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Amygdala volume and social network size in humans

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We found that amygdala volume correlates with the size and complexity of social networks in adult humans. An exploratory analysis of subcortical structures did not find strong evidence for similar relationships with any other structure, but there were associations between social network variables and cortical thickness in three cortical areas, two of them with amygdala connectivity. These findings indicate that the amygdala is important in social behavior.

For many species, but particularly for primates, living in groups is a major adaptive advantage¹. But living in a social group also presents its own challenges. To get along while getting ahead, it is necessary to learn who is who, who is friend and who is foe. It might be productive to form an alliance with certain group members in one context, but to outmaneuver them in another. The 'social brain hypothesis' suggests that, evolutionarily, living in larger, more complex social groups selected for larger brain regions with a greater capacity for performing relevant computations². On the basis of its central functional role^{3,4} and anatomic position⁵ in the social brain, investigators have proposed that amygdala volume should be related to the size of social groups, in part because the size of a brain region is one indicator of its processing capacity⁶.

Comparative neuroanatomical studies in nonhuman primates strongly support a link between amygdala volume and social network size⁷ and social behavior⁸. Species characterized by larger social groups have a larger corticobasolateral complex within the amygdala. The corticobasolateral complex conjointly expanded with evolutionarily newer cortex and the lateral geniculate nucleus, particularly the layers of the lateral geniculate nucleus that project to the ventral stream visual system⁷. Taken together, these comparative findings suggest that a larger amygdala provides for the increased processing demands required by a complex social life.

In this study we examined whether amygdala volume varies with individual variation in the size and complexity of social groupings within a single primate species, humans. In 58 healthy adults (22 females; mean age M=52.6, s.d. = 21.2, range = 19–83 years) with confirmed absence of DSM-IV Axis I diagnoses and normal performance on cognitive testing, we examined social network size and complexity with two subscales of the Social Network Index (SNI⁹). One SNI subscale (Number of People in Social Network) measures the

total number of regular contacts that a person maintains, reflecting overall network size. A second subscale (Number of Embedded Networks) measured the number of different groups these contacts belong to, reflecting network complexity. Despite the fact that the two social network variables were strongly correlated within the present sample (r = 0.86, P < 0.001), we opted to consider their separate relation to amygdala and hippocampal volumes. (For more details, see **Supplementary Results**.)

To assess amygdala (and, as a control region, hippocampal) volume, we performed quantitative morphometric analysis of T1-weighted MRI data using an automated segmentation and probabilistic region-of-interest (ROI) labeling technique (FreeSurfer, http://surfer.nmr. mgh.harvard.edu/). For methodological details, see **Supplementary Methods**. To adjust for differences in head size, amygdala and hippocampal volumes were divided by total intracranial volume, as performed previously^{10,11}.

Linear regression analyses revealed that individuals with larger and more complex social networks had larger amygdala volumes (**Fig. 1**). These relationships held when controlling for the age of the participant (because older individuals have, on average, smaller amygdala volumes than do younger individuals; **Table 1**). These relationships held when left and right amygdala volumes were analyzed separately (**Table 1**), indicating no lateralization of the effect.

To assess discriminant validity, we performed a linear regression using right and left hippocampal volumes (corrected for total intracranial volume) as independent variables and social network size and complexity as dependent variables while controlling for age (because hippocampal volume typically diminishes with age). For the whole group, these analyses showed no significant relationship

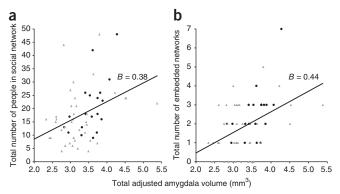


Figure 1 Amygdala volume correlates with social network size and complexity. (a,b) Plot of social network variables (y axis) against total adjusted amygdala volume (x axis). Data points from young participants, black circles; older participants, gray triangles. A line of best fit with standardized regression coefficients (B) is also displayed for the entire sample.

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Table 1 Linear regressions using amygdala and hippocampal volumes as independent variables and social network characteristics as dependent variables

	Amygdala		Hippocampus	
	Left	Right	Left	Right
Whole group (n = 58)		· ·		_
Social network size	0.38, 2.84 (0.006)	0.29, 2.15 (0.036)	0.23, 1.66 (0.103)	0.10, 0.72 (0.472)
Social network complexity	0.39, 3.13 (0.003)	0.30, 2.32 (0.024)	0.25, 1.89 (0.064)	0.15, 1.08 (0.286)
Young group $(n = 19)$				
Social network size	0.58, 2.96 (0.009)	0.54, 2.61 (0.018)	0.22, 0.94 (0.359)	-0.07, -0.27 (0.792)
Social network complexity	0.56, 2.81 (0.012)	0.57, 2.85 (0.011)	0.22, 0.94 (0.360)	-0.11, -0.45 (0.656)
Older group $(n = 35)$				
Social network size	0.32, 2.05 (0.048)	0.24, 1.52 (0.138)	0.27, 1.68 (0.102)	0.18, 1.11 (0.274)
Social network complexity	0.38, 2.50 (0.017)	0.28, 1.76 (0.086)	0.32, 2.06 (0.047)	0.27, 1.69 (0.099)
Males (n = 36)				
Social network size	0.31, 1.87 (0.07)	0.18, 1.06 (0.298)	0.19, 1.15 (0.259)	0.07, 0.38 (0.706)
Social network complexity	0.43, 2.79 (0.009)	0.27, 1.60 (0.118)	0.35, 2.19 (0.036)	0.22, 1.23 (0.203)
Females (n = 22)				
Social network size	0.52, 2.72 (0.013)	0.62, 3.53 (0.002)	0.20, 0.92 (0.367)	0.22, 1.00 (0.329)
Social network complexity	0.45, 2.27 (0.034)	0.60, 3.39 (0.003)	0.14, 0.64 (0.529)	0.20, 0.91 (0.372)

The table displays standardized regression coefficients (*B*), *t* values and *P* values (two-tailed, in parentheses). Results with *P* values < 0.05 are shown in bold. Volumes used were corrected for total intracranial volume. For the whole-group analysis, we controlled for age.

between hippocampal volume and either of the social network variables (**Table 1**). For the young and older subgroups, linear regressions showed a significant relationship only for older participants between left hippocampal volume and social network complexity (**Table 1**). Because hippocampal and amygdala volumes were themselves strongly correlated (left: r = 0.831, P < 0.001; right: r = 0.727, P < 0.001; combined: r = 0.815, P < 0.001), we conducted hierarchical linear regressions using amygdala and hippocampal volumes (corrected for total intracranial volume) as independent variables and social network characteristics as dependent variables. Increased amygdala volume remained significant when controlling for hippocampal volume (**Supplementary Table 1**).

To further investigate the specificity of the relationship between amygdala volume and social network characteristics, we conducted an exploratory analysis assessing the relationship between social network variables and all other subcortical volumes segmented by FreeSurfer. Linear regressions revealed that none of the other subcortical regions significantly correlated with either social network variable when controlling for age and correcting for multiple comparisons. (For more details, see **Supplementary Methods** and **Supplementary Results**.) Also supporting the discriminant validity of our primary finding, we found that amygdala volume did not relate to other measures of social functioning such as perceived social support 12,13 and life satisfaction 14 . (r values ranged from -0.26 to 0.27, P < 0.15 to P < 0.98; for more details about these measures, see **Supplementary Methods**.)

Finally, to explore the association between social network variables and cortical thickness throughout the cerebral cortex, we conducted a whole brain surface–based analysis (see **Supplementary Methods**); this analysis did not include subcortical structures (such as the amygdala). In the first fully corrected test, we found no regions that were correlated with the social network variables at conventional levels of statistical significance. In the second, more exploratory analysis, with a more lenient threshold (P < 0.01, uncorrected for multiple comparisons) we found that social network variables correlated significantly with the caudal inferior temporal sulcus, caudal superior frontal gyrus and subgenual anterior cingulate cortex. Separate analyses of young and older participants showed very consistent findings, supporting the reliability of these observations (for more details, see **Supplementary Results, Supplementary Fig. 1** and **Supplementary Tables 2** and 3).

To our knowledge, these findings demonstrate the first link between amygdala volume and social network characteristics within a single species. Although our findings do not test an evolutionary hypothesis specifically, they, along with cross-species studies in nonhuman primates^{7,15}, are consistent with the hypothesis that the primate amygdala evolved, in part, under the pressures of increasingly complex social life (for more details, see Supplementary Discussion). In addition, that individuals with larger subgenual anterior cingulate cortex and caudal inferior temporal sulcus volumes also reported larger and more complex social networks supports the hypothesis that the amygdala expanded in conjunction with some other brain regions to which it is densely connected⁷. The correlation found for the caudal superior frontal gyrus requires further investigation. Results from the exploratory analysis should be taken

as preliminary findings that could guide future work aimed at examining the distributed network of brain regions that might support social network size and complexity.

Humans are inherently social animals. We play, work, eat and fight with one another. A larger amygdala might enable us to more effectively identify, learn about and recognize socioemotional cues in conspecifics³, allowing us to develop complex strategies to cooperate and compete¹.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

C.I.W. and L.F.B. designed the study. R.J.D. and L.F.B. performed the research. K.C.B., R.J.D., B.C.D. and L.F.B. analyzed the data. K.C.B., B.C.D., C.I.W. and L.F.B. wrote the manuscript. B.C.D., C.I.W. and L.F.B. contributed to grant funding.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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