Original paper

Effects of septal ventral cuts on intermale aggressive behavior in castrated and non-castrated male rats.

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Abstract

The septum exerts an inhibitory influence for aggressive behavior in rats. In the present study, to clarify the role of the septal ventral fiber in regulating male to male aggression, ventral cuts (SC) were made in male rats and male intruder behavioral tests were carried out 3 times postoperatively at a week interval. Male rats with septal lesion (SL) or without the brain surgery (Intact) were prepared as positive or negative control groups. In addition, to investigate influence of androgen, castrated (OCX) rats with or without SC were made. The numbers of attack and bite during a 10-min period were recorded totally 3 times with a week interval. As a result, in non-castrated rats, the numbers and incidences of attack and bite in SC rats were statistically higher than those in Intact rats. Although number of these behaviors in the SL group was higher than those in the Intact group, there was no statistical difference. No rats showed biting behavior in Intact group. In OCX rats, the incidence and number of attack in the SC group was higher than those in rats without brain surgery. In contrast, no biting behavior was seen in OCX rats even if SC was made. These indicate that inhibitory signals for both attack and bite in the septum pass in the ventral fibers of the septum. Furthermore, androgen is more effective on biting when compare to attacking behavior.

Key Words：Intermale aggression; Septal inhibition; Androgen;Septal cut; Male rats;

Introduction

The septum is well known to play an important role in regulation of reproductive behaviors in both male and female rats. In male rats, since destruction of the septum had no influence on sexual interest against estrous female but inhibits mounting behavior (Kondo et al., 1990), the septum is an important in forming male sexual behavioral pattern. In female rats, the septum exerts an inhibitory influence on female typical sexual behavior, lordosis, conversely a facilitative influence in maternal behavior, because destruction of the septum enhanced lordosis and soliciting behavior (Yamanouchi,1997) and disrupted maternal behavior (Fleischer and Slotnick,1978). In both female sexual behavior and maternal behavior, ventral output fibers have been shown that are involved in septal functions (Yamanouchi, 1997; Koranyi et al., 1988).

Male reproductive behaviors are thought to be accompanied by aggressive behavior. A frontier report showed that septal lesions rendered male rats hypersensitive to sound and increased aggressive behavior, including biting (Brady and Nauta, 1953). Secundus reports also suggest that rage syndrome was evoked by septal lesions in rats (Schnurr, 1972; Thomas and Van Atta ,1972). Lesions in the septum caused agonistic response to stimuli by the experimenter and conversely electrical stimulation of it suppressed agonistic behavior in rats (Albert et al, 1979; Albert and Chew 1980). Suppression of activity of the lateral septum by infusions of local anesthetic into it were found to induce aggression (Albert and Wong, 1978). Intraspecific attack was also exaggerated by the septal lesions in the rat (Albert and Wong, 1978). These results indicate that the septum has a strong inhibition in regulation of most kinds of aggressive behavior (Albert and Walsh 1982; Chozick, 1985).

Aggressive behavior regulating mechanism is concerned with many neural substrates, in the hypothalamus (Kruk et al., 1983; Lammers et al., 1988), limbic cortex (Chain and Paxinos, 1974; Shibata et al.,1982) and lower brainstem (Kruk et al,1983: Lammers et al., 1988). However connections between these areas and the septum have not been analyzed yet. In this report, as first step to elucidate it, effects of cuts of ventral fibers of the septum on aggressive behaviors, especially attack and bite, toward male intruder were examined

Intermale aggression was reported to be dependent on the blood levels of androgen, because castration decreased the aggression in intruder tests in male rats (Barfield et al., 1972; Christie and Barfield, 1979b; Brain, 1983; Taylor et al., 1984). In contrast, androgen-complements led to the recovery of decreased aggression in castrated males (Christie and Barfield 1979a; Bermond et al., 1982). Furthermore, the presence of a female rat enhanced intermale aggressive behavior (Taylor,1975). One of foci of androgen in neural mechanisms for aggressive behavior is thought to be the hypothalamus, because aggression was enhanced by direct implantation of testosterone into the medial hypothalamus (Albert et al., 1987a). Furthermore, it was reported that direct application of testosterone into the septum enhanced aggression in male rats (Lisciotto et al., 1990). The second purpose of this experiment is to elucidate the relationships between septal inhibition and androgen. Effects of SC were observed on attack and bite in castrated or non-castrated male rats

Materials and Methods

Animals

Adult Wistar male rats (8 weeks of age, 300-375 g) for use in the experiment including as an intruder were purchased from Takasugi Animal Farm (Saitama, Japan) and kept under a controlled temperature (23-25 °C) and photoperiod (LD 14:10, lights off at 19:00 hr). Food and water were accessed ad libitum. All male rats were sexually in experience. All experiments were conducted according to the Regulations for Animal Experimentation at Waseda University (Permission No.08J011).

Eleven male rats were orchidectomized (OCX) under Isofluran anesthesia and 19 male rats did not undergo OCX. At the same time as castration, brain surgery was performed in 12 non-castrated male rats and 5 OCX rats. Seven non-castrated male rats did not undergo brain surgery (Intact group).

Brain surgery

Under Isofluran anesthesia, the brain surgery was performed. An anterior half-circle horizontal cut was made ventral to the septum in 6 non-castrated rats (SC group) and 5 OCX rats (OCX-SC group). Under a stereotaxic instrument with the incisor bar set at 3.3 mm below the interaural line (Paxinos and Watson 2007), the tip of an L-shaped Halász knife with a 2.5-mm horizontal blade was set at the level of 1.7 mm anterior to the bregma at the midline. The knife was then lowered to a point 7 mm ventral from the bregma and rotated 180 degrees anterohorizontally.

Bilateral lesions in the septum were made with a radiofrequency lesion generator (RFG-4A, Radionics Inc., Burlington, MA, USA) in 6 non-castrated male rats (SL group). Under a stereotaxic instrument an electrode (0.7 mm) was lowered 6 mm from the bregma level at a point 0.6 mm anterior to the bregma, 0.5 mm at the right and left from the midline. To produce lesions, a current was applied and the temperature at the electrode tip was kept at 55-56 °C for 1 min.

Behavioral tests

From the day of the brain surgery, all animals were kept in individual plastic cages (home cage, h, w, d: 20, 26, 45 cm, respectively). A behavioral testing was started 7 days after the surgery and carried out 3 times in total at one-week intervals. On the day of the test, observation was carried out from 19:00 to 21:00 under a red light. Two or 3 hrs before the test, home cages with the experimental rats were moved to the observation room for acclimation to the environment. Observation was started by putting a male rat into the home cage and the number of behavioral patterns was counted during a 10-minute period. Male rats of the same age as the experimental rats were used as the intruders. Rats for intruder were kept with two in a cage. During 3 behavioral tests, a different rat was used as an intruder in the cage of an experimental rat.

The number of attacking (AT) and biting behaviors (BT) during the 10-minute period were recorded in each test. When the experimental rats approached and threatened the intruder, the behavior was determined as an AT. The average of the total number of ATs in 3 tests was shown as a number of AT of each rat. Incidence was ratio of number of animals showing behavior in all 3 tests to all animals.

When the experimental rat bite the intruder's skin, the behavior was recorded as BT. As the AT, the mean number of BT in 3 tests was shown as the number of BT of each rat. The incidence score of BT was calculated in the same way as for AT. Latency was the time from the introduction of the intruder male into the home cage to the first appearance of the behaviors.

Histology of the brain

In order to examine the precise localization of the cuts and lesions histologically, each brain was removed and fixed in 10% formalin solution at the end of the behavioral test. Subsequently, frozen sections were prepared and stained with cresyl fast violet.

Statistics

Statistical analyses were performed using X^2 test for the incidence of the behaviors. For the comparison of the number of behaviors, one-way analysis of variance (ANOVA) followed by the Dunnet test were carried out. Results were considered to be significant, when p<0.05.

Results

Non-castrated groups

Only 1 rat in the Intact group showed AT in every 3 tests and 2 intact rats showed no AT through the tests. In contrast, all of 6 rats showed AT in every 3 tests in the SC groups (incidence, P<0.02, vs Intact). In SL group in non-OCX rats, as SC, all of 6 rats showed AT but 4 of them showed it every 3 tests. The mean number of AT per 10 min of the Intact group was 1.2 ± 0.4 (Fig.1). In contrast, numbers of AT in the SC group was 6.7 ± 1.4, which was higher than in the Intact group (P< 0.01).

The median latency of AT of the 3rd test in the Intact group was 270 sec (Min-Max:210-330). In the SC and SL group, the median latencies of AT were 107.5 sec (45-405) and 130 sec (10-420), respectively.

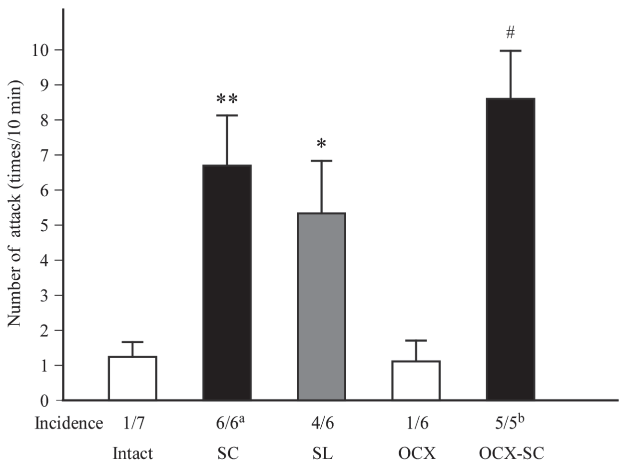

Fig. 1. Mean numbers of attack in intact, orchidectomized (OCX), non-OCX rats with a septal ventral cut (SC) or septal lesion (SL) rats. * P<0.05 vs Intact, **P<0.01 vs Intact, # P<0.001 vs OCX a P< 0.02, vs Intact; b P<0.02, vs OCX;

In the Intact group, there were no rats that showed BT in every 3 tests. In contrast, 5 of 6 SC rats showed BT in every 3 tests, (p<0.02, vs Intact). Number of BT in the

Intact group (1.0 ± 0.7) was lower than in the SC group (5.5 ± 1.9) ($p<0.05$) (Fig.2). The median latencies of BT of the 3rd test in the Intact, SC and SL groups were 580, 120 (45-220) and 255 (70-500) sec, respectively.

Castrated groups

In the OCX group, as in the Intact group, there was only 1 rat that showed AT in every 3 tests. All of 5 SC rats, even those that were castrated, showed AT in every 3 tests, which was statistically higher than in the OCX group (Incidence $P<0.02$) (Fig 1). The number of AT in the OCX-SC group was 8.6 ± 1.4, which was higher than in the OCX group (1.1 ± 0.6, $P<0.001$) and was comparable to those in the SC rats without gonadectomy (Fig. 1). Median latencies of AT of the 3rd test in the OCX and OCX-SC groups were 302.5 (200-405) and 40 (20-160) sec, respectively. None of rats in both the OCX and OCX-SC groups showed BT in all tests (Fig. 2)

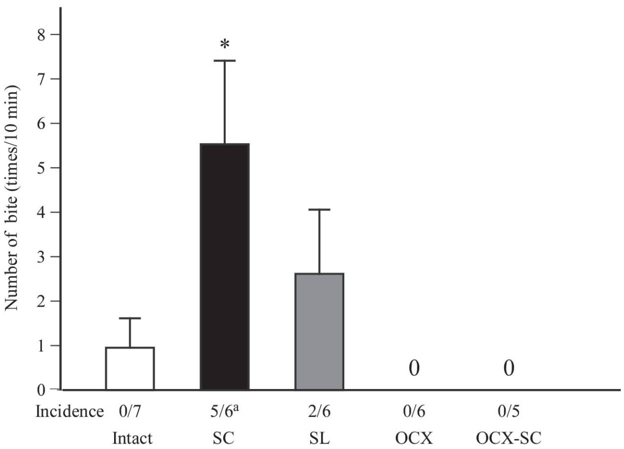

Fig. 2. Mean numbers of bite in intact, orchidectomized (OCX), non-OCX rats with a septal ventral cut (SC) or septal lesion (SL) rats.* $P<0.05$ vs Intat.
a $P<0.02$, vs Intact.

Precise location of the SC and SL

In the SC group, a trace of the knife was seen above the anterior commissar, extending from the anterior of island of Calleja to the anterior of end of the anterior commissure (Fig. 3). In some SC rats, parts of the cortex and midline of the septum were damaged by lowering of the knife. In the SL group, the main parts of the lateral septum were lesioned from the level of the anterior part of island of Calleja to the posterior end of the anterior commissure. In some SL rats, the ventral parts of the lateral and the dorsal parts of the medial nucleus were partially intact. The nuclei of the bed nucleus of stria terminalis and accumbens were intact.

Discussion

In this result, castrated rats showed the same low level of attacks as non-castrated rats. Castration was reported to reduce intermale aggressive behavior (Christie and Barfield, 1979b) and treatment with testosterone recovered it (Barfield et al., 1972; Christie and Barfield,1979a; Albert et al., 1986a). One of the explanations for this discrepancy is a difference in the threshold for androgen in the male rats used as experimental subjects in enhancement of aggression, because, in our rats, the number of attacks was very low even when not castrated. There are several kinds of motivation of attacking such as territorial aggression, offensive, defensive, predatory, fear-induced, irritation-induced aggression (Schnurr, 1972). Because of no

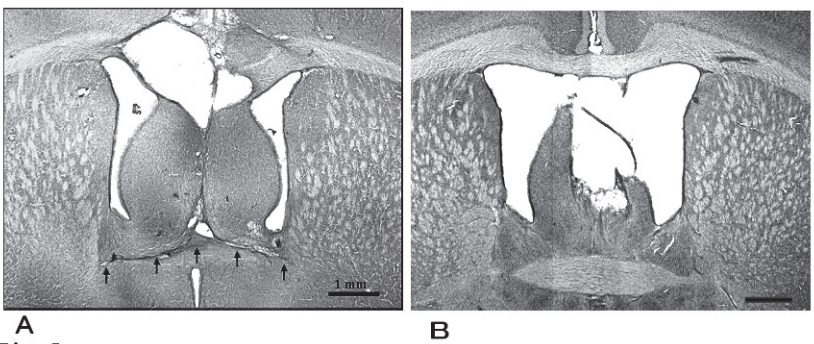

Fig. 3

Fig. 3. Representative photomicrographs of a frontal section of the septal level in rat with septal ventral cut (SC) and lesions (SL) , (A) and (B), respecitively (cresyl fast violet stain). Arrows indicate SC.

sexual experience in male rats used in this experiment, attack behavior is though to be caused mainly by territorial invasion. From this view, dependency on androgen in attacks induced by territorial aggression may be weak. This is supported by no statistical difference in mean numbers of attack among intact and OCX groups in this study.

In this experiment, septal lesions were effective in facilitating attacks and bites targeted at male intruders in non-castrated rats. These results are in agreement with many reports that the septal area plays an inhibitory role in inducing aggressive behavior (Albert et al., 1982; Chozick ,1985). In addition, the enhancement of aggression caused by SC was comparable to that caused by SL in the present results, suggesting that the ventral outputs and/or inputs of the septum were important in the control of aggression in an inhibitory fashion.

However, since attacks was facilitated by the SC in both rats with and without castration but number of attack in castrated rats with SC was comparable to that in non-castrated rats with SC, androgen is not influential to attacking behavior, although androgen plays an important role in intermale aggression (Simon, 2002). On the other hand, biting behavior was enhanced by SC in non-castrated rats but not in castrated rats. This indicates that biting behavior is strongly influenced by existence of androgen, when compared to attacking behavior.

It is known that the septum receives many vasopressin-projections (De Vries and Buijs, 1983) and these projections are influenced by testosterone (De Vries et al., 1984). Henk et al. (1997) showed from immnohistochemical and behavioral experiments that rats showing high intermale aggression had low levels of vasopressin immunoreactivity, and conversely, rats with low intermale aggression had high levels of vasopressin immunoreactivity. The bed nucleus of stria terminals is one of the origins of vasopressin neural fibers in the septum (De Vries and Al-Shamma,1990) and has been reported to play an important role in aggression in cats (Shaikh et al., 1986). In the present experiment, there is a possibility that the septal cuts interrupted vasopressin-afferents from the nuclei of the bed nucleus of the stria terminalis located at the anterior commisure level, because these nuclei extend both above and below this commissure and the cuts were located just above the commisure.

The SC enhanced biting as attacking in non-castrated but not castrated male rats in the present results. These results lead to a conclusion that septal ventral fibers strongly inhibit biting behavior and androgen is prerequisite for facilitation of biting behavior by SC. The difference of dependency on androgen between in attacking and biting behaviors may be caused by strength of aggressiveness or difference of motivation. In another point of view, since androgen was effective in inducing biting behavior even if a SC was performed, androgen acts on other regions than the septum in regulation of biting behavior.

The septum is shown to send their axons to many areas of the brain (Risold and Swanson, 1997). The ventral output fibers has been shown to go down in the preoptic area (POA) and to the lower brainstem such as the midbrain central gray (MCG) through the lateral and mediodorsal parts of the hypothalamus (Tsukahara and Yamanouchi K, 2001; Kouki and Yamanouch, 2007). There are reciprocal anatomical connections between the hypothalamus and septum (Risold and Swanson, 1997).

The hypothalamus including the POA contains large amounts of androgen concentrating neurons (Sar and Stumpf, 1975). The medial POA is also thought to play an important role in regulation of aggressive behavior, because POA lesions reduce aggressiveness (Albert et al., 1987b; Albert et al., 1986b). Furthermore, Albert et al. (1987a) reported that aggression was enhanced by direct implantation of testosterone into the medial hypothalamus being suggested that testosterone-sensitive neural circuitry in regulating intermale aggression exists in the medial hypothalamus.

Attack-inducing mechanism is existed in subfornical area in the hypothalamus including the preoptic area and ventromedial hypothalamic nucleus (hypothalamic attack area, HAA), because electrical stimulation to these areas in the male rat evoked fighting between males (Kruk et al., 1983; Lammers et al., 1988). The hypothalamic attacking area (HAA) projects axons to the lateral septum (Roeling et al., 1994; Siegel et al., 1999).The VMH lesion-induced aggressiveness has been suppressed by electrical stimulation of the lateral septum in the rat (Brayler and Albert, 1977). Thus, lateral septal projections sending inhibition for aggression is thought to be connected with HAA functions. The HAA projects also axons to the midbrain central gray (MCG) (Roeling et al., 1994; Siegel et al., 1999). It has been reported that the MCG is involved in aggressive behavior regulating - neural circuit that includes the intermediate HAA (Roeling et al., 1994; Mos et al., 1982; Mos et al., 1983). Thus, septal ventral fibers may include efferent fibers to these areas or afferent fibers from these areas. Further experiments are needed to clarify the neural circuit including the septal inhibition.

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Disclosure

None of the authors have any potential conflicts of interest associated with this research.

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精巣除去または非精巣除去雄ラットにおける雄間攻撃行動に対する中隔腹側切断効果

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要　旨

中隔には攻撃行動に対する抑制力がある。本研究では雄間の攻撃行動に中隔腹側神経線維がどのように関わっているか調べるため、中隔の腹側切断(SC)を雄ラットに施し、雄ラットの侵入者に対する行動テストを一週間おきに３回行った。また、ポジティブとネガティブの対照群として、中隔破壊（SL）群と脳の手術を行わない群（Intcat）をつくった。さらにアンドロゲンの影響を見るため、去勢（OCX）した雄ラットにSCを施す群と脳手術を施さない群を作った。１回の行動観察では１０分間のアタック行動と噛み付き行動を記録し、３回行動観察をおこなった。その結果、去勢を施していない雄ラットではSC群でアタックと噛み付きがIntact群より有意に回数、発現率とも高かった。SL群ではIntact群より高かったが有位差がみられなかった。Intact群では噛み付き行動が全く見られなかった。OCX ラットでは、SC 群のアタック行動が脳を手術していない群より明らかに高かったが、噛み付き行動はSCが施されていても見られなかった。これらの結果は雄ラットのアタック行動と噛み付き行動の中隔における抑制シグナルが腹側出力神経線維を通り下行する可能性を示している。さらに、アンドロゲンはアタック行動より、噛み付き行動に対する影響が強いことも明らかにされた。

Key Words：　雄間攻撃行動、中隔抑制力、男性ホルモン、神経線維切断、雄ラット。

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