et al., 1999), but also in the LH. It should be mentioned that Noesselt et al. (2005) noted differential activation for LVF fearful faces in both amygdalae, but they emphasized a significant advantage for the right amygdala. The bihemispheric LVF advantage may reflect the combined effect of an RH dominance for fear processing and the interhemispheric transfer of this information from the RH to the LH. Results from our same experiment also underscored the importance of hemifield rather than hemisphere superiority in the asymmetry of visuospatial attention (Siman-Tov et al., 2007). An LVF main effect was found bilaterally in activations of cortical and subcortical components of an attention-related network (e.g., IPS, frontal eye field, anterior insula, thalamus, and brain stem). It was suggested that this bihemispheric LVF superiority underlies visuospatial attention asymmetry in both normal (pseudoneglect) and pathological (hemispatial neglect) states (Orr & Nicholls, 2005; Mesulam, 1999). In addition, dynamic causal modeling analysis (Friston, Harrison, & Penny, 2003) showed asymmetric interhemispheric connections at the IPS level, suggesting a right-to-left advantage of attention-related information transfer (Siman-Tov et al., 2007).

The present report highlights a specific LVF advantage for fear processing. Although it appears reasonable that attention allocation and the response to potential danger will be handled by at least partially overlapping pathways, our results suggest two separate or partially segregated emotion- and attention-related pathways: an “emotion pathway” (represented by the amygdala) that shows an advantage for fearful stimuli with a Hemifield \times Valence interaction (Figure 3A), and an “attention pathway” (represented by the IPS) that shows LVF advantage irrespective of stimuli valence (Figure 4C). Interestingly, the pulvinar showed a modest LVF main effect along with the Hemifield \times Valence interaction, which might suggest its involvement in both pathways. The SC did not show this combined effect but the limitations of functional imaging of this region (Schneider & Kastner, 2005) should be considered when assessing this negative result.

In view of the previous dynamic causal modeling results showing asymmetric interhemispheric transfer of attention-related information, we suggest a right-to-left advantage in the interhemispheric transfer of fear-associated information. The level of interhemispheric communication cannot be inferred from our results: It may occur at the level of any of the subcortical structures investigated in the present study or via other subcortical or cortical structures. However, because the bihemispheric LVF advantage is already evident at the

SC level, intercollicular transfer is suggested. Intertectal connections have been described in both animals and humans (Tardiff & Clarke, 2002; Sprague, 1966); however, the nature of the information conveyed by the intercollicular commissure is still unclear (Tardiff & Clarke, 2002). Interestingly, asymmetric interhemispheric interactions via the intertectal commissure and asymmetries in the cross-sectional area of perikarya within both sides of the tectum have been suggested to underlie manifestations of visual lateralization within avians (Keyesers, Diekamp, & Gunturkun, 2000; Gunturkun, 1997; Gunturkun & Bohringer, 1987). Taken together, the nonhuman literature suggests that RH specialization for fear and danger could be determined at the very early level of the SC. This view is consistent with the central function of the SC in multisensory orientation and orienting movements, including saccadic eye movements (Sparks, 1999). The evidence in our current human study for a bicollicular leftward bias in fear processing might support asymmetric intertectal transfer of information from the dominant RH to the nondominant LH.

It should be mentioned that the results of the current study cannot support or refute the existence of a collicular–pulvinar–amygdala pathway. The study reveals a unique activation pattern within these structures but cannot attest to their interconnections. It is possible that other structures, both subcortical and cortical, show a similar activation pattern, that is, an LVF advantage for fear processing. In our study, no significant results were found for the pericalcarine region, the fusiform gyrus, or the IPS in this respect. However, mediation of the effect by other subcortical or cortical regions cannot be ruled out.

Lateralization of positive/approach emotions has been previously suggested in both human and animals (Quranta, Siniscalchi, & Vallortigara, 2007; Demaree et al., 2005), yet lateralization at the subcortical level is not well established. In our study, no significant lateralization pattern emerged for activations to happy faces. This may be due to lack of statistical power, relative inefficiency of happy faces as stimuli, or the use of unattended stimuli. It was previously shown that unattended happy faces are associated with decreased amygdala activity in contrast to unattended fearful faces (Williams, McGlone, Abbott, & Mattingley, 2005).

The evolutionary role of the left hemifield superiority for fear processing remains to be deciphered. Clearly, it must entail a substantial adaptive advantage outweighing the potential disadvantage of behavior predictability imposed by such lateralization. Based on a mathematical model, Vallortigara and Rogers (2005) and Ghirlanda and Vallortigara (2004) suggested that lateralization at the individual level enhances brain efficiency, whereas lateralization at the population level is the result of lateralization alignment among asymmetrical individuals aimed at achieving the advantages of being a part of a group. Lateralization of subcortical fear processing

might be related to lateralization of escape responses. Escape behavior asymmetries were reported in multiple species and are thought to be secondary to motor asymmetries (Vallortigara, 2000). The reason for the particular direction (RH/left hemisphere advantage) still needs to be explored.

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Reprint requests should be sent to Talma Hendler, Functional Brain Imaging Unit, Wohl Institute for Advanced Imaging, Tel Aviv Sourasky Medical Center, 6 Weizmann St. Tel-Aviv, Israel, or via e-mail: talma@tasmc.health.gov.il.

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