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ORIGINAL PAPER

Effects of superior colliculus ablation on the air-righting reflex in the rat

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Abstract To examine how the superior colliculus, the motor center of orientation and avoidance, could interact with postural reflexes, we investigated effects of unilateral and bilateral ablations on air-righting reflex movements in otherwise intact rats. Superior colliculus ablations variously modified righting movements: After falling from the supine position, the rats sometimes showed dorsiflexion instead of normal ventriflexion; the motor sequence of rotation from the fore- to the hindquarter was often modified to simultaneous rotation; lateral turn from supine to prone position was occasionally insufficient; body direction that was normally kept constant during falling was often changed; final posture sometimes deviated from the horizontal position. The first three abnormalities occurred almost twice in frequency as lesions increased from unilateral to bilateral ablation, and in unilaterally ablated rats, did so in righting contraversive to the lesions. Multiple influences of tectoreticular input to the air-righting reflex center are discussed.

Keywords Tectoreticulospinal pathway · Superior colliculus · Midbrain · Righting reflex

Introduction

When a rat was dropped from the supine position, it turned its head and body from the supine to prone position in the air, and took a posture for quadrupedal standing; this is called the air-righting reflex [1–6]. Previously we reported that even though midbrain rats could perform the air-righting reflex well, animals decerebrated at a higher level (striatal rats) exhibited an abnormal reflex action, which looked like freezing of on-going righting movements [5]. Freezing-like deterioration might be interpreted as an inhibitory projection to the reflex center, which presumably resides in the brain stem [1, 7]. It could be supposed that the basal ganglia, which had been released from cortical control by decortication, sent excessive inhibitory signals to the lower center, as in the case of Parkinson's disease [8, 9].

Among descending targets of the basal ganglia [10–13], one of the candidates is the superior colliculus, which has been known to be a center of orientation [12, 14–18] and avoidance [19–21] movements. Orienting and avoidance movements in relation to a target usually induce a postural change, which might evoke postural reflexes, but if it is evoked, the intended action could be disturbed. Therefore, a postural reflex, e.g., the vestibulo-ocular reflex, can be suppressed during such purposive movements, even though phasically, e.g., [22]. We hypothesized that the superior colliculus mediates inhibitory, descending influences from the basal ganglia on the air-righting reflex.

However, little is known about how the superior colliculus controls the motor center of the air-righting reflex. Pellis et al. [23] examined effects of superior colliculus ablation on the rat air-righting reflex. They observed that visual modulation of the air-righting reflex in which latency and movement duration were shortened by lowering the height from which the animals were dropped was not abolished by visual cortex lesions, but was abolished by superior colliculus ablation. As discussed by Pellis et al. [23], visual input seems to affect such parameters relating

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to excitation level rather than motor elements consisting of air-righting reflex. Accordingly, Pelli's et al. [23] reported sluggishness of air-righting movements in some rats with a lesion of the the superior colliculus. Nevertheless, superior colliculus ablation necessarily destroys descending tectal output, such as tectoreticulospinal or tectospinal pathways. Removal of descending output can change motor control of the head; it could affect the air-righting movement. However, details about movement disorder are not known. The present study investigated motor effects of superior colliculus ablation on the air-righting reflex in the rat. The ablation effects were so mild that freezing of the air-righting reflex in striatal rats may be evoked by extra pathways outside the superior colliculus.

Subjects and methods

A total of 14 adult male Wistar rats were used for the experiment under Yamagata University Commitee of Animal Experiments guidlelines. Under deep anesthesia (Nembutal, initial dose of 50 mg/kg i.p., supplemented with 10 mg/kg if necessary), rats were fixed in a stereotaxic frame and underwent a craniotomy to expose the dorsal surface of the superior colliculus by sucking overlaid structures, including the posterior cerebral cortex and the dorsal hippocampus. Under visual inspection, the superior colliculus was aspirated with a needle (2-mm outer diameter) connected to a vacuum pump. In one animal, an electrical lesion was made by passing a DC current (500 μA) through an enamel-coated, stainless steel electrode, which was positioned at every 0.5-mm point (mediolaterally, rostro-caudally, and dorso-ventrally) covering the whole superior colliculus region. Collicular ablations were given either unilaterally ($N = 5$) or bilaterally ($N = 4$; one of them was electrically ablated). Special care was taken that the lesions did not extend to the pretectal area, which is known to relate to vestibular and visual processing [24]. For controls, three intact animals and two sham-operated ones were used, in which the posterior and hippocampal cortices were removed. To reduce bleeding, the common carotid arteries were temporarily blocked during surgical operation on the brain. After the operation the animals were given antibiotics, sutured, and returned to a cage. The animals usually recovered from the operation on postoperative day 1 (p.o.d1); they could walk, eat, drink, and rear. Unilaterally ablated rats tended to show circling to the lesioned side, as has been reported by others [25], while in the bilateral animals, some walked straight forward even to an obstacle, and some showed circling. The experiment was usually performed on p.o.d1–3. In some cases, experiments were done p.o.d7 to see if any adaptive changes had occurred.

To induce the air-righting reflex, rats were at first pressed by hand in the supine position onto a ceiling plate of an experimental frame (about 2-m height). While a rat was being forced to take a supine posture, it sometimes tried to move and escape from the experimenter's hands. Then the experimenter continuously pressed the animal to the ceiling and waited until it did not move. When the animal was still, it was dropped to a soft cushion on the floor. While falling, it normally exhibited an air-righting action. Pictures of the movements while falling (usually the side view) were recorded on magnetic tapes with a digital video camera (30 frames/s) from a place about 2 m away. The animals were subjected to the righting test for about 10 trials per day; accordingly, about 30 righting movement records were obtained for each animal. Movie files recorded on digital magnetic tapes were stored on a personal computer, and data were transformed into series of still pictures (jpeg format). Righting movements were examined frame by frame on the computer.

Preliminary studies of comparison between righting movements of intact rats and those with the superior colliculus ablated suggested that the air-righting reflex in lesioned animals could be modified by several movement aspects (see 6 variables in "Results"). For each reflex trial, we examined if movement modification occurred for each variable and counted the number of occurrences to evaluate corresponding movement modification. Differences of frequencies of these occurrences (incidence ratio of respective movement modifications) among intact rats, rats with the superior colliculus unilaterally ablated, and those bilaterally ablated were assessed by chi-square test. A difference with $P < 0.05$ was considered significant.

After behavioral examination, the animals were killed; they were deeply anesthetized, thoracotomized, and perfused with 10% formaldehyde solution through the left ventricle. The removed brains were post-fixed for about 1 week, and 100-μm-thick sections were made for histological investigation.

Results

According to the previous study on air-righting movement [5], the movement was fairly stereotyped, as shown in Fig. 1a: when dropped from the supine position, the animal immediately ventriflexed the body, then twisted the head and the forequarter (FQ) almost simultaneously (laterally turned), slightly later turned the hindquarter (HQ), and finally took the landing posture, in which the head was elevated, the body was slightly dorsiflexed, and the four limbs were extended. However, rats with the superior colliculus ablated exhibited reflex movements that were variously modified (abnormalities). Movement variation

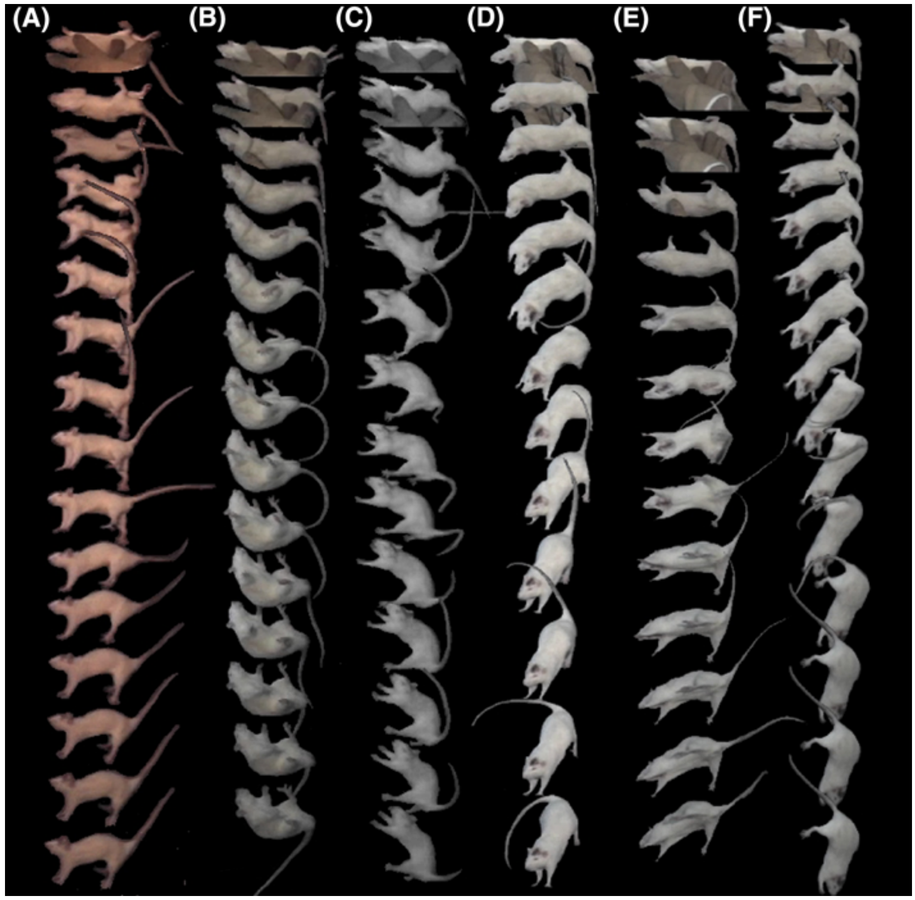

Fig. 1 Illustration of typical air-righting movements of an intact rat and rats with the superior colliculus lesioned. **a** An intact animal (control); **b**, **c** unilaterally ablated (two rats); **d**–**f** bilaterally ablated (one rat)

was qualitatively evaluated by using the following six movement variables:

1. For a gross action of the reflex (gross action), was the righting rotation longitudinal (rotation in the sagittal plane), lateral (leftward or rightward), or abolished?
2. For the immediate action at the beginning of falling (initial action), was it ventriflexion, not obvious, or dorsiflexion?
3. For the order of rotational movement of air righting with lateral turn (righting sequence), which rotated first, the FQ or the HQ, or did both rotate simultaneously?
4. For angular extent of the lateral turn (performance of lateral turn), was it insufficient, proper (almost 180°), or excessive?
5. For body orientation, did angular orientation of the body around the vertical axis remain unchanged during falling, or did it rotate either clockwise or counterclockwise (view from the top)?
6. For landing posture, was it horizontal or not (head down or head up)?

In intact animals (the first row of Table 1), the gross action of righting (variable 1) was exclusively a lateral turn (a total of 34 tests in 3 rats) with either left (27/34) or right (7/34) directions. The initial action immediately after falling (variable 2) was either ventriflexion (11/34) or the action was not obvious (23/34), but no dorsiflexion was observed (0/34). For righting sequence (variable 3), the FQ almost rotated at first and then the HQ (28/34, FQ/HQ in Table 1), whereas in a few cases the FQs and HQs rotated simultaneously (2/34). (In the remaining 4 cases, the order was undetermined because the experimenter's hands hid the early movements of righting.) In performance of the lateral turn (variable 4), the rotation was usually proper, almost 180° (29/34), but sometimes insufficient (5/34); there were no excessive rotations of more than 180°. The orientation (variable 5) normally remained unchanged (27/34), whereas clockwise (5/34) or counterclockwise (2/34) rotation occurred at times. The landing posture (variable 6) was almost horizontal in the vertical plane (30/34); head-up (2/34) or head-down (2/34) postures were, however, taken in some cases. Rats with the posterior and hippocampal cortices ablated (2 rats partially decorticated) showed almost the same righting as intact animals (compare the first and second rows of Table 1). Thus, for control, total frequencies of intact and partially decorticated rats were used (the third row of Table 1).

Table 1 Movement aspects of air-righting reflex by variables indicated in rats with intact superior colliculus (control)

Animal	Gross action	Initial action		Righting sequence		Performance of lateral turn		Orientation		Landing posture	
	Lateral turn	Ventriflexion	Not obvious	FQ/HQ	Simul.	Proper	Insufficient	Unchanged	Changed	Not tilted	Tilted
Intact ($N = 3$)	34/34	11/34	23/34	28/34	2/34	29/34	5/34	27/34	7/34	30/34	4/34
	100.0%	32.4%	67.6%	82.4%	5.9%	85.3%	14.7%	79.4%	20.6%	88.2%	11.8%
Partially decorticated ($N = 2$)	34/34	9/34	25/34	28/34	6/34	33/34	1/34	23/34	11/34	25/34	9/34
	100.0%	26.5%	73.5%	82.4%	17.6%	97.1%	2.9%	67.6%	32.4%	73.5%	26.4%
Total	68/68	20/68	48/68	56/68	8/68	62/68	6/68	50/68	18/68	55/68	13/68
	100.0%	29.4%	70.6%	82.4%	11.8%	91.2%	8.8%	73.5%	26.5%	80.9%	19.1%

Movement aspects indicated by variables are listed with frequencies of occurrence. In righting sequence, FQ/HQ means lateral turn with first forequarter rotation and then a hindquarter one. Simul. means simultaneous rotation of the fore- and hindquarters

Rats with the superior colliculus ablated exhibited various abnormalities in air-righting reflex. The two kinds of ablation, aspiration and electrically lesioning (see "Methods"), gave similar results, so that the two results were combined and used for analysis. Results from ablated animals were based on data obtained at p.o.d1–3. Nevertheless, the righting action was sometimes abolished in beginning trials, especially at p.o.d1. The suppression of the air-righting reflex might be due to superior colliculus ablation, if it provided facilitatory influences on the air-righting center. However, it was difficult to discriminate such specific effects of the ablation from general suppression of reflex excitability at a very acute stage. Thus, if the air-righting reflex was abolished in the beginning trials, and evoked afterwards, the abolished trials were not included in the followings. Further, there was no clear indication of adaptive change at p.o.d1–3. Moreover, the abnormalities observed at p.o.d1–3 seemingly remained unchanged, at least until p.o.d7; this was examined in some animals. In the following, abnormalities in unilaterally ablated and bilaterally ablated animals are described separately.

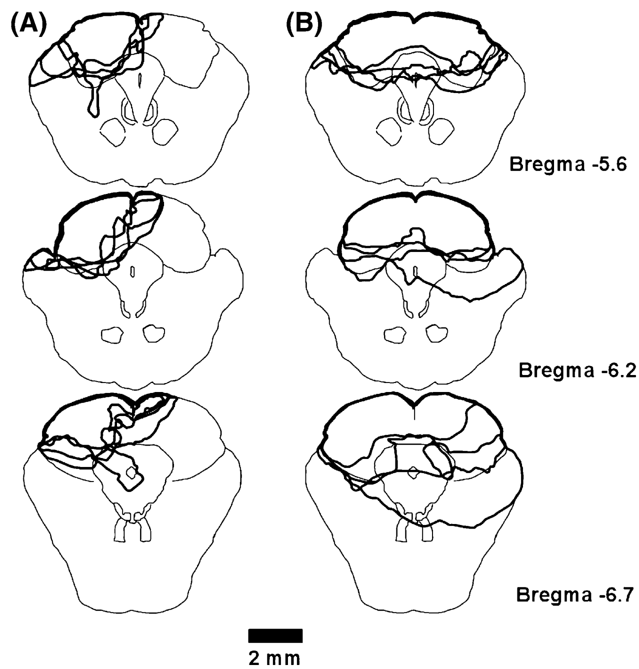

Fig. 2 Extents of superior collicular lesions depicted in transverse planes at three rostrocaudal levels. **a** Unilaterally ablated (4 rats); **b** bilaterally ablated (4 rats)

Effects of unilateral ablation of the superior colliculus

In five rats, the superior colliculus was ablated unilaterally on the left side. Figure 2a shows the extent of the ablations of four rats. The lesion extents were traced from histological sections onto templates at three rostrocaudal coordinates of the entire colliculus [26]. The ablations included almost the whole of the unilateral superior colliculus rostrocaudally as well as dorsoventrally. (The histological data of the remaining rat were unavailable, but the behavioral results appeared similar to those of the others, so that behavioral data were included in the following analysis.)

For the gross action (variable 1), the rats often exhibited air-righting movements with lateral turn (164/171, 95.9%), but in rare cases they fell without clear action of righting (7/171, 3.5%), as shown in Fig. 1b, where the rat at first showed ventriflexion immediately after falling, and then fell with the HQ first. In righting with lateral turn ($N = 164$), some were different from those of the control. With respect to the initial action (variable 2), the dorsiflexion led to righting at times (13/164). This is shown in Fig. 1c. Such dorsiflexion was never seen in controls.

As for the righting sequence (variable 3), in control the air-righting movement usually occurred first in the FQ and then the HQ (82.4%), or simultaneously (11.8%). On the other hand, in the unilaterally ablated rats, simultaneous

Table 2 Comparison of movement aspects between air-righting reflexes with left- and rightward turn in rats with the left superior colliculus ablated

	Initial action			Righting sequence		Performance of lateral turn		Orientation		Landing posture	
	Ventriflexion	Not obvious	Dorsi-flexion	FQ/HQ	Simult.	Proper	Insufficient	Unchange	Change	Not tilted	Tilted
Leftward (ipsiversive) ($N = 75$)	16/75	55/75	4/75	47/75	19/75	61/75	14/75	25/75	50/75	37/75	38/75
	21.3%	73.3%	5.3%	62.7%	25.3%	81.3%	18.7%	33.3%	66.7%	49.3%	50.7%
Rightward (contraversive) ($N = 89$)	32/89	48/89	9/89*	18/89	67/89**	58/89	31/89*	36/89	53/89	56/89	33/89
	36.0%	53.9%	10.1%	20.2%	75.3%	65.2%	34.8%	40.4%	59.6%	62.9%	37.1%

Initial action, righting sequence, and performance of lateral turn increase frequencies of occurrence of abnormalities in contraversive lateral turn versus ipsiversive turn. *$P < 0.05$, **$P < 0.01$ in chi-square tests

rotation of the FQ and the HQ (e.g., Fig. 1c) was more frequently observed (86/164, 52.4%); a clear sequence of fore-to-HQ rotation occurred less frequently (65/164, 39.6%).

Concerning the performance of the lateral turn (variable 4), the turn was sometimes insufficient to obtain a correct prone posture for landing (45/164, 27.4%). The body orientation (variable 5) often altered by about 45 degrees or more during falling. The rotation was either clockwise (50/164, 30.5%) or counterclockwise (53/164, 32.3%); it remained unchanged in the remainder (37.2%), which was contrasted to the control value of 73.5%. In the landing posture (variable 6), proper horizontal prone posture was less frequent (93/164, 56.7%); instead, head-up (41/164, 25%) or head-down (29/164, 17.7%) attitudes were taken. Frequencies of occurrence of abnormalities mentioned above (variables 3–6) were significantly larger than those of control animals ($P < 0.01$).

In air-righting reflex with lateral turn, the turning direction did not depend on the side of the ablation; the animal with the left colliculus ablated showed 75 leftward and 89 rightward rightings in a total of 164 actions. It was, however, noticed that righting abnormalities were more frequently observed in the axial rotation toward the right side (contraversive turn). Table 2 compares frequencies of occurrence of righting abnormalities between rightings with ipsiversive (leftward) and contraversive (rightward) turns. The most obvious asymmetry in frequency of occurrence between righting directions was the righting sequence (variable 3). In ipsiversive righting, the normal sequence of the first FQ and second HQ rotation was usually observed (47/75), but in contraversive righting abnormal simultaneous rotation of both quarters was prevalent (67/89). The initial action (variable 2) and performance of the lateral turn (variable 4) were also asymmetric. Anomaly of dorsiflexion was observed about two times more in the contraversive righting (9/89) than in the ipsiversive one (4/75). Insufficient rotation occurred also about two times more in contraversive righting (31/89) than in the ipsiversive one (14/75). Differences of occurrence of these abnormalities depending on the direction of the lateral turn were statistically significant, as shown by asterisks in Table 2. The other abnormalities, such as horizontal orientation (variable 5) and landing posture (variable 6), were independent of righting direction.

Frequencies of co-occurrence of righting disorders were examined to disclose correlation of occurrence. No significant correlation of occurrence of righting disorders was found.

Bilateral ablation of the superior colliculus

Lesioned areas in bilaterally ablated rats were shown in Fig. 2b. The ablations almost covered the whole of the superior colliculus bilaterally.

Anomalous righting movements in these animals are exemplified by one rat in Fig. 1d–f. They frequently righted with lateral turn, but were incapable of righting (f). In righting with lateral turn, dorsiflexion of the head and upper body (d, e), simultaneous rotation of FQ and HQ (e), insufficient turn (e), disorder in horizontal orientation (d), and anomaly in landing posture (d) occurred at times. These abnormalities were similar to those of unilaterally ablated rats, but frequencies of their occurrence were different. From qualitative comparison of the frequency of occurrence, abnormalities were classified into two groups; in one group the frequency of occurrence increased almost twice as much, and in the other it was nearly the same between unilateral and bilateral ablations. As shown in Table 3, the anomalous movements belonging to the first group were dorsiflexion and simultaneous rotation (variables 2 and 3). Those belonging to the second group were insufficient turn, orientation change, and non-horizontal landing posture (variables 4, 5 and 6). Statistical evaluation showed increases in the frequency of occurrence of abnormal movements were significant in the first groups (as shown by asterisks in Table 3), but not in the second groups. The two kinds of abnormality were not exclusive from each other; both appeared in individual animals regardless of ablations.

Discussion

Pellis et al. [23] showed that the superior colliculus is essential for visual modulation of the air-righting reflex as it adjusted the onset and speed depending on the height from which the rat was dropped, and such modulation was absent in rats with a damaged superior colliculus. Effects of superior colliculus lesions on righting movement have not been examined in detail. The present study revealed that ablation of the superior colliculus modified the performance of the air-righting reflex in rats in various ways. Most prominent features of movement disorder were related to the initial action (variable 2) and the righting sequence (variable 3); normal ventriflexion was sometimes replaced by dorsiflexion, and the sequence of the first FQ and the second HQ rotations was frequently abolished, resulting in simultaneous rotation of both quarters. Careful examination, while based on qualitative analysis without blind tests, revealed not only righting with movement disorder, but also normal righting in some trials of each animal. This implied that the superior colliculus influenced the center of the air-righting reflex, but the action was not indispensable for activation of the reflex.

The superior colliculus has been thought to be the center of orienting action, by which the animal moves the eyes, head, or body to face a novel object that is of interest [12, 14–18]. In rodents it is presumably involved in negatively orienting action, avoidance and defensive actions [19–21]. Generally, such movements more or less bring the animal into a position deviating from the proper upright posture targeted by the righting reflex. Therefore, to complete the orienting action, the righting reflex should be suppressed. The suppression might be performed via the superior colliculus. If this is the case, ablation of the superior colliculus might facilitate the righting reflex. However, ablation effects in the present study could not be interpreted as a simple facilitation of the reflex, since there were degraded righting actions rather than exaggerated ones, suggesting that the collicular projection to the air-righting reflex center could not be inhibitory, as was the simple expectation, but may be multiple and complex. In this line, we supposed that inhibitory effects from the basal ganglia to the air-righting center, which were expected for freezing-like righting movements in striatal rats [5], may not be transmitted via the superior colliculus, but they may be due to direct projection to the midbrain tegmentum [9–11]. Nevertheless, to understand the involvement of the

Table 3 Comparison of movement aspects of air-righting reflex among control, unilaterally ablated, and bilaterally ablated rats

Animals	Gross action	Initial action			Righting sequence		Performance of lateral turn		Orientation		Landing posture	
	Lateral turn	Ventriflexion	Not obvious	Dorsiflexion	FQ/HQ	Simul.	Proper	Insufficient	Unchange	Change	Not tilted	Tilted
Control	68/68	20/68	48/68	0/68	56/68	8/68	62/68	6/68	50/68	18/68	55/68	13/68
	100.0%	29.4%	70.6%	0.0%	82.4%	11.8%	91.2%	8.8%	73.5%	26.5%	80.9%	19.1%
Unilaterally	164/171	48/164	103/164	13/164	65/164	86/164##	119/164	45/164##	61/164	103/164##	93/164	71/164##
ablated ($N = 5$)	95.9%	29.3%	62.8%	7.9%	39.6%	52.4%	72.6%	27.4%	37.2%	62.8%	56.7%	43.3%
Bilaterally	110/117	38/110	52/110	20/110##, **	21/110	72/110##, **	68/110	42/110##	53/110	57/110##	63/110	47/110##
ablated ($N = 4$)	94.0%	34.6%	47.3%	18.2%	19.1%	65.5%	61.8%	38.2%	48.2%	51.8%	57.3%	42.7%

The same format as Table 1. All variables significantly increased abnormalities by superior collicular lesions in comparison with control ($P < 0.05$). The initial action and righting sequence increased frequencies of occurrence, comparing unilaterally and bilaterally ablated animals. Chi-square test was performed for each variable; ## $P < 0.01$ comparing control and ablated rats; ** $P < 0.01$ comparing unilaterally and bilaterally lesioned animals neuronal substrate for freezing-like righting, further studies are required.

Instead of having an inhibitory function, the superior colliculus could facilitate the righting center, because ablation of the superior colliculus tended to weaken excitability of the reflex. The facilitating effect could be related to lateral turn of the FQ, so that removal of the facilitatory action by tectal ablation resulted in reduction of the leading role of the FQ as the primary motor segment of the righting [1, 7].

According to Pellis et al. [23], visual input seemed to affect general excitability for air-righting, such as onset latency and movement speed, rather than individual, specific motor elements of righting. We considered that specific motor effects in abnormal righting in this study were most probably due to removal of the descending tectal output. It might, however, be thought that some defects depended on sensory disorder for orienting and avoidance, and were induced indirectly and not via descending projection, or that deficient righting might be evoked by abnormal excitation of some descending neurons spared from the ablation. To examine these possibilities, further studies are required. In the following discussion, we assumed the abnormalities observed after superior colliculus ablation were primarily evoked by ablation of the direct, descending projection from the superior colliculus to the brain stem.

Comparing effects of unilateral and bilateral ablations, we can qualitatively distinguish two kinds of abnormalities; in one group that consisted of dorsiflexion, and simultaneous fore- and HQ rotation, their frequencies of occurrence increased after bilateral ablation, but in the other group, including insufficient turn, tilted landing posture, and orientation change, their frequencies of occurrence remained at nearly the same level. Furthermore, in unilaterally lesioned rats, abnormal movements belonging to the former group were more frequently observed in contraversive righting, but abnormalities of the latter group were independent of the righting direction. It was suggested that the former abnormalities were likely to be attributed to unilateral projection neurons of the superior colliculus (unilaterally affected abnormalities), whereas the latter to bilateral ones (bilaterally affected abnormalities).

Electrical stimulation of the superior colliculus is known to elicit contraversively orienting movements of the eye, head, and body in many vertebrates [14, 20, 27, 28], and its ablation presumably results in neglect of salient stimuli presented on the contralateral side [29, 30]. Neuronal substrates for the orienting behavior are largely thought to be crossed tectoreticular and tectospinal neurons, descending the predorsal bundle via the dorsal tegmental decussation [12, 14–21]. Considering that orienting movement was rather similar to the axial rotation of the air-righting reflex toward the same side, we supposed that the unilaterally affected abnormalities were related to the crossed descending neurons of the predorsal bundle, unilateral ablation of which presumably decreased facilitating effects on the air-righting center of the opposite side, resulting in motor deficiencies in the contraversive air-righting reflex. If this was the case, the air-righting center may control the righting reflex toward the ipsilateral side. However, in rodents, stimulation of the superior colliculus could evoke avoidance behavior [19–21], which was likely to be initiated by the ipsilaterally descending pathway [19, 21, 27–29, 31]. Thus, it is possible that the unilaterally affected abnormalities were primarily due to the ipsilaterally descending pathway.

However, bilaterally affected abnormalities could be induced by some tectoreticular neurons sending axon collaterals to the ipsilateral midbrain tegmentum before crossing [17, 18, 32]. Nevertheless, tectal output neurons with bilateral axon collaterals were reported to be rather few [33]. Furthermore, there was a question as to why these abnormalities occurred with similar frequencies between unilaterally and bilaterally ablated animals. One of the possibilities is that unilateral ablation of the superior colliculus might deactivate bilaterally projecting neurons located in the intact side through commissural interaction within the superior colliculus [34–37]. To better understand the descending pathways responsible for unilaterally and bilaterally affected abnormalities, further studies are required.

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