Statistical analyses

To account for the non-independence of individual observations within a year, and the large differences in sample size among groups, analyses were, where possible, performed on yearly means for the relevant sub-group. When appropriate, yearly means were square-root or arc-sine transformed before analysis[24]. All presented means and parameter estimates are back-transformed.

All statistical analyses were performed using the SAS statistical package using the GLM and GENMOD procedures[25]. Non-significant interactions were removed first, starting with the least significant, followed by non-significant single terms, again starting with the least significant. When interactions were significant, the main effects were kept in the model, regardless of their significance. All tests are two-tailed.

Selection analyses

Local survival was used as a measure of viability, which is defined as the probability that a bird is observed breeding again on Vlieland the next year. Local recruitment was used as a measure of fecundity, and is defined as the number of offspring produced in all clutches in a year observed to be breeding on Vlieland in subsequent years. We can therefore not distinguish between mortality and emigration of both fledglings and adults. Both processes do however have a similar effect on the population level. Only clutches from which at least one chick fledged were included in analyses of recruitment.

To quantify selection acting on clutch size, we calculated standardized selection gradients (β') by regressing relative fitness (fitness divided by the mean fitness in that year) on standardized clutch size (clutch size relative to the mean in that year, divided by the standard deviation)[26]. Significance of selection gradients was determined from a generalized linear model with binomial and Poisson errors, using standardized clutch sizes. If significant, origin of birth was included in the model. Selection gradients were calculated for both the period from 1955 until 1975, and for 1975 until 1995. As a result of the small sample sizes in the West, especially in the first period, analyses were limited to females breeding in the East.

Animal model analysis

Genetic parameters were estimated using an animal model, which uses all available information on both ancestors and descendents to separate an individual's phenotype into an additive genetic component (or breeding value) and other random and fixed effects[27,28]. The amounts of variance accounted for by the random effects (additive genetic variance V_A, permanent environmental variance V_{PE}, and residual variance V_R) were estimated using a Restricted Maximum Likelihood (REML) technique implemented in the software package VCE4[29], and were equal to 0.58, 0.42 and 0.94, respectively. The narrow sense heritability $\pm$ s.e. of clutch size on Vlieland across the period 1965–2003 (defined as V_A/V_P) was 0.30 $\pm$ 0.028. Best Linear Unbiased Predictions (BLUPs) of breeding values were obtained for all individuals in the pedigree using the software package PEST[30]. See Supplementary Information for more details on pedigree reconstruction and which fixed and random effects were included in the animal model.

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Correspondence and requests for materials should be addressed to E.P. (e.postma@nioo.knaw.nl).

A mechanism for impaired fear recognition after amygdala damage

Ralph Adolphs[1,2], Frederic Gosselin[3], Tony W. Buchanan[1], Daniel Tranel[1], Philippe Schyns[4] & Antonio R. Damasio[1]

[1]*Department of Neurology, University of Iowa, Iowa City, Iowa 52242, USA*
[2]*Division of Humanities and Social Sciences, California Institute of Technology, Pasadena, California 91125, USA*
[3]*Departement de Psychologie, Université de Montréal, Montréal H3C 3J7, Canada*
[4]*Department of Psychology, University of Glasgow, Glasgow G12 8QB, UK*

Ten years ago, we reported that SM, a patient with rare bilateral amygdala damage, showed an intriguing impairment in her ability to recognize fear from facial expressions[1]. Since then, the importance of the amygdala in processing information about facial emotions has been borne out by a number of lesion[2–4] and functional imaging studies[5,6]. Yet the mechanism by which amygdala damage compromises fear recognition has not been identified. Returning to patient SM, we now show that her impairment stems from an inability to make normal use of information from the eye region of faces when judging emotions, a defect we trace to a lack of spontaneous fixations on the eyes during free viewing of faces. Although SM fails to look normally at the eye region in all facial expressions, her selective impairment in recognizing fear is explained by the fact that the eyes are the most important feature for identifying this emotion. Notably, SM's recognition of fearful faces became entirely normal when she was instructed explicitly to look at the eyes. This finding provides a mechanism to explain the amygdala's role in fear recognition, and points to new approaches for the possible rehabilitation of patients with defective emotion perception.

Patient SM is a 38-yr-old woman whose brain lesion encompasses all nuclei of the amygdala bilaterally, as well as a small portion of the

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adjacent entorhinal cortex, yet spares all other subcortical and cortical structures, leaving her with essentially normal basic perception, memory, language and reasoning insofar as these do not involve the processing of emotional material[7]. However, her processing of emotionally and socially meaningful information is impaired, as it is in nonhuman animals with amygdala damage. For example, she does not show normal conditioned fear responses[8], and her social behaviour is indiscriminately trusting and friendly[9]. Over more than a decade of testing, she has consistently shown a severe and selective impairment in the ability to recognize fear from facial expressions[1,7], although she is able to recognize fear from complex visual scenes and tone of voice. So far, she remains the human subject with the most selective amygdala damage and with the most selective impairment in fear recognition from faces; however, no mechanism has yet been provided to link these two conditions.

We began by exploring SM's ability to make use of visual information from specific regions of the face. SM and normal control subjects were each shown approximately 3,000 trials of sparsely revealed faces varying in gender and emotional expression (fear or happiness)[10,11]. In each trial, random locations on one of the face images were made visible with gaussian 'bubbles' in five one-octave bands of spatial frequencies (see Supplementary Fig. 1), and viewers were asked in a two-alternative discrimination task to judge whether the revealed features expressed fear or happiness. We chose to contrast these two expressions because SM differs most in her ability to recognize them (entirely normal recognition of happiness, severely impaired recognition of fear)[1,7], and because they differ most in terms of the facial features used for their identification[12]. For each subject, recognition performance was kept constant at 75% for each emotion by interactively adjusting the number of bubbles during the task. This corresponded to an average of 16.5 bubbles (s.d. = 3.1, range = 13–23.4) per image for the normal controls, whereas SM required 30.8 bubbles per image. The number of bubbles required to identify correctly a face as fearful or happy was equivalent; the difference in number of bubbles (fearful faces minus happy faces) was −0.03 bubbles for control subjects and +0.05 bubbles for SM.

Is SM's requirement for more bubbles relative to control subjects due to a decrease in her use of visual information over all facial features, or can it be attributed to a failure in using information from specific facial features? We performed a linear regression using the location of the bubbles on the face images and the subject's discrimination accuracy on each trial to reveal the regions of the face used to discriminate between fear and happiness. Whereas normal subjects used information predominantly from the eyes in high spatial frequencies (from 5.59–22.38 cycles per degree), SM failed to make the same use of eye information (Fig. 1a, b). For the highest spatial frequency band information from the eyes, SM's mean *Z*-score was equal to 0.59 s.d. below her global mean (that is, her use of the eyes at high spatial frequency was worse than her mean use of all face regions across all spatial frequencies), whereas the *Z*-scores of control subjects ranged from 0.42 to 1.50 s.d. above the mean (average = +0.79). Whereas every normal subject made use of visual information from the eye region in the highest spatial frequency band ($P < 0.05$), SM did not.

Moreover, SM did not use information in the face other than the eyes more effectively than control subjects when discriminating fear; the difference image of the visual information used more by SM than by control subjects does not reveal any such features (Fig. 1b). Although SM failed to use information from the eyes in high spatial frequencies in gaussian bubble trials showing either fearful or happy faces, she did make normal use of the mouth region (Fig. 1c). This finding probably explains her intact ability to recognize happiness, and her equivalent performance at discriminating between fearful and happy faces in the described task—because we offered her only two options, her intact ability to use the smile to identify happiness should result in successful identification of fear by exclusion.

SM's failure to use information about the eyes stood out as abnormal in comparison with every one of the ten normal control subjects we tested (Supplementary Figs 2 and 3). In order to establish further the specificity of SM's deficit, we performed the same two-alternative discrimination task in 13 subjects with unilateral amygdala damage and with normal fear recognition. All made normal use of information from the eye region of the faces (see Supplementary Fig. 4).

Although the large number of trials required precluded testing SM's ability to discriminate fear from all other basic emotions on this particular task, such data have been obtained in a separate study in normal individuals[12]. When asked to discriminate between each of the six basic emotions (happiness, surprise, fear, anger, disgust and sadness) and neutral expressions in a seven-alternative discrimination task, normal subjects consistently and specifically make the most use of high spatial frequency information from the eyes for discriminating fear. It is interesting to note that discrimination of

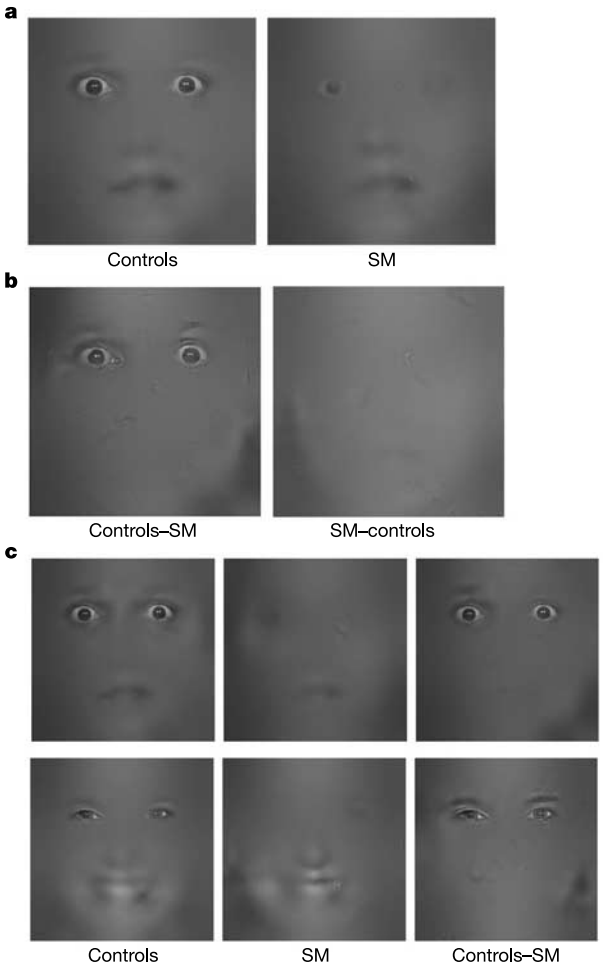

Figure 1 SM fails to make use of visual information from the eyes in faces. **a**, Information from faces used to discriminate fear from happiness in ten control subjects (left panel) or SM (right panel). **b**, Difference images showing the facial information used more by control subjects than by SM (left panel), or more by SM than by control subjects (right panel). Unlike control subjects, SM does not use high spatial frequency information about the eyes, nor does she use any information that the controls do not. **c**, Visual information used in those trials in which fearful faces were shown (top row) or happy faces were shown (bottom row). SM fails to make use of the eyes for either emotion, but is able to use information about the mouth normally.

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two other emotions, sadness and anger, also makes substantial use of the eye region, and that recognition of these two emotions, in addition to fear, has been most consistently reported to be impaired after amygdala damage in other patients[3]. The highly selective impairment in fear recognition in SM's case is probably attributable to her ability to make compensatory use of information outside the eye region for those other emotions; however, this strategy is insufficient in the case of fear.

In a control task using identical stimuli and procedure to those described above, subjects were asked to discriminate the gender of the faces rather than their emotion. SM's performance was normal in all respects for this task: she required the same number of bubbles (average number required by control subjects = 46.5, s.d. = 9.5; number required by SM = 39.5) and she used exactly the same effective visual information (the difference image for control subjects minus SM was uniformly grey). Notably, both SM and controls used high spatial frequency information from the eyes and mouth in the gender discrimination task (see Supplementary Fig. 5), indicating that SM is indeed capable of using such information, although she fails to do so spontaneously when judging emotion.

The discrimination task using the gaussian bubbles method provided an unbiased and homogeneous sampling of all regions of the face that might be important for fear recognition, but used rather artificial stimuli that might be processed differently than actual faces, and was restricted to comparisons between two emotions (fear and happiness). We thus conducted a further experiment to assess directly the importance of the eyes within facial images and broaden the scope of our conclusions. Subjects were shown whole facial images expressing the six basic emotions, as well as the same images with the eyes digitally erased, and we assessed their accuracy in recognizing the emotion in each image. Whereas control subjects were significantly less accurate at recog-

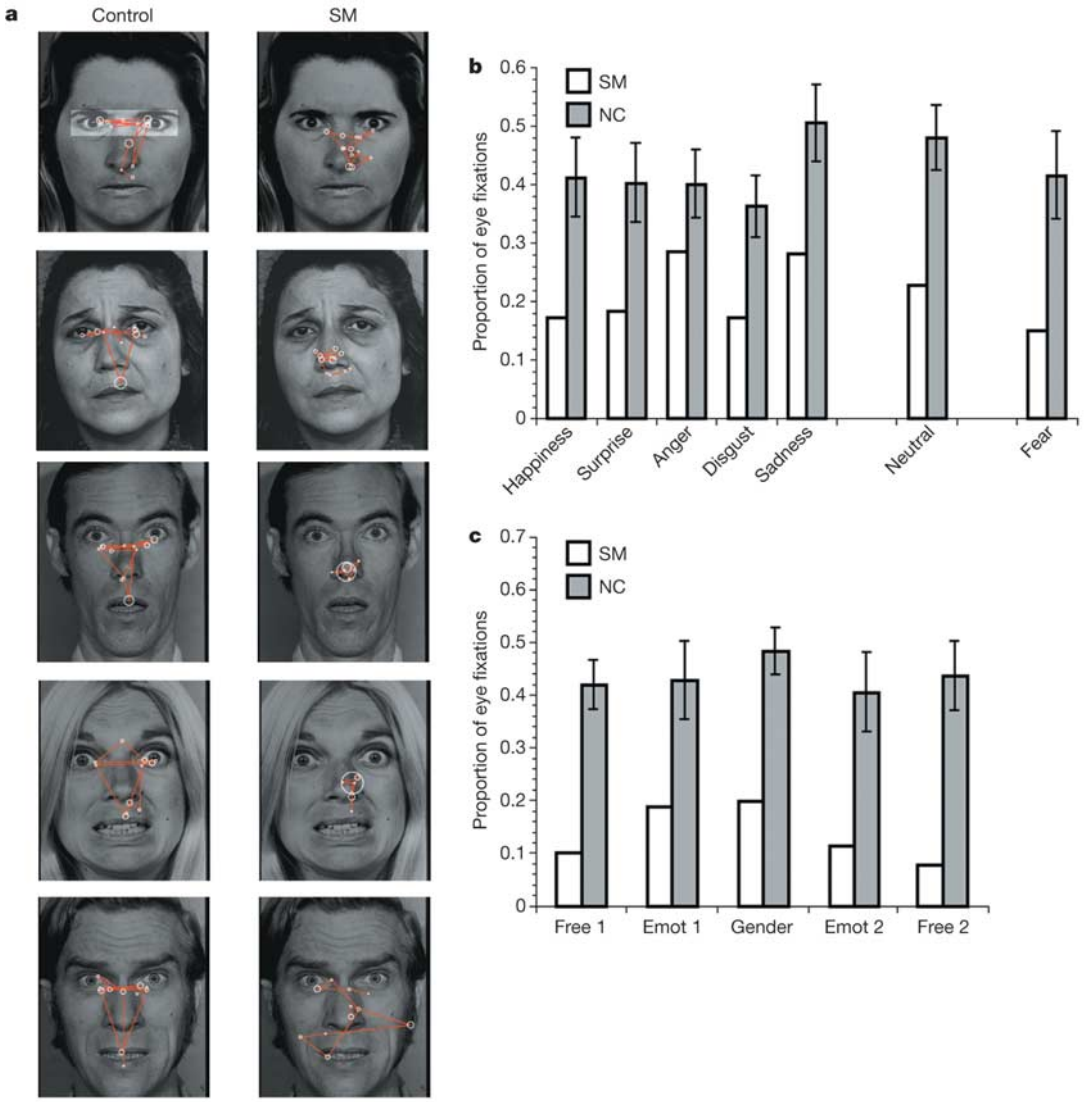

Figure 2 SM fails to fixate on the eyes when viewing facial expressions. **a**, Saccades (red lines) and fixations (white circles, where circle size corresponds to fixation duration) made by a typical normal control subject (left column) and SM (right column) when judging the emotion shown in sample expressions (from top to bottom) of anger, sadness and three fear faces. A lightly shaded box around the eyes is present in the top left image, showing the region (defined *a priori*) used to calculate the proportion of fixations shown in **b**. **b**, The proportion of fixations made by SM (white bars) and normal control subjects (NC, grey bars, mean ± s.e.m.) on the eye region of face images when judging different emotions, calculated as the number of fixations to the eye region divided by the total number of fixations made on the face. **c**, The proportion of fixations made specifically to facial expressions of fear, under the five different viewing conditions detailed in the Methods, shown in their order of presentation from left to right (Free = passive viewing, Emot = emotion judging). SM's proportion of fixations on the eyes is abnormally low for all conditions.

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nizing fear when the eyes had been erased ($P < 0.005$, paired t-test), SM showed no change in her performance accuracy (0.33 in both conditions). No control subject ever approached SM's performance in fear recognition for whole faces (lowest control performance of 0.67 accuracy) whereas three out of twelve control subjects were as impaired as or worse than SM when the eyes had been erased. Notably, this pattern extended to other emotions (see Supplementary Table 1), as the recognition accuracy of control subjects dropped when the eyes were erased, but SM's accuracy did not. These findings confirmed that SM fails to make normal use of information from the eye region of faces when judging facial emotions.

The findings thus far raised the possibility that SM's impairment might result from a failure to direct her gaze to the eyes in the first place. To test this idea, we monitored eye movements while subjects viewed prototypical facial expressions of all basic emotions[13,14] under five conditions: passive viewing (done twice), emotion recognition (done twice) and gender recognition (done once). Normal control subjects reliably explored the face, fixating mostly on the eyes (Fig. 2a); this is a pattern observed in humans as young as 7 weeks old[15] as well as in nonhuman primates[16]. SM showed a highly abnormal fixation pattern: she did not explore the face normally, and systematically failed to fixate on the eye region. This impairment was evident for fear as well as other emotions (Fig. 2b). SM's fixations on the eyes were fewer than those of any normal control subject, and were significantly fewer than the control group for all but one condition (the first emotion judgement task 'Emot 1' in Fig. 2c, $P < 0.2$; all other conditions, $P < 0.05$; two-tailed Z-tests).

A control task verified that SM's abnormal fixations do not arise from cueing particular locations during the experimental procedure. Specifically, the fixation cross that preceded each face stimulus in the above experiments was located in the centre of the screen, roughly coincident with the subsequent location of the nose in each face. A further two blocks of trials presented the same faces, but preceded by a fixation cross coincident with either the left or right eye rather than the nose, and asked subjects to judge the emotion. SM's proportion of fixations to the eyes remained abnormally low (0.24 for both trial blocks versus 0.49 and 0.48 respectively for the control subjects), and her fear recognition remained impaired (0.33 and 0.17 correct for the two trial blocks versus 0.81 and 0.79 for the control subjects).

We interpreted the above findings to mean that SM is impaired in recognizing fear because she is unable to make use of diagnostic information from the eye region that is normally essential for recognizing fear, and that this inability is related to her lack of spontaneous fixation on the eye region of faces. This interpretation would predict that manipulating how she inspects faces might influence her ability to recognize emotion. Accordingly, we re-assessed her emotion recognition while instructing her specifically to look at the eye region of faces. As instructed, SM looked at the eyes in the facial expressions presented (Fig. 3). Her impaired recognition of fear was completely reversed (that is, attained normal levels) with this simple instruction. We verified this result on two separate occasions, counterbalancing the order of the 'instruction' task and the previously described free viewing task (Fig. 3 and Table 1).

However, a single instruction to direct her gaze onto the eye region of facial images was insufficient to rehabilitate permanently SM's impaired fear recognition. When we subsequently showed her the face stimuli under unconstrained viewing conditions, she failed to fixate the eye region spontaneously and reverted to her previously impaired fear recognition. Thus the impairment could be rescued by instruction to fixate the eye region of faces, but the improvement lasted only as long as the instruction remained explicit. This finding opens the possibility for developing a strategy that could consistently direct her gaze to the eye region of faces, perhaps with additional instruction and training.

In over a decade of repeated testing, SM has not learned to recognize fear in faces[7], and does not appear to have improved her defective social judgements[9]. This collection of impairments is consistent with an inability to search automatically for environmental clues whose presence signifies potential threat or danger. Not only does the amygdala feed back to the visual cortex[17], modulating even relatively early visual information processing[18,19], but as the present study suggests it might also influence the visual information that our eyes seek in the first place. This mechanism could be a component of the amygdala's role in the resolution of ambiguity in facial expressions[20] and the modulation of attention[18,21,22]. Thus, we believe that the impaired fear recognition arising from damage to SM's amygdala is not due to a basic visuoperceptual inability to process information from the eyes, but is instead a failure by the amygdala to direct her visual system to seek out, fixate, pay attention to and make use of such information to identify emotions. This interpretation entails a revision of

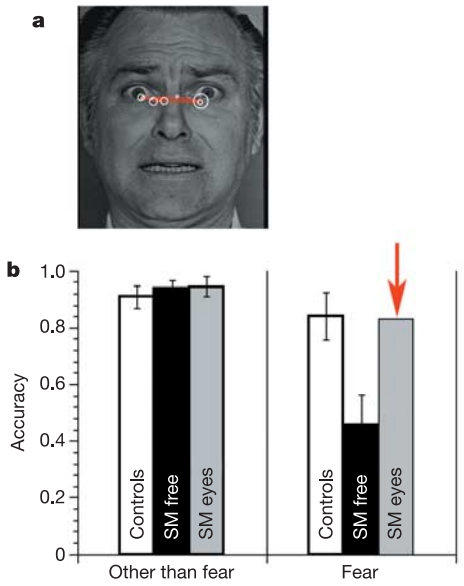

Figure 3 Instructed viewing of the eyes improves impaired fear recognition in SM. **a**, When instructed to fixate on the eyes in facial expressions of fear, SM is able to do so. **b**, Accuracy of emotion recognition (±s.e.m.) for ten control subjects (white) and SM. Whereas SM's recognition of fear is impaired when allowed to look at the stimuli freely (SM free, black bars), her performance becomes normal relative to control subjects when instructed to fixate on the eyes (SM eyes, grey bar, red arrow). The impairment is specific to fear recognition (left panel shows mean recognition accuracy for all emotions other than fear).

Table 1 **Mean accuracies in emotion recognition for SM and control subjects**

Emotion	Controls	SM (free)	SM (eyes)
Happiness	1.00	1.00	1.00
Surprise	0.96	1.00	1.00
Anger	0.82	0.88	0.82
Disgust	0.76	0.85	0.90
Sadness	1.00	0.96	1.00
Fear	0.84	0.46	0.83

Subjects (SM and ten control subjects) were shown six different exemplars of each of six emotions using face stimuli[13] identical to those used in prior studies[1], and were asked to identify the appropriate emotion by pushing a button. The experiment was conducted twice with controls and four times with SM: twice when she was allowed to look freely at the images (free), and twice when instructed to fixate on the eyes (eyes). The only significant difference between SM and control subjects is in her recognition of fear under the free viewing condition ($Z = -2.385$, $P < 0.01$, one-tailed t-test).

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our previous conclusions[1] about the face processing abilities of SM: although she can generate a normal performance score on discrimination and recognition tasks for some emotions (such as happiness), her use of visual information is abnormal for all facial emotions, not only fear.

Our study is in line with recent findings that the amygdala participates in processing information about the eye region of faces[6,23,24]. Such a functional specialization might account for the role of the amygdala in processing emotions related to behavioural withdrawal[25], fear[26], threat or danger[3,7]. A strategy of directing one's own gaze onto the eyes of others would serve to seek out potential sources of salient social information[27], and it seems plausible that other impairments in social judgement resulting from bilateral amygdala damage[9] could be attributed, at least in part, to the same mechanism. It is intriguing to consider the possibility that disorders such as autism, which also features impaired fixations to the features of faces[28,29] and impaired processing of emotion from faces[30], might benefit from instructed viewing as we found in SM. □

Methods

Subjects

We tested subject SM, a 38-yr-old woman with bilateral amygdala damage, 30 neurologically normal females of comparable mean age (37.5 yr, s.d. = 3) and 13 neurological subjects with focal, unilateral amygdala damage due to temporal lobectomy (five subjects with right lobectomy (three females, two males) and eight subjects with left lobectomy (three females, five males), with a mean age of 37.4 yr, s.d. = 12). SM participated in all experiments, and control subjects participated as specified below. All subjects had normal or corrected-to-normal visual acuity, normal basic visuoperception (for example, from the Benton facial recognition task) and IQ in the normal range.

Bubbles task

SM, along with ten normal control subjects and all 13 subjects with unilateral amygdala damage, were seated 1 m in front of a 17-inch LCD display in a dimly lit room. Images ($5.72° \times 5.72°$) 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 discrimination task: either a discrimination between fear and happiness, or between male and female. Each block of trials consisted of one discrimination task. Faces were drawn randomly from the four exemplars shown in Supplementary Fig. 1 (see Supplementary Information for construction of stimuli), and sparsely sampled in the two-dimensional image plane and in five spatial frequency bands as described in detail elsewhere[10,11] (see Supplementary Fig. 1). Gaussian bubbles were adjusted to maintain 75% correct discrimination performance for each subject. The emotion discrimination task consisted on average of 2,970 trials (3,072 trials for SM), and the gender task consisted on average of 2,048 trials. These were broken down into multiple sessions, for a cumulative testing time of 6–10 h per subject.

Faces with eyes erased

Twelve normal controls and SM were shown the same faces as in the eye-tracking tasks below, in two blocks separated by approximately 1 h. In the first block the eye region of the faces was replaced with a grey rectangle and in the second block the same faces were shown with the eyes present. Subjects were asked to pick one of the six emotion labels that best matched the stimulus.

Eye-tracking tasks

Eighteen normal control subjects and SM participated in this experiment. One experiment (ten subjects) consisted of five blocks of the conditions listed below, where each condition contained 39 face images from the Ekman data set, identical to those used in other studies[1] (six images of each of the six basic emotions and three neutral images). All stimuli were preceded by a 2 s interstimulus interval consisting of a grey screen isoluminant with the face stimuli, followed by a 1 s central fixation cross, followed by the face image for 5 s. The five blocks were presented in fixed order for all subjects as follows: (1) passive viewing; (2) judging the emotion, where subjects were asked to push one of six buttons corresponding to the emotion labels; (3) judging the gender, where subjects were asked to push one of two buttons; (4) judging the emotion (same as block 2); and (5) passive viewing (same as block 1).

A second experiment was run with SM and eight control subjects, using identical conditions to block 2 above, but with the fixation cross located in a position coincident with either the left or the right eye in each face (two blocks run for each subject).

Eye movements were measured with an infrared pupil-centred corneal-reflection eye tracker (Applied Science Laboratories, Model 504). The criterion for identifying a fixation was that the viewer's gaze drifted by less than 1° within 100 ms.

Data analysis

For the two-alternative discrimination task, we performed multiple linear regression using the gaussian bubble parameters (x and y coordinates specifying the bubble location on the two-dimensional face image, and a third parameter specifying spatial frequency scale) and the subject's accuracy throughout the task. This in effect yielded a three-dimensional regression coefficient volume, which was transformed into a Z-score volume. This Z-score volume was visualized by assigning a threshold at $P < 0.05$.

For the eye-tracking tasks, we drew a box around the eye region of each stimulus (Fig. 2a) and counted the number of fixations made in this region during the entire 5-s presentation of the stimulus. This was then expressed as a proportion of the total number of fixations made on the entire face.

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Correspondence and requests for materials should be addressed to R.A. (radolphs@hss.caltech.edu).

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