

The human amygdala drives reflexive orienting towards facial features

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The human amygdala is reliably activated by facial expressions [1], but the precise functional relevance of such activity change is not well understood, because most previous studies did not allow for separating effects of the emotional expression from the distribution of specific facial features and neglected corresponding attentional processes. Findings on rare patients with bilateral amygdala damage indicate that the amygdala might be involved in triggering shifts of overt attention towards specific facial features such as the eyes [2]. Moreover, it was reported that healthy individuals show a preference for attending to the eye region across different emotional expressions [3]. This early attentional bias was linked to amygdala activity [4], and was found to be most pronounced for fearful faces and less pronounced for happy facial expressions [3,5]. These findings indicate that healthy individuals show a tendency to automatically attend to facial features that are diagnostic of the current emotional state of conspecifics [6]. Here, we examined an otherwise healthy, male adult individual (MW) with unilateral right-sided amygdala loss in a novel, eye-tracking-based face perception task in order to clarify the functional role of the amygdala complex in driving attentional orienting. Compared to a sample of matched controls, MW showed an isolated deficit in reflexive gaze shifts towards diagnostic emotional facial features during brief stimulus presentations as compared to normal performance during longer viewing periods. These results suggest that the amygdala is implicated in quickly detecting diagnostic facial features in the

visual periphery and driving reflexive saccades towards these locations.

The amygdala lesion of MW (Figure 1A) was detected incidentally when he participated in a neuroimaging study. The lesion is very circumscribed and encompasses the whole amygdaloid complex in the right hemisphere, presumably with the exception of marginal cortical parts. Damage to neighboring tissue is negligible and only concerns minor parts of the superior temporal gyrus and the hippocampus proper region. The history of the lesion is unclear, but the radiological assessment led to argue for an impact trauma in early childhood. MW and ten carefully matched controls (Figure S1 and Table S1 in the Supplemental Information) took part in an experimental task that quantifies reflexive and sustained aspects of visual attention during face processing [3]. Angry, fearful, happy, and neutral facial expressions were presented either briefly (150 ms) or for a longer duration (5,000 ms) while measuring eye movements. Faces were unpredictably shifted either downwards or upwards on each trial, such that participants initially fixated either the eye or the mouth region. Thus, attentional aspects of face processing were isolated while controlling for the differential distribution of diagnostic features. This design allowed us to quantify the target of the first saccade after stimulus onset as well as the total dwell time for the eye and the mouth region when stimuli were shown for a longer duration (see Supplemental Experimental Procedures).

As depicted in Figure 1B, control subjects showed a marked tendency to primarily fixate the eye region when faces were shown for a longer duration. Consistent with previous findings [3], however, this bias was less pronounced for happy facial expressions, indicating a preference for fixating facial features that are diagnostic for the current emotional expression [6]. Although MW (diamonds in Figure 1) tended to fixate the eye region longer than controls across all facial expressions, he showed a similar modulation of his gazing pattern by the currently depicted emotional expression.

In a second step, we analysed whether the first saccade after

stimulus onset was directed towards the facial feature that was presented out of fixation. Thus, when the eyes were presented at fixation, we identified the number of downward fixation changes toward the mouth; when the mouth followed the fixation cross, we calculated the corresponding proportion of upward saccades toward the eyes. These numbers were divided by the total number of valid trials in each condition and analyzed separately for short and long viewing durations. Similar to the dwell times, control subjects preferred shifting the current focus of attention towards the eye region, with a markedly reduced bias for happy facial expressions (Figure 1C). Interestingly, MW showed an isolated deficit in attentional orienting for brief stimulus presentations with less than 10% of saccades across all trials (Figure 1C, left), whereas for longer viewing durations, his gazing pattern was highly similar to healthy controls (Figure 1C, right; cf. Figure S2). These results can be explained neither by a slower coding of visual input nor by longer saccadic latencies in MW since he showed similar classification accuracies of emotional expressions and only slightly prolonged saccadic latencies as compared to the control group (Supplemental Information).

For short viewing durations, saccades only occur after stimulus offset and, thus, do not allow for extracting further information from the display. Such gaze changes can be considered reflexive, since they are triggered by the stimulus, and are automatically executed irrespective of whether the stimulus is still present on the screen or not. For longer viewing durations on the contrary, saccades allow for further exploration of the currently shown facial expression and, therefore, share features with voluntary attentional control. MW showed a dissociation between reflexive and sustained aspects of visual attention. This indicates that the functional integrity of the amygdala is crucial for quickly detecting diagnostic facial features in the visual periphery and reflexively shifting attention towards such stimulus elements.

Interestingly, a rare patient with bilateral amygdala damage

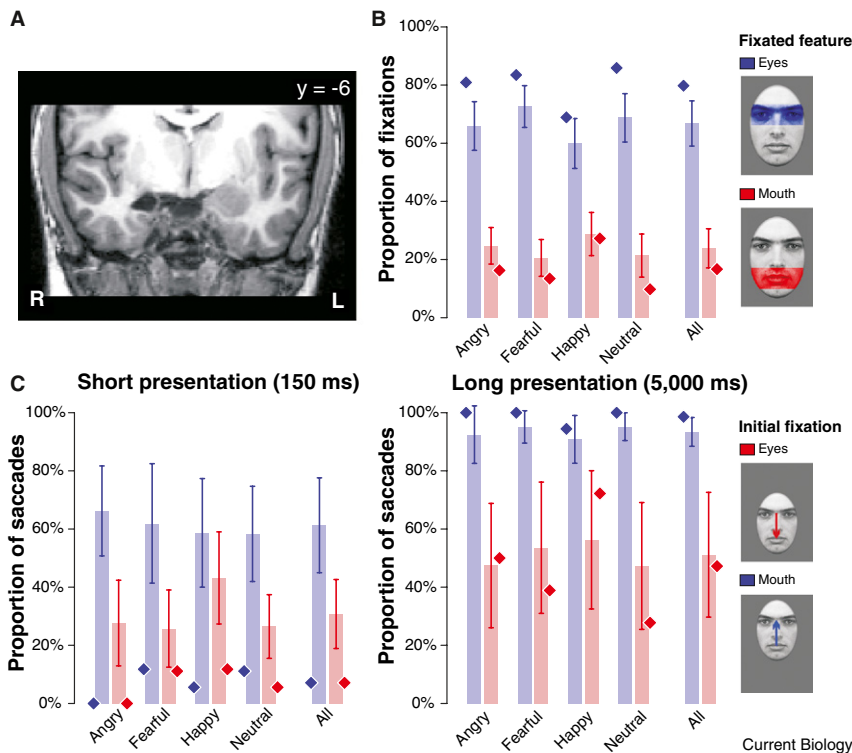


Figure 1. Location of the amygdala lesion of MW and experimental results. (A) The amygdala lesion of MW shown on a coronal slice of a structural MR image at $y = -6$ (MNI coordinates). (B) The relative dwell time on the eye and mouth region compared to the whole face as a function of the emotional expression. (C) The proportion of saccades as a function of the emotional expression and the initial fixation, with data for short presentation times (150 ms) on the left and long stimulus durations (5,000 ms) on the right side. Bars on the right side in B and C show data pooled across emotional expressions. Data for the control subjects (bars) are shown as mean \pm 95% confidence intervals of the mean. Data of MW are depicted as diamonds.

did not show saccades towards the eye region, even when stimuli were presented for longer durations [2], and also failed to show such a pattern during real social interactions [7]. It thus seems possible that the spared left amygdala of MW allowed for a partial compensation of his deficits in early visual attention. The finding that longer stimulus durations were sufficient to normalize the gazing pattern of MW, however, might be taken to suggest an involvement of cortical brain regions [8] in driving attentional orienting during face processing in MW. Especially frontoparietal regions that were frequently shown to mediate stimulus-driven and goal-driven attentional orienting might contribute to ameliorating MW's deficit in reflexive gaze shifting when providing sufficient visual input.

To sum up, our study demonstrates that the amygdala is involved in quickly detecting salient and

diagnostically relevant facial features in the visual periphery and enables attentional orienting towards these locations by driving reflexive eye movements. Future studies are desirable to rule out that damage to neighboring tissue contributed to the current effects and to evaluate whether these results can be generalized to non-social stimuli. Furthermore, patient studies seem interesting since the current data suggest a link between previously reported abnormalities in gazing patterns and dysregulations of the amygdala in certain clinical groups. For example, patients with social anxiety disorders show amygdala hyperexcitability along with abnormal scanning of facial features [9]. Patients with autism spectrum disorders, on the contrary, tend to avoid looking at the eye region of conspecifics and at the same time exhibit reduced amygdala activity [10]. It remains an important challenge for future research to further explore

the potential link between amygdala function and attentional regulation during the processing of social information in clinical groups.

Supplemental Information

Supplemental Information includes experimental procedures, results, two figures and two tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.09.008>.

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