

Asymmetrical use of eye information from faces following unilateral amygdala damage

Frédéric Gosselin^{1*}, Michael Spezio^{2,3}, Daniel Tranel⁴ & Ralph Adolphs^{3,5}

1 Département de psychologie, Université de Montréal, Montréal, Québec, Canada

2 Department of Psychology, Scripps College, Claremont, CA 91711

3 Division of the Humanities & Social Sciences, California Institute of Technology M/C 228-77, Pasadena, CA 91101

4 Department of Neurology, University of Iowa 52242

5 Computation & Neural Systems, California Institute of Technology, Pasadena, CA 91101

* Corresponding author:

Frédéric Gosselin

Département de psychologie

Université de Montréal

C.P. 6128, succ. Centre-ville,

Montréal, Québec

H3C 3J7, Canada

Phone: (514) 343-7550

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Abstract

The human amygdalae are involved in processing visual information about the eyes within faces (Morris et al., 2002; Whalen et al., 2004), and play an essential role in the use of information from the eye region of the face in order to judge emotional expressions (Adolphs et al., 2005), as well as in directing gaze to the eyes in conversations with real people (Spezio et al., 2007). However, the roles played here by the left and right amygdala individually remain unknown. Here we investigated this question by applying the “*Bubbles*” method, which asks viewers to discriminate facial emotions from randomly sampled small regions of a face, to 23 neurological participants with focal, unilateral amygdala damage (10 to the right amygdala). We found a statistically significant asymmetry in the use of eye information when comparing those with unilateral left lesions to those with unilateral right lesions, specifically during emotion judgments. The findings have implications for the amygdala’s role in emotion recognition and gaze direction during face processing.

We previously reported that the human amygdalae are essential for processing information about the eyes in images of faces from an experiment conducted on SM, a rare patient with bilateral amygdala damage. In that study (Adolphs et al., 2005), SM and normal comparison participants were presented with randomly sampled regions of faces expressing fear or happiness, and were asked to discriminate the facial expressions. The correlation between performance accuracy and the location of the regions of the face that were revealed on each trial showed that normal participants predominantly used the eye region of the face on the task, whereas SM made essentially no use of the eyes at all. These findings fit with functional imaging studies demonstrating amygdala activation in response to fearful eyes (Morris et al., 2002), an effect reported even under conditions of subliminal presentation (Whalen et al., 2004).

It remains unclear how precisely to interpret these findings. For instance, in the study with SM (Adolphs et al., 2005), it was found that instructing SM to direct her gaze and visual attention to the eyes within faces improved her recognition of the emotion shown. This finding suggested that the amygdala is not solely essential for processing information from the eye region as such, but perhaps plays a more instrumental role in allocating attention to the eyes in the first place. Such an interpretation is supported by two recent fMRI studies. In one study (Gamer & Büchel, 2009), it was found that amygdala activation predicted when subjects shifted their fixation from the mouth region of faces towards the eye region of faces: a higher probability of switching gaze towards the eyes correlated with greater amygdala activation. Importantly, this finding held even though the face stimuli were presented so briefly that subjects' shift in gaze towards the eye region of faces in fact never landed on the eyes, a clear indication that the

amygdala does not merely respond to looking at the eyes, but rather participates in directing gaze towards them. Consistent with this instrumental rather than reactive picture of amygdala function, another study found that the amygdala showed differential activation for fear as compared to neutral faces even when the eye region of faces was erased (Asghar et al., 2008). These findings are in line with an emerging view of the amygdala in allocating processing resources towards salient stimuli that are initially unpredictable (Herry et al., 2007) or ambiguous in order to resolve them (Whalen, 2007).

Yet all these studies leave open the question of how the left and the right amygdala contribute individually to this processing. One possibility is that each amygdala contributes equally to processing information from both eyes; this would lead one to hypothesize that unilateral amygdala damage impairs the use of information from both eyes symmetrically, only less so than would bilateral amygdala damage. Another possibility is that each amygdala preferentially processes a somewhat different set of facial features, or perhaps features from different sides of the face; this possibility would be consistent with lateralized activation of the amygdala in several neuroimaging studies (e.g., Carlson, Reinke & Habib, 2009; Baas et al., 2004; Costafreda et al., 2008). Given the amygdala's key role in processing information about the eyes in faces, we here investigated a specific question: how do the left and right amygdala process information from the left and right eye region of faces? We investigated this question under free viewing conditions that precluded examination of how information from left and right visual hemifields might be processed; instead our investigation focused on possible asymmetries between left and right amygdala damage, on the one hand, and use of information from the left and right eye regions of the face (throughout our paper, we use "left" and "right" always as seen from the perspective of the subject). We tested 23 neurological participants with

unilateral amygdala damage on the same task that we had used previously to demonstrate bilateral amygdala involvement in processing eye information (Adolphs et al., 2005).

Methods

Participants. A total of 23 neurological participants were tested, all with unilateral amygdala damage (10 with right lesions; see Table 1 for details). All participants had normal or corrected-to-normal visual acuity, normal basic visual perception, and all but one were fully right handed. Nineteen of the participants had lesions resulting from unilateral temporal lobectomy to treat pharmaco-resistant epilepsy, two had surgical resection for a benign tumor, one had surgical resection for a cyst, and one had evacuation of a clot. It is important to note that such lesions, while typically used in studies that investigate unilateral amygdala damage, also variably encompass entorhinal cortex, medial temporal and temporal polar cortex, as well as white matter. Given that the amygdala receives its primary visual input from the adjacent inferior temporal cortex, the lesions probably compromised not only the amygdala itself, but also its source of visual input. All neurological participants were selected from the Patient Registry of the Department of Neurology at the University of Iowa; their neuroanatomy was obtained from detailed 3-D reconstructions of their brains from MR images or CT scans. For comparison, we also tested 12 neurologically and psychiatrically healthy individuals whose performances on our task were comparable to those of healthy individuals in previous studies. All procedures were carried out with the approval of the Institutional Review Boards at the University of Iowa and the California Institute of Technology and all subjects gave informed consent.

“Bubbles” task. The task was identical to one we have used before to investigate the amygdala’s role in the use of facial information (Adolphs et al., 2005). Briefly, participants were

seated 1 m in front of a 17-inch LCD display in a dimly lit room. Images (256 x 256 pixels; 5.72 x 5.72 deg of visual angle) were shown at the centre of the screen one at a time with no time limit, until the subject pushed one of two buttons required for the fear vs. happiness discrimination. Faces were drawn randomly from four exemplars (two females—one happy and the other fearful—and two males—one happy and the other fearful) as well as their mirror images (for a total of 8 base images), and randomly sampled using Gaussian apertures in the two-dimensional image plane and in five spatial frequency bands. Spatial filtering was achieved with Laplacian pyramid transforms (Burt & Adelson, 1983). The number of bubbles was adjusted on a trial-by-trial basis to maintain correct responses at a rate of 75%. Each subject completed 512 trials in approximately one hour. More details about this task are provided elsewhere (Adolphs et al., 2005; Gosselin & Schyns, 2001; Spezio et al., 2007a, 2007b), and a schematic showing the stimulus construction is shown in Figure 1.

As a comparison task, a subset of the same participants (6 with right lesions and 12 with left) additionally completed the identical task as described above, but with a gender discrimination instruction rather than an emotion discrimination. In this case, they had to push a button to indicate whether the sparsely revealed face was male or female, instead of whether it was fearful or happy.

Analysis of performance data. We performed least-square multiple linear regressions on the location of the bubbles and the accuracy of the subject's response on each trial to pinpoint the facial features that different observers used to discriminate fearful vs. happy faces. The plane of regression coefficients yielded by this operation is called a classification image: it reveals which locations on the face image (i.e., which parts or features of faces) are systematically associated with emotion discrimination performance on our task. We computed one such raw classification

image per subject per band of spatial frequencies.

Results

We first calculated the pixelwise classification image for each of our three subject groups (left amygdala lesioned, right amygdala lesioned, healthy comparison), that is, the effective information used by each group to discriminate happy from fearful faces. We pooled individual raw classification images per subject group, smoothed the resulting group classification images, transformed them into Z-scores, and, to determine whether visual information correlated reliably with accuracy, we applied corrected statistical tests (Pixel test; $p < 0.05$; Chauvin et al., 2005; Figure 2). Two aspects of these classification images are noteworthy: First, the right amygdala group classification images contain in total fewer significant pixels (11,029) than the left amygdala classification images (16,961), and the left amygdala classification images contain fewer significant pixels than the healthy comparison classification images (23,305). Second, the classification images of the three groups are qualitatively quite similar, with the notable exception of the 27.5-13.75-cycles-per-face (cpf) classification images—only the eye on the right side of the face reaches significance in the left amygdala group, only the eye on the left side of the face reaches significance for the right amygdala group, and both eyes reach significance for the healthy comparison group.

We also looked at all pairwise statistical contrasts between these group images. Consistent with what we had found previously in another study (Adolphs et al., 2005), the classification images for both left and right amygdala lesion groups did not differ significantly overall from those observed in healthy individuals. We therefore undertook a more sensitive analysis that compared, within each amygdala subject, the differential use from the left and right

eye regions alone (an ROI-based approach).

To increase signal-to-noise ratio, we summed all raw classification images across bands of spatial frequencies and transformed them into Z-scores. We then smoothed the individual classification images with a Gaussian filter ($FWHM= 4.36$ pixels) and Z-scored each image. Each Z-score is thus a weighted sum of an area containing several pixels. Finally, we subtracted the maximum Z-score within the eye region shown on the left side of the image (each eye region was delimited by an elliptical disc with a horizontal and a vertical diameter equal to 64 and 32 pixels, respectively, Figure 3) from the maximum Z-score within the eye region shown on the right side of the image in every smoothed individual classification image (we use “left” and “right” always from the perspective of the subject viewing the stimuli). The resulting laterality indices—Z-scored by dividing by $\sqrt{2}$ —are plotted as a function of subject groups in Figure 3.

Several patterns are noteworthy from this analysis. Most importantly, a two-tailed t-test assuming unequal variances indicated that participants from the right amygdala lesion group had a more negative laterality index (i.e., greater use of left eye than right eye; mean=-0.4092; std=0.3911) than did participants from the left amygdala lesion group (mean=+0.1338; std=0.5246; $t[20.9929]=2.8435$; $p=0.0097$). There was no difference between female ($N=14$; mean laterality index=-0.1895; std=0.5750) and male (mean laterality index=+0.0334; std=0.4711) participants in laterality index overall (two-tailed t-test: $t[19.5975]=1.0145$; n.s.) nor within each lesion group. These statistical patterns as well as all the others reported in this article remained significant with nonparametric tests (Wilcoxon signed-rank).

Eighteen of the 23 participants (7 with right lesions) had completed an additional 512 trials during which a gender judgment was required instead of an emotion discrimination on the same face stimuli. Laterality scores were derived exactly as already described. These 18 individuals showed a significant difference in use of information from left and right eye regions

as described above when an emotion judgment was required (two-tailed t-test: $t[15.9416]=3.1577$; $p=0.0061$; mean laterality index of right amygdala group= -0.5582 ; $std=0.3658$; mean laterality index of left amygdala group= $+0.1284$; $std=0.5566$), but no difference when a gender judgment was required (two-tailed t-test: $t[15.9922]=0.4402$; n.s.).

If one takes the use of eye information observed in healthy comparison subjects (dashed line in Figure 3) as the comparison for evaluating asymmetries in the use of eye information in the lesion groups, then Figure 3 suggests that the group difference during emotion judgment we report here is driven primarily by an effect in the group with left, but not with right, amygdala lesions. In particular, the group with left amygdala lesions appears to make preferential use of information from the eye region shown ipsilateral to the intact (right) amygdala. The reason for this is that healthy comparison subjects, as a group, already show an asymmetric use of eye information: they have a mean laterality index of -0.2558 ($std=0.2697$), i.e. a preference for use of information from the eye region on the left side of the image over that on the right side of the image. This laterality was significantly different from zero (two-tailed t-test: $t[11]=-3.2858$; $p=0.0073$). If we contrast the amygdala lesion groups' laterality indices relative to those of the healthy comparison group, we find that the group with left amygdala lesions shows a significant shift from normal (towards an asymmetric use of the right eye region; two-tailed t-test: $t[18.2254]=2.3608$; $p=0.0296$), whereas the group with right amygdala lesions shows a non-significant shift (towards the left eye region) from the normal comparison group (two-tailed t-test: $t[15.5476]=-1.0499$; n.s.).

Discussion

Using the “*Bubbles*” method together with a new way to analyze lateralized use of information from the left versus the right eye within faces, we found that unilateral damage to the amygdala results in an asymmetry in how such information is used. Specifically, we found that:

1. There was a statistically significant difference in laterality indices between the group with left amygdala lesions compared to the group with right amygdala lesions.
2. This difference was due to a preferential shift towards processing information from the eye region on the side of the image ipsilateral to the intact amygdala (contralateral to the lesion).
3. These effects were found only when participants made fearful versus happy emotion discriminations, and not when they were asked to discriminate gender.

The emotion discrimination data for 13 of our 23 subjects with unilateral amygdala damage (5 with right lesions) have been analyzed in a preliminary way and yielded results that did not differ statistically from normal comparison subjects as was previously reported (Adolphs et al., 2005, Supplementary Online Information), a null-finding that we replicated here. There are two singly necessary and jointly sufficient reasons why this prior study (Adolphs et al., 2005) did not find the pattern of asymmetric eye use we report here. First, the sample size was smaller, limiting statistical power. Second, no analysis comparing use of left and right eye information was carried out in that prior study. Our present results argue for an important revision to effects of unilateral amygdala damage: there are no global effects on the use of facial information, but instead specific shifts in how information from each of the two eye regions is used (see also Akiyama et al., 2007; Cristinzio et al., 2010; Palermo et al., 2010).

Perhaps the most surprising aspect of our findings is that the amygdala appears to be associated with preferential use of information in the ipsilateral rather than the contralateral eye

region on our task. It is important to note that our stimuli were not presented tachistoscopically, and that therefore the left and right eye regions in the stimuli cannot be equated with left and right visual fields. Nonetheless, given that fixations will fall over both sides of the face under free-viewing conditions with the relatively long stimulus duration that we used, one would expect a correlation between the side of the eye region and visual hemifield: fixations onto the right side of the face will ensure that the left eye region is in the left visual field, and conversely fixations onto the left side of the face would ensure that the right eye region is in the right visual field. As well, fixations onto the center of the face at stimulus onset (which was the location of our fixation cross preceding each trial) would ensure such lateralized input from the eye region until participants began to make their first saccades. Under experimental conditions nearly identical to ours, it has been shown that occipito-temporal regions of the healthy brain process information from the eye region contralaterally up to about 200 ms after stimulus onset (Schyns et al., 2003; Smith, Gosselin & Schyns, 2004; Smith, Gosselin & Schyns, 2007; Smith et al., 2009). All these considerations would lead one to expect a correlation between seeing the left eye in the left hemifield and the right eye in the right hemifield on average across our trial. Our finding is therefore surprising in light of evidence from studies in human and nonhuman primates that each amygdala receives visual information primarily from the contralateral visual field, via visual cortices in the temporal lobe (Amaral et al., 1992). Neurons in temporal area TE of the monkey, for example, show foveal/contralateral processing within fairly restricted spatial receptive fields (2.8 to 26 degrees of visual angle; Op De Beeck & Vogels, 2000). On the other hand, the amygdalae also receive some indirect visual input via the pulvinar thalamus (Romanski et al., 1997) which contains neurons that show bilateral receptive fields at least in some subdivisions in monkeys (Petersen et al., 1985) and also appears to process bilateral visual field information in humans (Cotton & Smith, 2007). Furthermore, lesions to the pulvinar

in humans can result in impairments in object-based space as well as retinotopic-based space, raising the possibility of ipsilateral effects (Ward & Arend, 2007). Additional subcortical pathways to the amygdala may also provide routes for ipsilateral visual information (Usunoff et al., 2007).

One possible interpretation of the surprising ipsilateral relationship we noted above, is that the amygdala may not be important for sensory processing of visual input about the ipsilateral eye region. Our conjecture here is as follows. Given the amygdala's instrumental role in disambiguating salient information we discussed in the Introduction, it may not be correct to conceive of the ipsilateral eye processing effect that we found as resulting from a stimulus-response mechanism in the (remaining intact) amygdala. Rather, it may be revealing an orienting or attentional role towards the ipsilateral eye region. Consistent with this idea is a recent report that suggests an ipsilateral field bias for visual attention correlates with BOLD signal in the amygdala (Carlson, Reinke & Habib, 2009), although by and large attentional effects also favor contralateral rather than ipsilateral biases. Future studies that vary attentional load, or that independently manipulate the left and the right eye region under gaze-contingent viewing conditions, could help to resolve these possibilities.

Next we consider how one might interpret the effects of unilateral amygdala damage on our asymmetry index, as compared with the healthy comparison group. Our interpretation of this comparison begins with the small negative laterality bias we found in the normal comparison group itself, suggesting that healthy individuals, on average, make slightly more use of the eye region on their left than the eye region on their right. While this finding will need to be replicated in a larger sample, it fits with other results from the literature on face processing, which have shown that face information on the viewer's left side dominates in processing faces (Gilbert & Bakan, 1973; Grega et al., 1988) and in making a variety of judgments including emotional ones

from faces (Burt & Perrett, 1997). In terms of the amygdala's role, the recent study by Carlson, Reinke & Habib (2009) suggests that it is the left amygdala's ipsilateral attentional bias that may be contributing to the laterality effect seen in healthy individuals. This interpretation would predict that left amygdala damage should shift laterality indices away from the normal left-eye preference and towards a more positive laterality index. We in fact observed a shift towards a mean positive laterality index, suggesting that left amygdala damage may in fact unmask a similar ipsilateral attentional bias by the intact right amygdala (see also Gamer & Buechel, 2009; Cristinzio et al., 2010). Conversely, right amygdala damage should leave the normal leftward laterality bias exerted by the left amygdala unopposed and show an even larger negative laterality index than seen in controls, just as we observed. To summarize: our results thus support the idea that the left amygdala subserves a role in preferential processing of eye information on the viewer's left while the right amygdala subserves a role in preferential processing of eye information on the viewer's right.

Finally, the leftward laterality bias we observed in healthy individuals will be important to follow up. We have observed individual differences in neurologically healthy participants in the same emotion-judgment task employed here: many individuals show a statistically significant asymmetry in their use of information from one of the two eyes. One possibility is that these individual differences in normal individuals could result partly from differences in amygdala function, an idea that could be tested in future studies combining the "*Bubbles*" method with fMRI.

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Table 1: Demographic and neuropsychological characterization of the participants. Data are broken down for those with unilateral left or right lesions. VIQ, PIQ, FSIQ are verbal, performance, or full-scale IQ from the Wechsler Adult Intelligence Scale (WAIS-R or WAIS-III).

	N	Age	Education	VIQ	PIQ	FSIQ
Left	6M/7F	46±8	13±2	93±12	103±12	97±11
Right	3M/7F	43±14	14±2	102±13	105±12	104±11

Figure Legend

Figure 1. Construction of the “bubbles” stimuli. One of the face base images (top) was decomposed into octaves of spatial frequencies (second row). These were each convolved with Gaussian apertures (the “bubbles”, third row) to yield the sparsely filtered images shown in the fourth row. When spatial frequency channels were recombined, they yielded the final stimulus image shown at the bottom.

Figure 2. Average information from faces used to discriminate fear from happiness by left and right amygdala neurological participants, and by control participants (top). Significant areas are shown in red superimposed onto the spatial information breakdown in bandwidths of one octave (four bottom rows). There is no statistically significant pixel in the coarsest bandwidth. Furthermore, there is no statistically significant difference between the groups on this measure.

Figure 3. Difference in use of information from the right eye and the left eye. We plot a laterality index as the peak classification image value in the eye region on the left side of the image (from the viewer’s perspective) minus the region on the right side of the image in individual participants. Each amygdala lesion group showed a bias in favor of using information from that side of the face ipsilateral to their intact amygdala, resulting in a statistically significant difference in the laterality index between the two groups ($p < 0.01$, two-tailed). The inset shows the left and right eye regions as bright blobs superimposed on the average of the four facial expression photos used in the experiment. These were used as regions of interest to derive the difference in use of information from the eye displayed on the right and left side of the face.

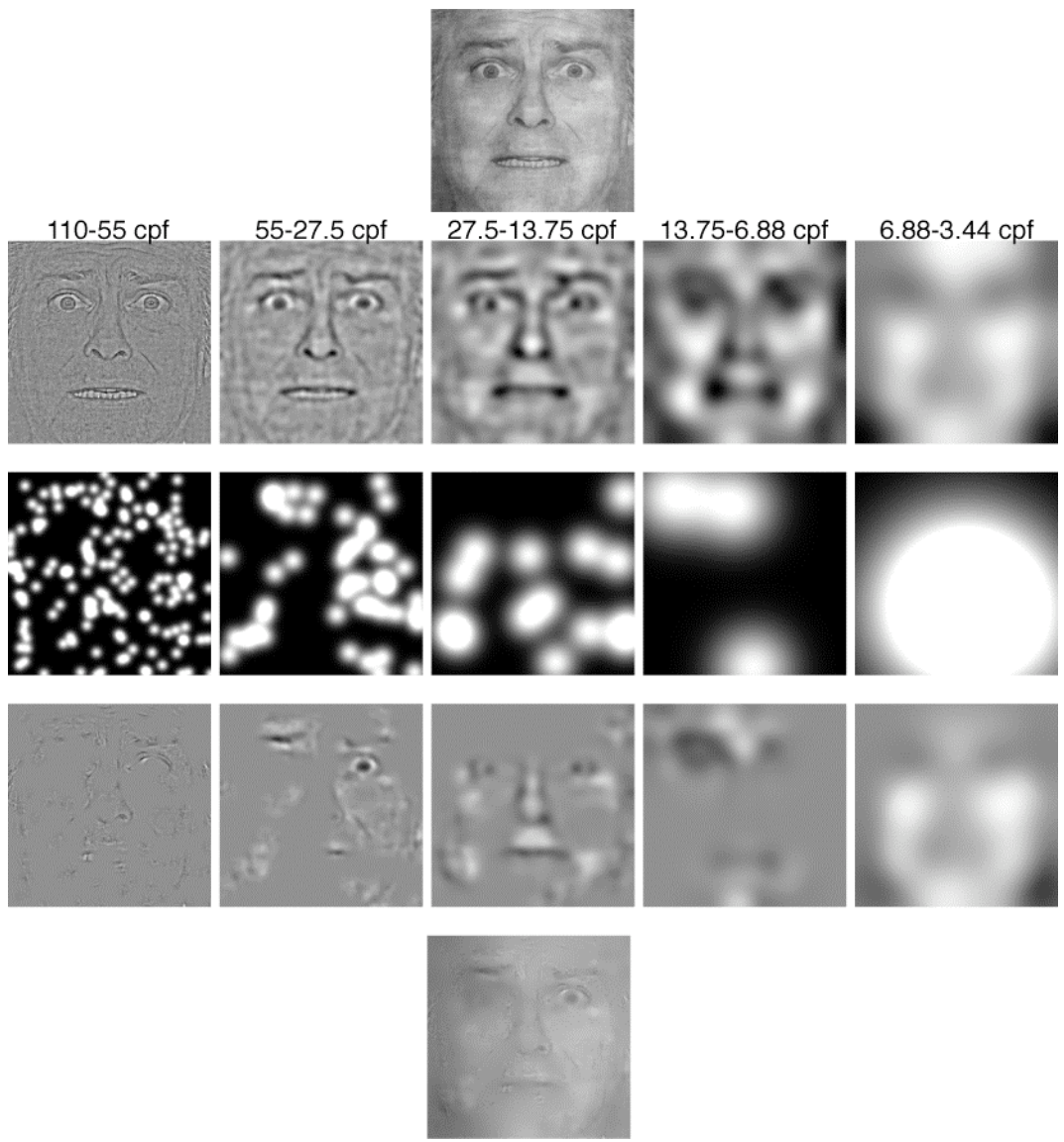


Figure 1.

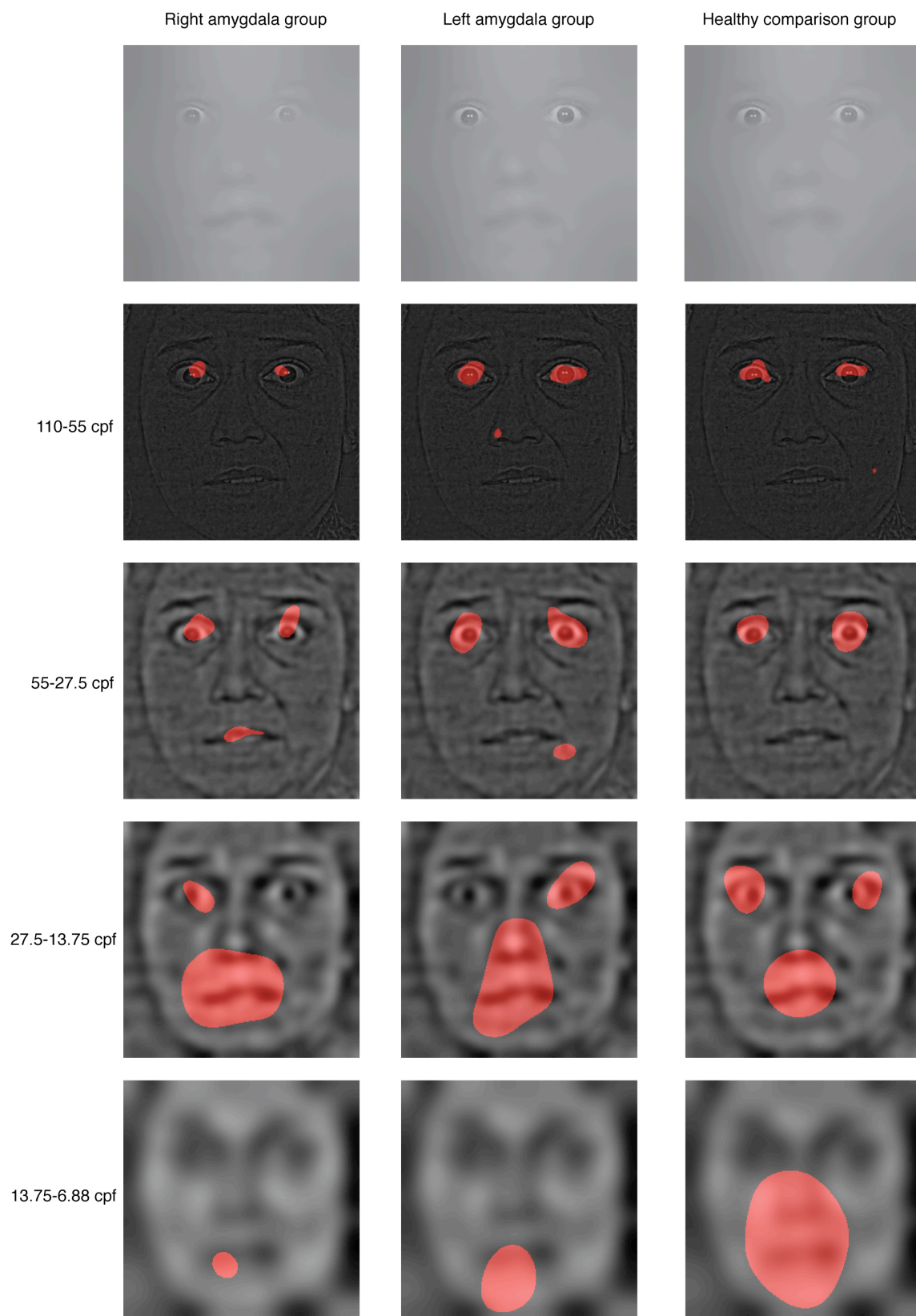


Figure 2.

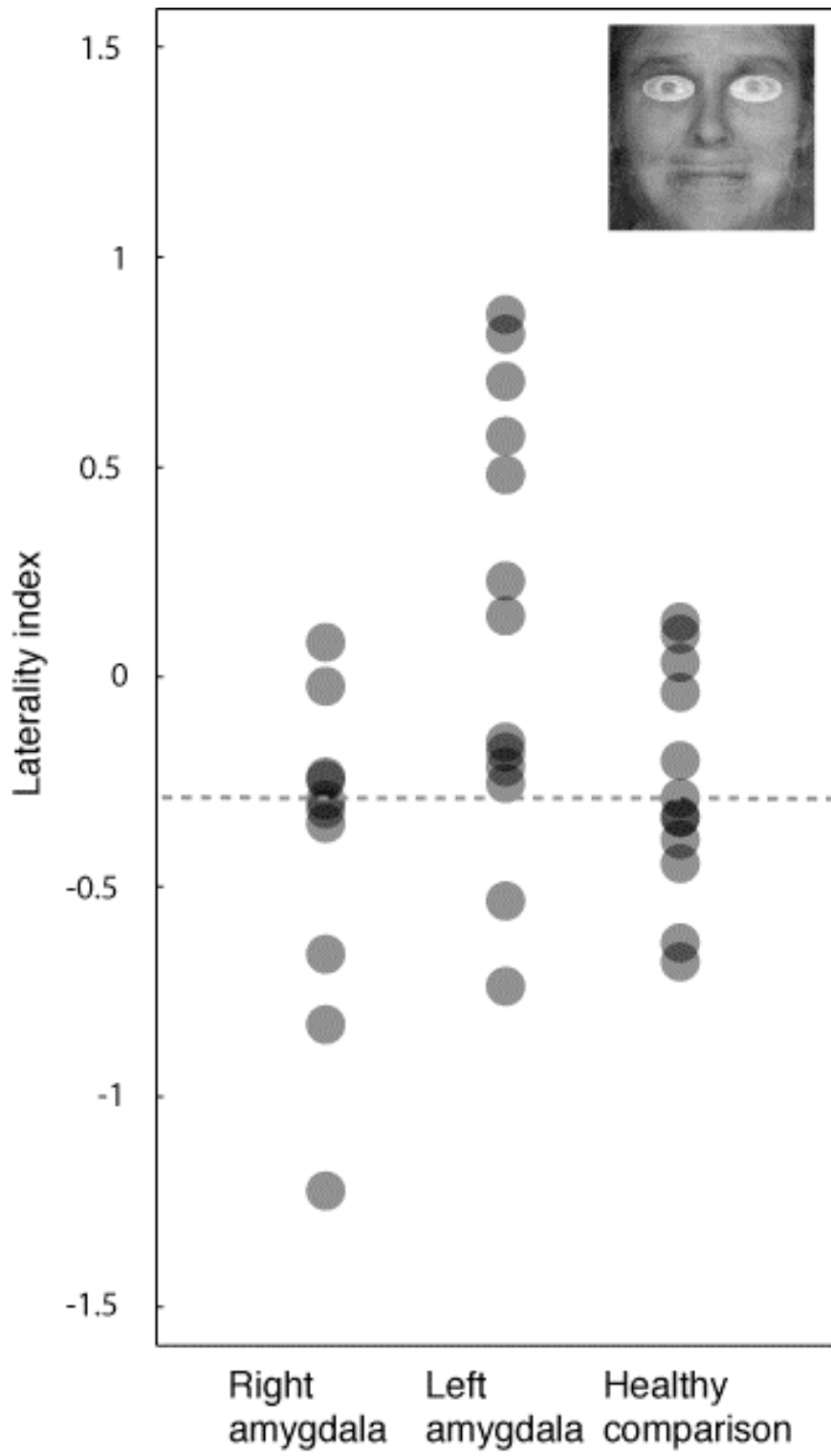


Figure 3.