The squirrel monkey as a model in the study of the central control of vocalization

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Abstract

In the squirrel monkey (*Saimiri sciureus*), the electrical activity of single neurones was compared in the periaqueductal grey of the midbrain and the reticular formation of the medulla oblongata during vocalization, using a recently developed telemetric technique. The results show that both structures contain neurones with vocalization-correlated activity. There are characteristic differences between the two structures, however. Neurones showing changes in discharge rate with changes in fundamental frequency were only found in the reticular formation, whereas neurones firing immediately before vocalization, but not during vocalization, were almost exclusively found in the periaqueductal grey. It is concluded that the reticular formation is involved in vocal motor coordination, while the periaqueductal grey mainly serves gating functions.

**Keywords**: Neurobiology; Phonation control; Telemetry; Vocal pattern generation; Squirrel monkey

1. Introduction

The squirrel monkey (*Saimiri sciureus*) is a small New World primate that, due to its rich vocal repertoire, its membership in the primate order, and its handy size, has become the most extensively investigated species in studies on the central nervous control of vocalization. Specifically, the squirrel monkey’s vocal range reaches from pulsed, purring-like sounds with a fundamental frequency of 40 Hz to high-pitched, peep-like sounds with a fundamental of 16,000 Hz, thus encompassing more than eight octaves. The repertoire contains harmonically structured as well as noisy calls, constant-frequency and frequency-modulated calls, calls with...
a rather constant amplitude course and calls with marked amplitude modulations, single syllable calls as well as calls consisting of rhythmic repetitions of specific elements. The brain of the squirrel monkey, despite a weight of only 26 g, resembles the human brain to a much higher degree than that of the cat or rat. This makes it possible to homologize specific brain areas between man and squirrel monkey in a very differentiated way. Finally, the small body weight of only 600-1200 g makes handling of squirrel monkeys, and thus experimentation, much easier than in macaques with a body weight of several kg.

2. Methods

In order to find out which brain areas are involved in the central control of phonation, we use the method of extracellular recording with microelectrodes. By this technique, the electrical activity of single neurones is registered in various brain regions during vocalization. The advantage of this method over other methods, such as the functional magnetic resonance imaging technique, positron emission tomography, electroencephalography or magnetoencephalography is that it combines high spatial resolution with high time resolution. The main drawback of the technique is its invasive character which precludes its systematic use in humans.

Until recently, it was only possible to record single-cell activity in monkeys restrained in a chair. In these experiments, the head was fixed and the neuronal activity was transmitted via cables to the recording equipment. In this artificial situation, it was a serious problem to make the animal produce large numbers of vocalization. In the last years, we succeeded in developing a telemetric technique which now allows us to record single-cell activity in freely moving animals within their social group [2]. In this situation, animals vocalize a lot and collection of vocal data is no more a problem. The animals have a platform implanted on the skull in a stereotactic operation. On the platform, custom-made microdrives are fixed by which the microelectrodes can be lowered into the brain. There is a dual-channel amplifier and transmitter on the platform. One channel is used to transmit the neuronal activity to a receiver outside of the animal room. The other channel receives its input from a piezo-ceramic element fixed to the platform. This element registers the skull vibrations taking place during vocalization. By comparing the output of the skull vibration sensor with that of the room microphone, it is possible to decide whether a given vocalization stems from the experimental animal or its group mates.
3. Results

Our single-cell recordings concentrated on two structures, both of which have been proposed by several authors to be involved in vocal motor coordination [3-6]: one is the periaqueductal grey of the midbrain and the other is the reticular formation of the medulla oblongata. Altogether, 483 neurones were recorded from these structures. The results show that both structures contain neurones with vocalization-related activity changes. The characteristics of the activity changes, however, differ between the two structures. While the majority of the vocalization-related reticular neurones (91%) were active during vocalization, starting either somewhat before or at vocalization onset, the majority of the periaqueductal neurones (58%) showed an increased activity immediately before vocalization onset, but not during vocalization. Such an exclusive pre-onset activity occurred in only 6.6% of the reticular vocalization-related cells. Out of the altogether 224 neurones in the periaqueductal grey and reticular formation that were active during vocalization, 83 showed a change in discharge rate with changing fundamental frequency. All 83 neurones were located in the reticular formation; none of the periaqueductal neurones showed a correlation with fundamental frequency modulation. On the other hand, a cell type was found in the periaqueductal grey that could not be found in the reticular formation. This cell type reacted to vocalizations uttered by other animals; the reaction, however, only occurred if the vocalizations were responded to by the experimental animal. That is, if the experimental animal heard vocalizations of group mates, but did not react vocally to them, no activity occurred. If vocalizations were heard and responded to, periaqueductal neurones fired throughout the interval between perceived vocalization and produced vocal response. In other words, the neurones behaved like an audio-vocal interface.

4. Discussion

The finding that there are neurones in the reticular formation showing a vocalization-correlated activity which directly reflects changes in fundamental frequency suggests that the reticular formation is involved in vocal motor coordination. This suggestion is supported by observations coming from electrical brain stimulation, lesioning and anatomical studies. Electrical brain stimulation experiments in the squirrel monkey have shown that there are numerous sites in the reticular formation of the lower brainstem yielding vocalization when electrically stimulated [7]. These vocalizations, in contrast to those elicitable from the fore-
brain and midbrain, do not sound like natural species-specific calls, but exhibit an abnormal acoustic structure. This abnormal structure can be interpreted as due to direct interference of the artificial pulse pattern forced upon the vocal pattern-generator activity by the electrical stimulation. Lesioning studies in the squirrel monkey have revealed that small lesions in the reticular formation can cause dysphonia [8]. Anatomical studies, furthermore, have shown that large parts of the reticular formation have direct connections with the motoneurones innervating the laryngeal muscles, jaw, lip and tongue muscles as well as with pre-motor neurones controlling the expiratory muscles [9, 10].

With respect to the periaqueductal grey, our recording results suggest that this structure is not involved in vocal motor coordination in a strict sense, that is, in the integration of vocal fold movements, expiration and supralaryngeal (articulatory) movements. Its function rather seems to be that of a gating mechanism, coupling sensory and motivation-processing structures with the vocal motor-coordinating mechanisms in the reticular formation. This interpretation is supported again by electrical brain stimulation, lesioning and anatomical studies. Electrical stimulation of the periaqueductal grey produces natural species-specific vocalizations in all species tested until now [for a review, see 11]. The fact that the vocalizations do not bear an artificial character suggests that the vocalizations are elicited from a level above that of motor coordination. If the periaqueductual grey, together with the laterally bordering tegmentum, is destroyed, mutism emerges [11]. This does not only hold for animals, but also for humans [12]. Anatomical studies, finally, show that the periaqueductal grey projects into that part of the reticular formation which is connected with the laryngeal and articulatory motoneurones as well as the expiratory pre-motor neurones [13].

References


