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The amygdala: is it an essential component of the neural network for social cognition?

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Abstract

Observations from human subjects with focal brain lesions and animal subjects with experimental lesions have implicated a variety of brain regions in the mediation of social behavior. Previous studies carried out in the macaque monkey found that lesions of the amygdala not only decrease emotional reactivity but also disrupt normal social interactions. We have re-investigated the relationship between amygdala lesions and social behavior in cohorts of mature and neonatal rhesus monkeys who were prepared with selective and complete bilateral ibotenic acid lesions of the amygdaloid complex. These animals display clear alterations in emotional and social behavior. We interpret these changes as due to a loss of the ability to evaluate environmental stimuli as potential threats. However, adult animals with bilateral lesions of the amygdala demonstrate normal, and even increased, social interactions with conspecifics. Moreover, neonatal animals, prepared with amygdala lesions at 2 weeks of age, also demonstrate species typical social behaviors such as the generation of facial expressions, grooming and play behavior. These results argue against the idea that the amygdala is essential for the interpretation of social communication or for the expression of social behavior. Because it does appear to participate in the evaluation of the "safety" of social interactions, we believe that it does have a role in modulating the amount of social behavior in which an organism will participate. However, our current answer to the question posed in the title of this paper is no!
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It has been known for more than a century that damage to the temporal lobe in non-human primates is associated with dramatic changes in socioemotional behavior [3]. Macaque monkeys with these lesions typically are more tame, demonstrate abnormal food preferences and have alterations of sexual behavior [11,12]. Subsequent studies with more selective lesions provided evidence that damage restricted to the region of the amygdala can produce most of these changes in behavior [1,18].

One of the earliest studies explicitly designed to evaluate changes in social behavior in macaque monkeys following amygdala damage was carried out by Rosvold et al. [15]. They established artificial social groups of male rhesus monkeys and studied the dominance hierarchy that emerged. They then carried out two-stage bilateral destructive lesions of the amygdala of the most dominant animals and studied the dominance hierarchy as the group reorganized. The common finding was that the lesion led to a decrease in social dominance with the lesioned animal typically falling to the most subordinate position of the group.

A more extensive group of studies was carried out by Kling and coworkers in a variety of primate species in both captive and free ranging environments [6–10]. In a classic study, Dicks et al. [4] retrieved rhesus monkeys from social troops on the island of Cayo Santiago. These animals were subjected to bilateral amygdalectomy and then returned to their social groups. While it was difficult to follow the minute-to-minute interactions of the lesioned animals, the typical finding was that they were invariably ostracized and would often perish without the support of the social group.

From the results of these and similar studies carried out by several laboratories, Brothers [2] formalized the view that the amygdala is one of a small group of brain regions that form the neural substrate for social cognition. This

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view predicts that the amygdala is essential for certain aspects of the interpretation and production of normal social gestures such as facial expressions, body postures, etc. It also predicts that damage to the amygdala would invariably lead to a decrease in the amount, or quality of, conspecific social interactions.

While the evidence in favor of a prominent role for the amygdala in social function is substantial, there are also a number of problems with the way in which many of the earlier non-human primate studies were conducted. Virtually, all of the lesion studies involved destructive lesions of the amygdala that not only damaged cells within the amygdala itself, but also damaged fibers that travel through and around the amygdala from other brain regions. Many of the lesions also directly involved surrounding brain regions. Some of the lesions in the study by Rosvold et al. [15], for example, heavily involved the temporal polar cortex. Another problem is that most of the studies of post-surgical alterations in social behavior were qualitative or anecdotal. It was rare that a full array of primate interactions was evaluated and even rarer that the frequency or duration of behaviors was quantified. In some cases, lack of social interaction could be explained due to reasons other than the brain damage. For example, in the matrilineal social system of macaque monkeys, young, male monkeys often emigrate from their natal troops to other troops. This has the obvious merit of maintaining genetic diversity in the population. If a male who emigrates attempts to return to its natal troop, however, it is typically rebuffed. Therefore, it is not clear in some of the naturalistic studies whether the amygdala lesioned animals were ostracized due to the effects of the lesion or because the troop had interpreted that the animal was an émigré.

We have re-investigated the contribution of the macaque monkey amygdala to social behavior using a more controlled and quantitative approach both to the production of the lesions and to the subsequent behavioral observations. A complete account of the effects of amygdala lesions on dyadic social interactions in the mature macaque monkey has been published recently [5]. A preliminary report on the effects of neonatal amygdala lesions on the emergence of social behavior has also been published [14]. In the remainder of this article, we will briefly summarize the major findings of these studies and then comment on the implications of these findings for considering the amygdala an essential component of the network for social cognition.

Male rhesus monkeys with bilateral ibotenic acid lesions of the amygdala, and age- and sex-matched control monkeys were observed during a variety of social encounters. All monkeys were born and raised in different outdoor cages and had comparable ranks in their respective dominance hierarchies. The neurotoxic lesion technique has the merit of removing the neurons of the amygdala while sparing fibers that pass through it. Fig. 1 illustrates the near complete loss of neurons in the amygdala at a mid rostrocaudal level in one of the subject animals.

We will summarize below some of the data from dyadic interactions in which the amygdala lesioned animals and age-, sex- and dominance-matched control animals interacted with “stimulus monkeys” (two males and two females). A variety of both affiliative (groom, present sex, etc.) and agonistic (aggression, displace, etc.) behaviors were quantitatively recorded using the Observer program (Noldus) while animals interacted in a large (18 ft × 7 ft × 6.5 ft—shown in Fig. 2) chain link enclosure. Each experimental animal interacted with each stimulus animal for 6 and 20 min periods

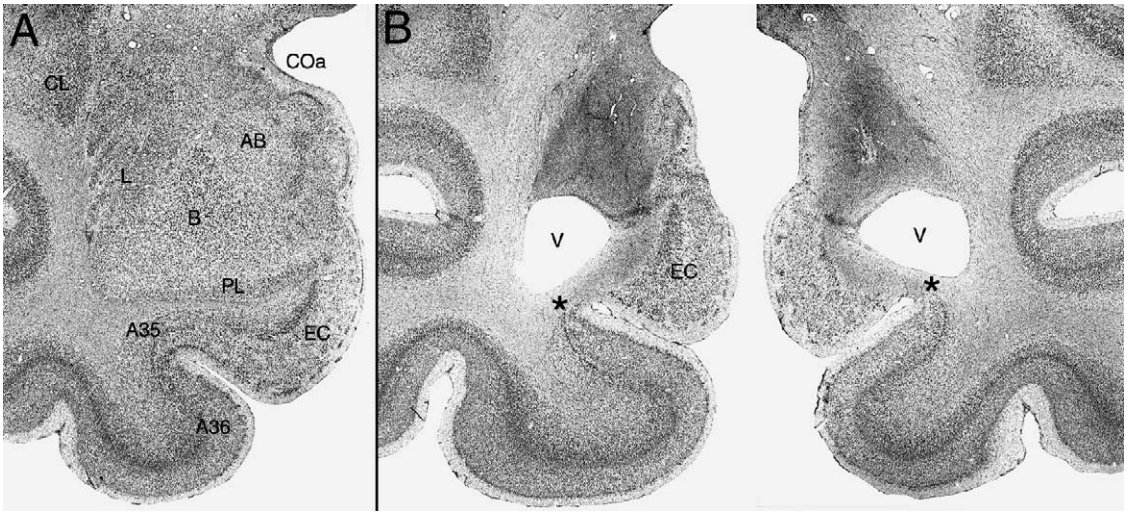

Fig. 1. Photomicrographs of Nissl-stained coronal sections through a mid rostral caudal level of the macaque monkey amygdala. Panel (A) shows the left side in a control brain and panel (B) shows the left and right sides in one of the animals that had received a bilateral ibotenic acid lesion of the amygdala. The amygdala in the lesioned animals has shrunken substantially, shows few viable neurons, and the subjacent ventricle has expanded. Abbreviations: A35, A36, areas 35 and 36 of the perirhinal cortex; AB, accessory basal nucleus; B, basal nucleus; CL, claustrum; COa, anterior cortical nucleus; EC, entorhinal cortex; L, lateral nucleus, PL, paralaminar nucleus; V, ventricle; asterisk marks minor damage of area 35 of the perirhinal cortex in the lesioned brain.

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