Audio-Visual Targeting Reaction after Unilateral Lesions of the Superior Colliculus in Cats

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Key words: superior colliculus and orienting, lesions, audio-visual targeting

Abstract. Cats were trained to visually localize one of eight loudspeakers distributed in different spatial locations. The animals localized the activated sound source through a directed movement of ears, eyes and head towards it. The number of correct targeting reactions triggered by a tone stimulus from different spatial positions was strongly impaired in the operated animals in comparison to controls. The number of correct responses was higher when the tone stimulus was presented from the side of the lesion. The role of the superior colliculus in the integration of audio-visual targeting reaction is discussed.

Introduction

The role of the superior colliculus (SC) in visually guided behavior has been well established in several mammal species (11, 29, 30, 34, 40). Many authors were able to show that after its removal, different types of visuomotor behavior are impaired (2, 7, 15, 17, 18, 39). The effect of the SC lesion is stronger when the task requires visual spatial localization and orientation (3, 20, 23, 44). In animals with unilateral lesions the deficits are restricted mainly to the opposite half of the hemifield (34). Electrophysiological data have shown that the SC is spatio-topically organized, as demonstrated by stimulation and by single cell recording (5, 10, 27, 37). An electrical stimulation of this structure induces coordinated movements of pinna, eyes and head (9, 14, 28, 29, 38,
41). Visual and auditory space are behaviorally integrated and probably this integration has a neural basis in the functional organization of the SC. It is interesting to note that a loss of orientation ability not only to visual but also to other stimuli modalities has been demonstrated. Schneider (31) and Sprague and Meikle (34) described a decrease of reactivity to auditory and somatosensory stimuli after SC lesions. The evidence of spatially ordered auditory and auditory-visual neurons in the SC and anatomical connections with some parts of the auditory system (12, 22, 36) led us to assume that the SC may also be involved in auditory induced orienting movements. The present work is devoted to studying the effect of unilateral lesions of the SC on the ability of the animals to visually target tone-sources placed in different spatial locations.

METHODS

The experiments were carried out at approximately the same hour male cats, weighing about 3 kg. The experimental group consisted of 5 operated cats and the control group of 10 normal cats. The operated animals were kept in individual cages until the fifth day after operation. Then they lived as did the normal cats, in groups of 5 animals in big home cages. All cats were food deprived during 23 h. They received food (meat) only during the experimental sessions. Water was available ad libitum.

Surgery. Operations were performed under nembutal anesthesia (40 mg/kg i. p.). Unilateral lesions were produced by direct current (10 mA, 10 s) passed through a tungsten electrode, isolated except for a 1 mm tip and stereotaxically guided. The coordinates were taken from the stereotaxic atlas of Snider and Niemer (32). In two cats the right SC and in three cats the left SC were coagulated. After the operation antibiotics were administered.

Postoperative testing and training procedure. Starting from the second postoperative day the visual placing reaction, spontaneous behavior in the home cage, reactivity to auditory, visual and somatosensory stimuli, food intake and pupillary reflex were observed. The weight was controlled daily. Six days after the operation the animals were submitted to training during 30 daily sessions in the experimental box. The experiments were carried out at approximately the same hour of the day in a cage (80 × 80 × 80 cm). Eight loudspeakers placed in the corners of the cage were used to stimulate the animal. The acoustic stimulus was a tone of 1000 Hz with a duration of 500 ms, 80 dB intensity and with an inter-stimulus interval of about 1 min. The tone was
administered at random, 16 times per session when the cat was sitting in the middle of the cage in a straight ahead position. In relation to this position four loudspeakers were placed in front of the cat and four behind it. The cat had to target visually the activated loudspeaker by a goal directed movement. A response was considered correct only when the cat targeted the activated loudspeaker at the first attempt. To prevent habituation each correct response was rewarded by a piece of meat (conditioned audio-visual targeting reaction). The results were statistically analysed with the t-test for independent or dependent samples.

**Histology.** When testing had been completed the cats with collicular lesions were anesthetized again and perfused through the heart with saline, followed by 10% formaline. The brains were removed. The tissue containing the lesion was blocked and embedded in paraffin. 60 μm sections were cut and stained with eosine.

**RESULTS**

**General postoperative behavior.** Post-operative behavior was not strongly disturbed. Changes in daily food and water intake were not observed. The visual placing reaction was normal in all cats except in cat No. 1 in which it became normal six days after the operation. The pupillary reflex was present in all five cats. Only in one cat (No. 3) a slight mydriasis contralateral to the lesion could be observed during the first three days after the operation.

The following behavioral changes were observed in the home cage. Targeting reactions elicited by different auditory stimuli were directed mainly to the side of the lesion independently of the sound source position. Visual stimuli in the hemifield contralateral to the lesion were often neglected. Movements of both pinnas during mechanical stimulation could be elicited, but during spontaneous or orienting behavior the pinna ipsilateral to the lesion was used more intensively. Hyperactivity or other functional alterations of movements were not observed.

**Comparison of the ability to target sound sources between normal and operated cats.** In both groups — operated and control — each tone stimulation induced an orienting movement. Differences between both groups were obvious in the ability to target the sound source. The targeting reactions of the operated animals were often not directed to the activated loudspeaker, whereas the control group reached the performance level of 80% of correct reactions (Fig. 1). The number of correct targeting reactions of the operated group was significantly impaired in comparison with the controls \((t = 12.56, P < 0.001)\). Besides, the operat-
ed animals presented some other behavioral peculiarities in the localization of the sound source.

Comparison of the ability to target ipsilaterally and contralaterally placed sound source, in operated and normal cats. The control group did not show significant differences in the localization ability between the left and the right sides. The experimental group, on the contrary, presented an asymmetry in the localization ability (Fig. 2). The number of correct responses was significantly higher when the tone-stimulus was presented from the side of the lesion ($t = 4.33, P < 0.01$).

![Fig. 1. Percentage of correct audio-visual targeting reactions in the operated and control groups.](image1)

![Fig. 2. Percentage of correct audio-visual targeting reactions in the experimental group (unilateral lesion of SC) to sound sources placed ipsilaterally and contralaterally to the lesioned side.](image2)
the tone was produced by loudspeakers placed on the contralateral side a targeting reaction was also elicited, but it was mostly directed to the ipsilateral, “wrong” side. Sometimes it was observed that after contralateral posterior tone stimulation the cat turned over 180° through the ipsilateral, “wrong”, side and correctly localized the sound source. Independently of the stimulated side, the response of the pinna ipsilateral to the lesion was more intense than the contralateral one.

**Upwards and downwards localization ability: comparison between operated and normal cats.** The control group did not exhibit any significant difference in the localization of upper and lower loudspeakers. In the operated group a clear up-down asymmetry, although without statistical significance, was observed. Lesioned cats localized the lower placed sound sources better than the upper ones. Only one cat (No. 2) preferred the upper sources. No correlation between the placement and the extent of lesions and these behavioral differences was found.

**Localization ability inside and outside the visual field: comparison between normal and operated cats.** The cats of both groups — operated and control — showed significantly more correct targeting reactions to sound sources placed in front of the animals in contrast to those placed behind them ($t = 3.13$, $P < 0.01$ in controls; $t = 11.67$, $P < 0.01$ in operated). Figure 3 illustrates this difference in the lesioned cats. These differences in performance were stronger for the operated group, as shown by comparing the number of correct responses to the frontally placed loudspeakers between both groups ($t = 12.66$, $P < 0.001$) and by comparing correct responses to the rear loudspeakers ($t = 11.19$, $P < 0.001$).

![Figure 3](image-url)

Fig. 3. Percentage of correct audio-visual targeting reaction in the experimental group (unilateral lesion of SC) to sound sources placed inside the visual field (anterior loudspeakers) and outside the visual field (posterior loudspeakers).
Simplification of the test for operated animals. Control experiments were performed with the operated cats. Their ability to target was tested using only two sound sources instead of eight. If the sources were placed within the visual field ipsilateral to the lesioned colliculus, the animals reached 80% correct responses in 2–3 sessions. But if the sound sources were placed on the contralateral side, the animals were unable to show any increase in the number of correct responses. Depending on the cat, after a certain number of sessions (5 to 10) the animals changed their behavior, either they did not respond to the tone stimulus during the experiment or they exhibited some signs of neurotic behavior.

Anatomical results (Fig. 4). The lesions in all cats were very similar in size, which ranged between 23% (Cat 1) and 28% (Cat 2) of the SC’s tissue. All lesions involved the superficial, intermediate and deep collicular layers. The lesion was placed in the medial zone of the SC leaving the lateral part undamaged. Cats 3 and 4 showed an extension of the lesion into the underlying periaqueductal gray. The lesion of cat 4 was shifted 1–2 mm posteriorly in relation to the other animals.
DISCUSSION

Unilateral lesions of the superior colliculus produced a deficit in the ability to localize stationary sound sources. This deficit concerned the sources placed contralaterally to the operated side more than those placed ipsilaterally, and the ones outside the visual field more than those inside it. These results seem to support the hypothesis that not only visually but also acoustically induced targeting reactions are based on the functional integrity of SC. To explain these deficits a number of causal possibilities can be invoked: visual or/and acoustic perceptual deficit, motor disturbances or a deficit in the integration of perceptual and motor functions of the brain.

The analysis of the animals' behavior does not seem to speak in favor of a specific deficit of auditory nature. Auditory stimuli were perceived and followed by a targeting reaction. As shown in our results, only the correct localization in space is influenced by SC lesions.

The observations in the lesioned cat do not indicate a specific deficit in visual perception either. The cats were able to follow a moving visual object, the visual placing reaction was present and they moved quite normally in their home cage. The deprivation of visual information in normal cats caused strong alterations in spontaneous behavior and in their ability to target sound sources in space by an audio-visual targeting reaction (6).

The size of the collicular lesion seems to be important because it can cause not only visual deficits, but also some peculiar motor phenomena. Lesions involving more than 85% of the structure, including the underlying tegmentum, produced very strong behavioral disturbances such as spontaneous compulsive ipsiversive circling (45). Smaller lesions without tegmental involvement did not produce such motor alterations. Masterton and Thompson (19) have found alterations of head movements to contralateral visual stimuli, but not to contralateral auditory stimuli. In the present work ipsiversive circling was not found, and the discrepancies with Masterton and Thompson (19) may probably be explained by the location and size of the lesion.

The integration of sensory and motor functions could be taken as an explanatory basis to understand the results of this work. The most striking effect of the unilateral lesion of the SC was the production of a deficit in the integration of spatial auditory cues with the goal directed motor output. The animals showed a deficit in the anterior-posterior, contralateral and up-down localization of the sound sources. Some authors describe a deficit in discrimination learning after SC lesions.
Spatial factors may be of great importance in visual discrimination learning (1, 35). Therefore it cannot be excluded that orientation or attention deficits are responsible for impaired discrimination learning after SC lesions. Milner et al. (20) in rats and Butter et al. (3) in monkeys, showed that learning is decreased only in those cases when a spatially directed orienting reaction is necessary. The experimental situation here discussed can be described as a spatial-auditory test with a visual goal-directed movement. It is well known that a motor pattern similar to that of the audio-visual targeting reaction has been elicited by direct electrical stimulation of the SC, the direction of movement being contralateral to the stimulated colliculus (38, 41, 29). Even more, there is experimental evidence (14, 29, 38) demonstrating that the direction of the electrically elicited orienting movements is determined by the position of the electrode in the tectum. Recently Stein and Claman (38) have described a topographical representation of the pinna movement in the intermediate and deep collicular layers. The pinna movements, as Siegmund and Santibáñez-H. (33) pointed out, play an important role in the audio-visual targeting reflex in cats. Anatomical studies have demonstrated that the SC has efferent connections reaching the facial nucleus (8, 13). In our experiments the operated cats used the pinna ipsilateral to the lesioned colliculus more than the contralateral one, regardless of the laterality of the activated sound source. The SC is a structure rich in efferent connections (8, 16), some of them belonging to the acoustic modality. The external and pericentral nuclei of the inferior colliculus, the nucleus of the trapezoid body, the dorsomedial periolivary nucleus, the nucleus of the lateral lemniscus and part of the auditory cortex (4, 25, 42) send fibers to the SC. Some of these structures are involved in the identification of the laterality of the sound (24).

On the other hand, the observations of different authors (5, 10) have provided evidence that the SC is able to integrate multimodal sensory inputs reflecting their spatial distribution. It has been shown that auditory and visual receptive fields of bimodal neurons in the deep layers of SC are roughly superimposed in space (in the contralateral hemifield). Other types of neurons are related to the eye movements and some are able to fire in complete darkness and before eye movements, as has been described in monkeys (21). The multimodal neurons could be responsible for the integration of audio-visual space and the motor neurons can be triggered by these multimodal neurons independently of the activating sensory modality.

The results of our work can be interpreted as a consequence of the disturbance of the multimodal spatial representation in the SC.
REFERENCES

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Accepted 1 September 1982