Korean J. Zool. 39:1-11, 1996

Specific Effects on Monocular OKN Directional Asymmetry of Unilateral Microinjections of GABA Antagonist into the Mesencephalic Structures in the Chicken

Myoung Soon Kim

Department of Biology, College of Natural Science, Woosuk University, Chonju 565-800, Korea

The SR 95531, a GABA antagonist was microinjected into either the pretectum nuclei (nucleus Superficialis Synencephali nSS) or the nBOR (nucleus Ectomammilaris nEM) of chickens. Monocular optokinetic nystagmus (OKN) was reorded by the search coil technique before and after unilateral intracerebral drug administration. Unilateral microinjections of SR 95531 into either the nSS or nEM induce a reversible increase of gain in OKN directed by contralateral eye for both directions of stimulation. The administration into the nSS increased directional asymmetry by increasing the T-N component velocity gain more strongly than the N-T component velocity gain. On the other hand, the unilateral administration of the drug into the nEM suppressed the diretional OKN asymmetry by increasing the N-T component velocity gain more strongly than the T-N component velocity gain. The nSS seems especially involved in monocular OKN in response to a T-N stimulation, while the nEM seems more involved in the OKN response to N-T stimulation. These results indicate that the drug suppresses GABAergic inhibition at the mesencephalic level. The increase in gain of OKN directed by the ipsilateral eye to microinjected nuclei could account for the strong interactions existing between these two mesencephalic structures responsible for horizontal OKN.

KEY WORDS: Accessory Optic System, $GABA_A$ Receptor, Microinjection, Optokinetic Nystagmus, Chicken

Optokinetic nystagmus (OKN) is a visuomotor reflex stabilizing the image on the retina with respect to movements of the animal or of its environment. The OKN is a stereotyped pattern of eye motion composed of smooth compensatory movements in the direction of the stimulus and of resetting fast phases in the opposite direction.

Directionality of horizontal monocular OKN is one characteristic of this reflex. In the chicken, monocular OKN is asymmetrical, the temporal-nasal (T-N) stimulation being more efficient than the nasal-temporal (N-T), to evoke the reflex (Fite *et al.* 1979; Gioanni *et al.* 1981; Wallman and Velez 1985).

In previous work, it was proposed that GABAergic mechanism might be involved in the control of OKN directional characteristics in the frog (Yücel *et al.* 1990) as well as in the chicken (Bonaventure *et al.*, 1992). Indeed, systemic injections of GABA antagonists provoked a reversible increase in both components of monocular OKN, increasing the N-T components more than the T-N one, so that the directional asymmetry of the OKN was strongly reduced. On the other hand, intravitreal injections of GABA antagonists into the open eyes of chickens, induced spontaneous nystagmus and was only slightly modified by stimulation.

This effect could be explained by action of the GABA antagonists on the central structures responsible for OKN, such as the nucleus Lentiformis Mesencephali (nLM) (Brecha *et al.*, 1980; Fite *et al.*, 1979; McKenna and Wallman 1985; Simpson *et al.*, 1988), and not at the retinal level.

It has been shown that the high density of GABA localized in the nBOR of birds (Britto *et al.*, 1989), and the nBOR and nucleus Lentiformis Mesencephali in frogs could be engaged in the control of monocular OKN asymmetry (Yücel *et al.*, 1991).

The pretectum nucleus also known as nucleus Lentiformis Mesencephali (nLM) or nucleus Superficialis Synencephali (nSS) in birds is regarded as homologous to the mammalian nucleus of the optic tract (NOT). This pretectal nucleus receives a direct retinal projection.

The involvement of the nLM in the horizontal OKN was substantiated by experiments using lesions, stimulations (Gioanni *et al.*, 1983a) and metabolic labelling with 2DG in the chicken (McKenna and Wallman, 1981, 1985b) and pigeon (Chown *et al.*, 1984). These experiments show that these nuclei play an essential role in the elaboration of the horizontal OKN in the T-N direction for the contralateral eye.

The other mesencephalic structure involved in OKN is the nBOR, also called the nucleus Ectomamillaris (nEM) in birds. It is composed of three parts: the nBOR proper, dorsal nBOR and lateral nBOR (Brecha *et al.*, 1980). All receive completely crossed retinal projections. Involvement of the nBOR in the vertical OKN genesis was clearly demonstrated by experiments using lesions (Wallman *et al.* 1981b), metabolic labelling with 2DG (Frost *et al.*, 1980; McKenna and Wallman, 1981, 1985a) or electrophysiological unit recordings (Burns and Wallman 1981; Gioanni *et al.*, 1984; Frost *et al.*, 1980). However, its implication in the N-T horizontal OKN is less clearly understood (Gioanni, 1983b). According to Fite *et al.* (1979), the nBOR is only involved in high frequency OKN.

The present study was undertaken to examine the specific relationships between the above GABAergic systems and horizontal OKN generation, especially with respect to directional asymmetry. For this purpose, a GABA antagonist was microinjected into either the pretectum or nBOR of chickens, and the monocular OKN of each eye was recorded.

Materials and Methods

Animal preparation

Forty-two adult (4-5 weeks old) Leghorn chickens at a weight of 0.8 to 1.2 kg, were used for this study. Monocular eye movements were recorded by means of the search coil technique, before and after unilateral microinjection of SR 95531 into the nSS or the nEM. The recorded eye (i.e. the open, stimulated eye) was either contralateral or ipsilateral to the injected structure. The eyelids of the closed eye were sutured, under light general anesthesia (ether), one hour before recording.

Stimulation

To evoke horizontal OKN, chickens set at the center of a drum (545 mm in diameter and 550 mm in height) with alternating black and white vertical stripes of 4° 65 (19 mm) equally distributed on its inner surface. The optokinetic drum rotated clockwise or counter-clockwise at 3 constant speeds (8, 15 and 60 deg/s). Animal was kept constant at 750 lux measured at the level of the chicken's eye. The lamp illuminating the drum was powered by direct current to prevent stroboscopic interferences with the drum stripe motion at the highest speed.

Search coil recording

One pair of coils (300 mm in diameter) carrying a current of 50 kHz frequency, generates a homogeneous magnetic field. The sensor coil (1 mg, 75 turns, Sokymat) was fixed on the eyeball with a drop of glue just before beginning of experimentation; this was performed while the chicken was under general anesthesia (ether). The animal was then placed in the center of the magnetic field.

Before each recording, the system was calibrated, the linear relationship between the

angular displacement of the sensing coil and the induced voltage was verified. The constant slow phase speed was analysed by tracing the cumulative curve of 3 successive eye movements at steady state velocity following elimination of eye resetting fast phases. The resetting fast phase frequency was the number of eye resetting fast phases during 10 s. Statistical analyses were performed using the Wilcoxon signed-ranks test.

Chicken Preparation for recordings and intracerebral microinjection

Chicken were prepared the day before recording, under general anesthesia obtained by an intraperitoneal injection of equithesin (0.25 ml/ 100 g); a nut was fixed to the skull by means of dental cement, and 7 metal screws (1 mm) were implanted in the dorsal skull.

A permanent stainless steel injection guide cannula (0.4 mm outer diameter, 0.3 mm inner diameter, 15 mm length) was stereotaxically implanted at either the level of the nEM or nSS. The coordinates varied slightly according to each animals weight; Anterior/Posterior (A/P) 4.4-4.5, Median/Lateral (M/L) 2.4-2.5 and Dorso/Ventral (D/V) 1.5-2 for the nEM, and A/P 5.75-6, M/L 4.1-4.4 and D/V 3.5-4 for the nSS, according to the Atlas of Tiehoven and Juhasz (1964) and Karten and Hodos (1967). A stainless steel sterile mandrel (0.27 mm diameter) was introduced into the cannula to avoid obstruction. Extenciline was intramuscularly injected to limit the risk of bacteria infection.

The day of experimentation, the chicken's head was restrained by attaching the nut to a bar placed in the drum. The mandrel was subsequently pulled out and replaced by a stainless steel injection cannula (outer ψ 0.28 mm, inner ψ 0.18 mm). The injection cannula was connected to a microliter Hamilton microsyringe via polyethylene tubing filled with distilled water and the drug. A small air gap separated the two liquids. Pressure

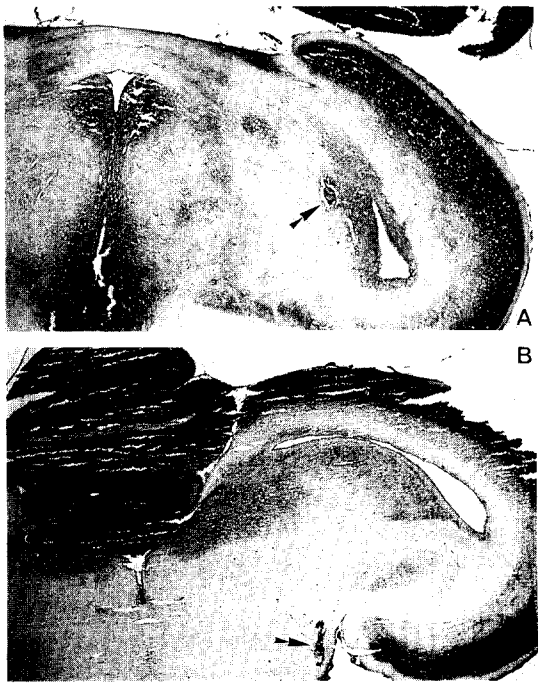

Fig. 1. Photographs showing a coronal section (40 μm) of the mesencephalic region of the chicken. Arrows indicate the cannula position localized in the nSS (A) and in the nEM (B).

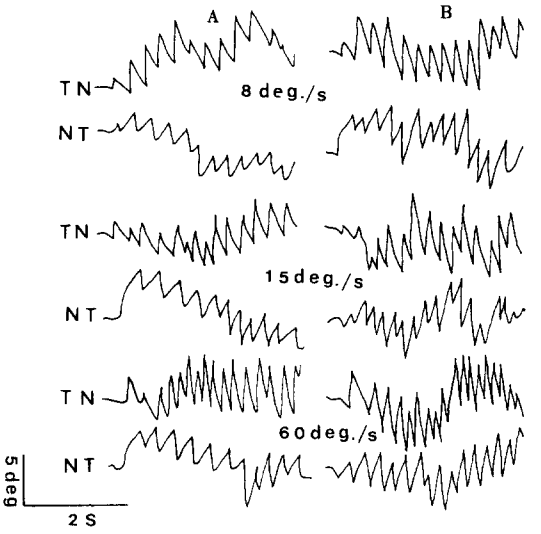

Fig. 2. Coil recordings of monocular eye OKN evoked by three different constant drum speeds in a monocular viewing condition, before (A) and after microinjection of SR 95531 into the nSS contralateral to the recorded eye (B). The direction of the stimulus T-N or N-T, as well as the drum speed are indicated on the left of the figure. The OKN fast phase is downwards for a T-N stimulation, upwards for a N-T stimultion. OKN gain (or slow phase velocity) increased after SR 95531 administration for both directions of stimulation.

injection of 0.3 μl was delivered over 20 s, and the movement of the air gap down the tubing was indicative of a successful injection. Following treatment, the injection cannula was kept in place for 60 s, and then slowly removed.

Monocular eye movement recordings of either eye were made before and after implantation as well as following drug administration.

Drug injection

The injected drug was SR 95531, a recently synthesized GABA antagonist (Chambon *et al.*, 1985), which like bicuculline, specifically binds to the $GABA_A$ receptor. It has previously been shown that SR 95531, systemically or intracerebrally injected in the frog, like bicuculline, suppressed monocular OKN directional asymmetry, but was more efficient and more prolonged effects than bicuculline (Bonaventure *et al.*, 1985; Yücel *et al.*, 1991). It was diluted in phosphate buffered saline (PBS) and prepared daily (pH 7.3). The concentration used was 0.1 mM and the injected quantity was 0.3 μl.

Histological control

Histological controls were performed for all chickens, following a 10 day post survival time, in order to localize the cannula tracks.

In some chickens, a volume of 0.5 μl of fast blue stain was injected (under general anesthesia) via the permanent intracerebral cannula.

Transcardial perfusion with saline (0.9% NaCl) followed by formaldehyde (10%) was performed under general anesthesia. Coronal frozen brain slices were sectioned at 40 μm and stained with cresyl violet. All animals in which cannula tracks could not be localized were excluded from this study. The unilateral representation of the cannula track in the nSS and in the nEM is indicated on Fig. 1A and Fig. 1B respectively.

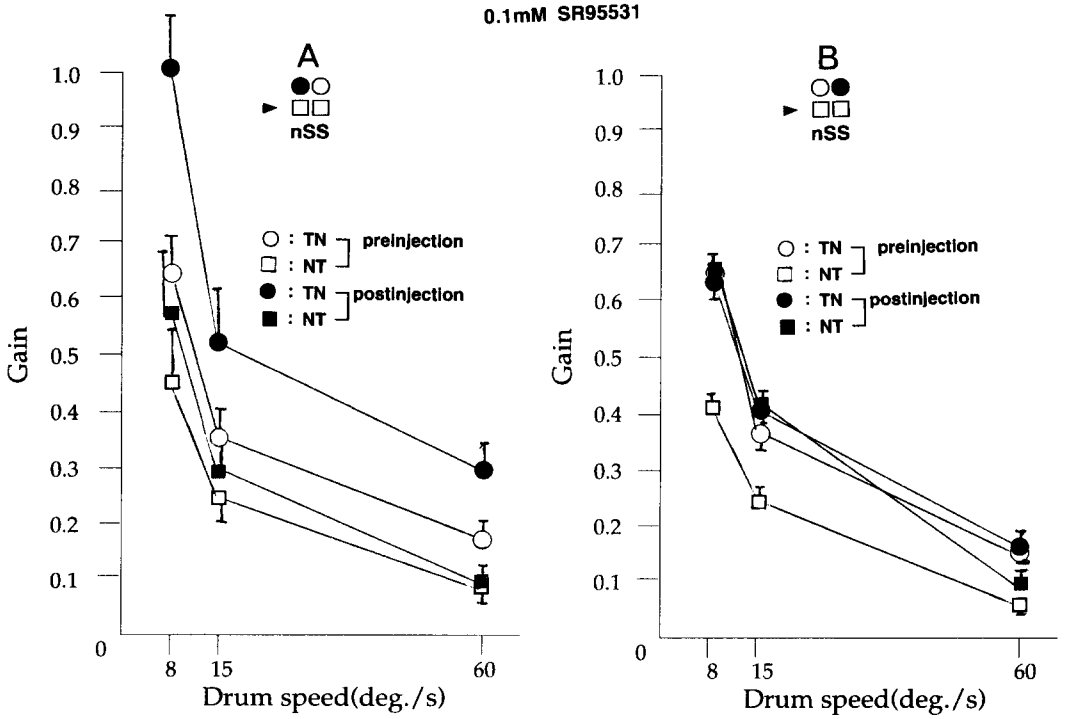

Fig. 3. Mean values of the OKN gain for three different drum speeds, before (white symbols) and 20 min after microinjection of SR 95531 (dark symbols) into the nSS contralateral to the recorded eye (A) (n=17) or ipsilateral to the recorded eye (B) (n=4). The injected structure is indicated by the arrow; the open circle stands for the stimulated eye, the filled circle stands for the closed eye.

Results

Control monocular OKN (42)

The stimulated eye was always recorded. Before the injection no saccades nor spontaneous eye movements existed, either in light or dark conditions.

Optokinetic stimulation in the T-N direction was more efficient in evoking the reflex than the stimulation in the N-T direction, and the gain for a T-N stimulation was significantly higher ($P < 0.001$) than the stimulation the slow phase gain for a N-T stimulation at each drum speed tested (8, 15 and 60 deg/s) (Figs. 2A and 5A, Fig. 3 and 6, white symbols). Moreover, the measured slow phase gain was maximal at the lowest drum speed, and decreased with increasing drum speed for both directions of stimulation.

On the contrary, the resetting fast phase frequency (fpf) increased with increasing drum speed, up to 60 deg/s, for both directions of stimulation (Fig. 4 and 7).

The OKN fast phase frequency evoked by T-N stimulation was always higher than N-T stimulation. Moreover, the difference between the fpf measured during T-N stimulation and that measured during N-T stimulation was always significant ($P < 0.005$).

Neither cannula implantations nor microinjection of PBS into other brain structure affected main characteristics of chicken OKN: i.e. the slow phase gain and the resetting fast phase frequency.

Monocular OKN triggered by the eye contralateral to the injected nSS (17)

After intracerebral drug injection, spontaneous eye movements were observed in 4 chickens, and one chicken began having convulsions. These animals were exclued from the experiment.

The effect of drug injection upon OKN were

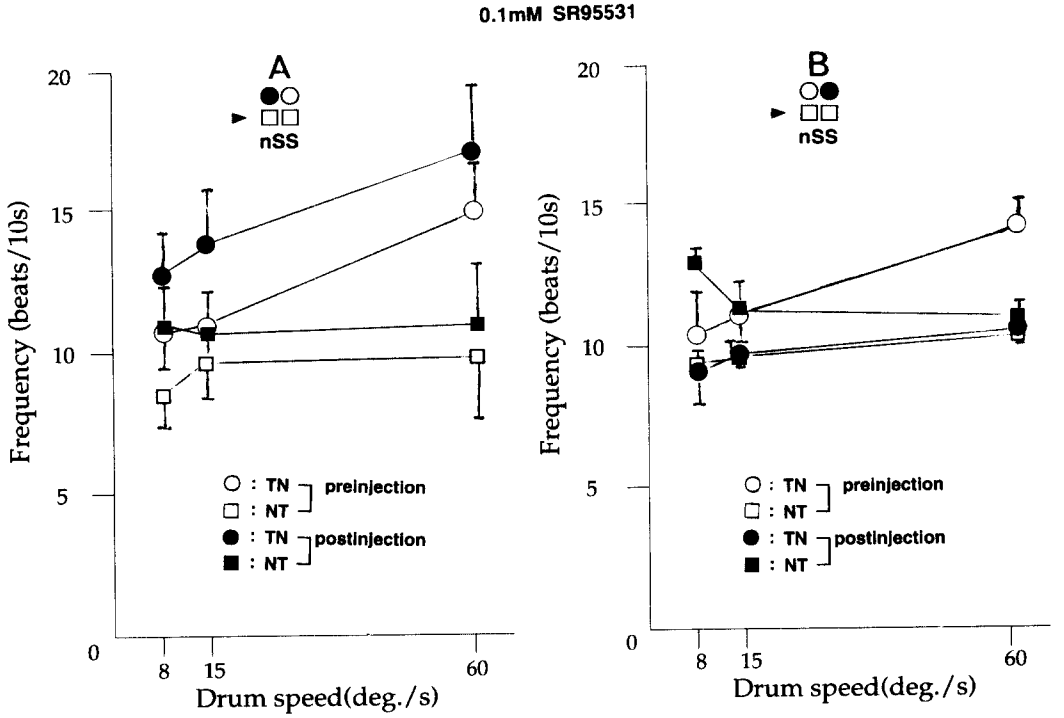

Fig. 4. Mean values of OKN fast phase frequency for three different drum speeds, before (white symbols) and 20 min after microinjection of SR 95531 (dark symbols) into the nSS contralateral to the recorded eye (A) (n=17) or ipsilateral to the recorded eye (B) (n=4). The injected structure is indicated by the arrow; the open circle stands for the stimulated eye, the filled circle stands for the closed eye.

generally detected at approximately 5 min after injection, reached a maximum within 20 - 30 min later and subsided within 1 h. All OKN characteristics increased for the 3 drum speeds tested, and for both T-N and N-T directions of stimulation (Fig. 2). The increase of slow phase gain was significant ($P < 0.005$) in all experimental conditions, and in both directions, except at a drum speed of 60 deg/s in the N-T direction (Fig. 3A). However, the increase in gain was always stronger with stimulation in the T-N direction.

The fpf was modified, increasing at all drum speeds and for both directions of stimulation in a similar manner; this increase was higher for a T-N stimulation than for a N-T one.

In the present experiment, the most prominent findings were the increases in velocity gain and fpf of the monocular OKN when the stimulation was in the T-N direction, pronouncing the directional asymmetry characteristics of monocular OKN.

OKN triggered by the eye ipsilateral to the injected nSS (4)

In this experimental condition, the velocity gain was increased for the N-T direction of stimulation, especially at the lowest drum speed; it was not modified in the T-N direction of stimulation (Fig. 3B). Thus, the directional asymmetry of monocular OKN totally disappeared for the weakest stimulation speeds, and was strongly reduced for the highest one.

The fpf in the OKN T-N component was slightly decreased, whereas it was only slightly increased in the OKN N-T component for the lowest drum speeds, but these modifications were not significant (Fig. 4B).

OKN triggered by the eye contralateral to the injected nEM (16)

After intracerebral drug injection, spontaneous eye movements were observed in one animal, another had convulsions. These animals were not included.

Recordings are shown on Fig. 5. OKN gain and fpf were strongly increased for the 3 drum speeds tested and both directions of stimulation.

The velocity gain was significantly increased ($P < 0.005$) especially at the lowest drum speeds and in the N-T direction of stimulation (Fig. 6A).

The directional asymmetry of the monocular OKN totally disappeared for the lowest stimulation speeds and was strongly reduced for the highest. The difference between mean values obtained for the OKN gain using a T-N stimulation and N-T stimulation was not significant ($P > 0.005$).

The fpf was modified in the same manner (Fig. 7A), increasing for the 3 drum speeds tested and both directions of stimulation. This increase was higher for the N-T direction of stimulation than for the T-N. Thus, the directional asymmetry of the monocular OKN was suppressed, at least at the lowest drum speeds and was strongly reduced at the highest one.

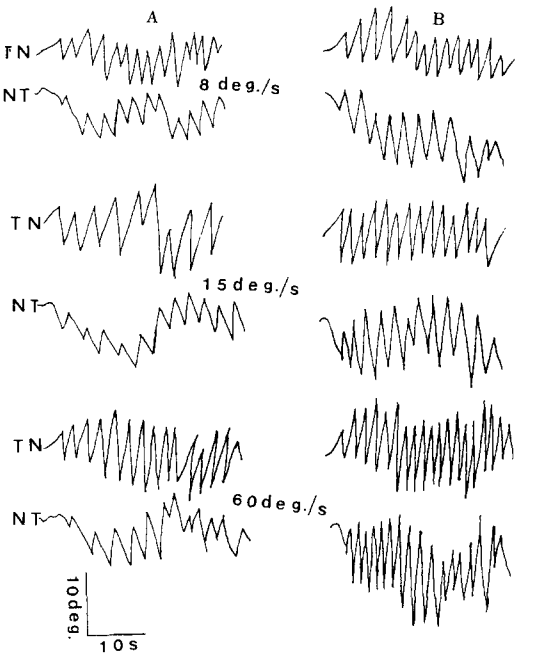

Fig. 5. Coil recordings of monocular eye OKN evoked by three different constant drum speeds in a monocular viewing condition, before (A) and after microinjection of SR 95531 into the nEM contralateral to the recorded eye (B). The direction of the stimulus T-N or N-T, as well as the drum speed are indicated on the left of ther figure. The OKN fast phase is downwards for a T-N stimulation, upwards for a N-T stimultion. OKN performances increased after SR 95531 administration for both directions of stimulation, but especialy for the N-T stimulation.

OKN trigged by the eye ipsilateral to the injected nEM (5)

The gain was only slightly increased at the lowest drum speeds and for both directions of stimulation, but it was not significant (Fig. 6B). The fpf was not modified (Fig. 7B).

Discussion

The results of the present study indicate that when injected into either the nSS or nEM, SR 95531 always induces an increase in the monocular OKN velocity gain as well as that of the fast phase frequency for both directions of stimulation. This increase was observed especially at the lowest drum speeds, regardless of the stimulated eye. This suggests that SR 95531 suppressed the inhibition of GABAergic mechanisms involved in OKN at the mesencephalic level. It also demonstrates the complementary participation of both structures to the generation of both T-N and N-T components of the monocular OKN.

The drug has little effect with a stimulation velocity of 60°/s. The reduced effects of drug injection at the highest drum speed suggest a specific corticofugal inhibition from the hyperstriatum (considered the visual cortex in birds) upon the mesencephalic structures for the highest velocity stimulation.

Stimulation of the contralateral eye to the injected structure always provoked an increase in OKN performances, larger than those observed after stimulation of the ipsilateral eye. This suggested that it is the direct relationship between the retina and the crossed mesencephalic nuclei. However, the effects related to the contralateral eye are different according to the side of injection.

When injected into the nSS, SR 95531

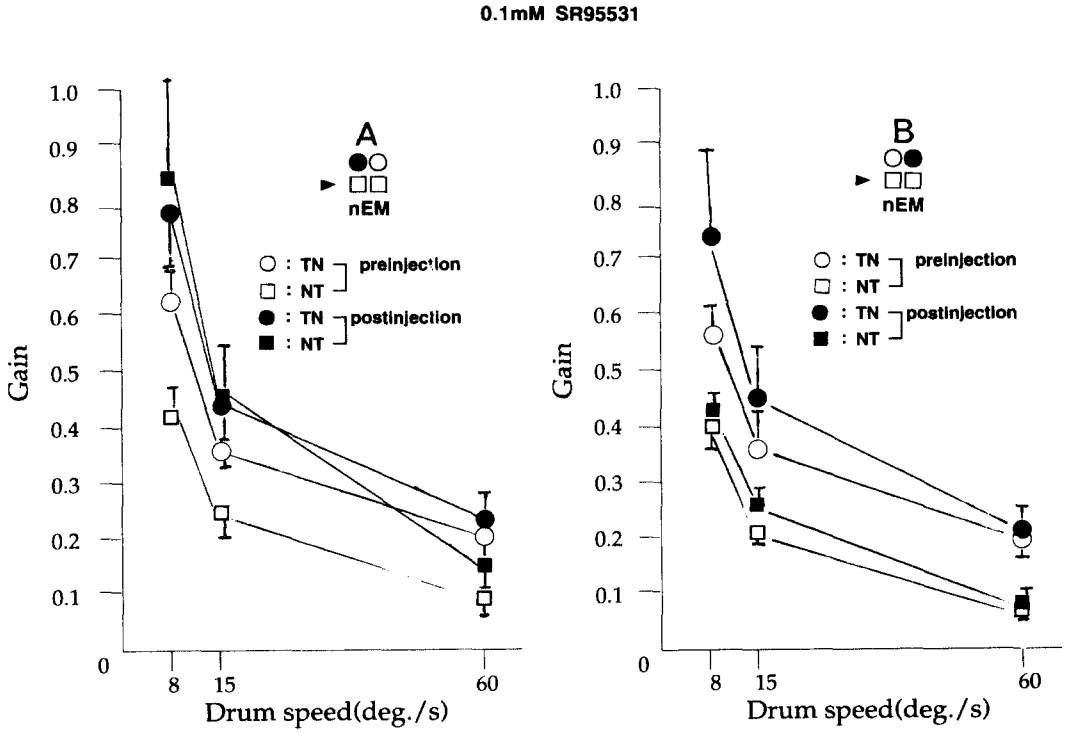

Fig. 6. Mean values of OKN gain for three different drum speeds, before (white symbols) and 20 min after microinjection of SR 95531 (dark symbols) into the nEM contralateral to the recorded eye (A) (n=16) or ipsilateral to the recorded eye (B) (n=5). The injected structure is indicated by the arrow; the open circle stands for the stimulated eye, the filled circle stands for the closed eye.

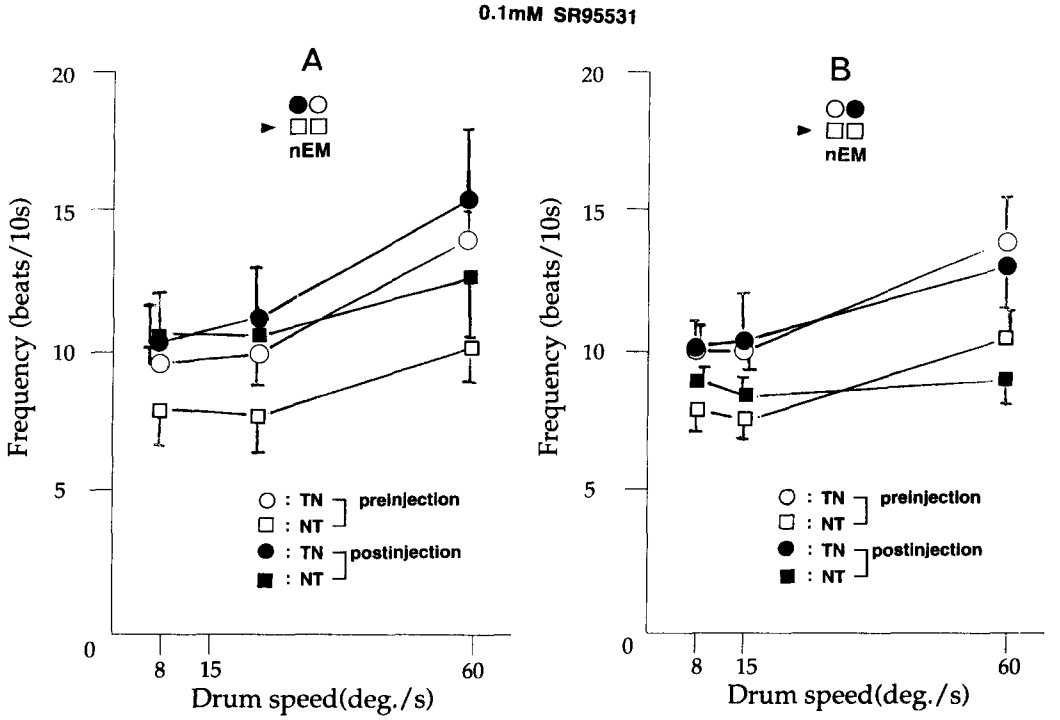

Fig. 7. Mean values of the OKN fast phase frequency for three different drum speeds, before (white symbols) and 20 min after microinjection of SR 95531 (dark symbols) into the nEM contralateral to the recorded eye (A) (n=16) or ipsilateral to the recorded eye (B) (n=5). The injected structure is indicated by the arrow; the open circle stands for the stimulated eye, the filled circle stands for the closed eye.

provoked a stronger increase in the OKN T-N component. When injected into the nEM, it was the N-T component which is the most strongly increased.

These results provide evidence of the fundamental role played by the nSS in the horizontal OKN related to the contralateral eye when the stimulation is TN. The nEM, which is considered essential in the generation of vertical OKN, was also shown to have a strong involvement in the horizontal OKN triggered by the contralateral eye in the N-T direction of stimulation.

These results confirm previous data in birds obtained by lesions, stimulations or 2DG labelling of pretectal nucleus (Gioanni 1983a, b; Chown *et al.*, 1984; McKenna and Wallman, 1981, 1985b) as well as in amphibians (Montgomery *et al.*, 1982; Manteuffel *et al.*, 1983) indicating the involvement of the nSS in the horizontal OKN resulting from T-N stimulation. They show that the AOS is involved in horizontal OKN also, especially for a N-T direction of stimulation; this confirms the data obtained by lesions (Gioanni *et al.*, 1983b).

It has shown that the GABA which is abundant in these mesencephalic structure, as evidenced by immunocytochemical techniques in rodents (Giolly *et al.*, 1985), avians (Britto *et al.*, 1989) and frogs (Yücel *et al.*, 1988), could control the directional asymmetry of horizontal monocular eye OKN.

The GABAergic systems could be responsible for the degree of horizontal OKN asymmetry by regulating the directional selectivity of the cells.

On the other hand, when the stimulated eye was either contralateral to the injected nSS or ipsilateral to the injected nEM, OKN performances were strongly increased when the stimulation was T-N and, in this case, the directional asymmetry of OKN was increased. When the stimulated eye was

contralateral to the injected nEM or ipsilateral to the injected nSS, OKN performances were strongly amplified when the stimulation was N-T. In this case, the directional asymmetry of OKN disappeared.

These data confirm that crossed interactions exist beside homolateral ones. Several observation have already suggested this possibility. In the pigeon, unilateral lesion of the nSS caused the abolition of the OKN induced by the ipsilateral eye as well, indicating an inhibitory effect between the two pretecta (Gioanni *et al.*, 1983b). Moreover, according to the latter report and our own observations, crossed interconnections seem to strongly influence on OKN than homolateral ones.

Tracing techniques have shown that reciprocal projections exist between the nEM in birds and the pretectal nuclei in Amphibians; but there are also afferences from the nEM to both ipsi- and contralateral nSS (Azevedo *et al.*, 1983; Brecha *et al.*, 1980; Gamlin, 1984; Montgomery *et al.*, 1985; Naujocks-Manteuffel, 1986). These morphological relationships clearly support the possibility of functional interactions. It is probable that the GABA is intimately involved in this processes but interactions at a higher levels such as in the cerebellum cannot be excluded.

Although the mechanisms of these interactions are still unknown, it seems that the directional selectivity of monocular eye OKN could be determined by the directional selectivity of cells in these mesencephalic structures. Thus, the spontaneous firing of neurons within the pretectum diplays a predominent depression after stimulation of the ipsilateral nBOR in pigeons (Baldo and Britto, 1990). In the Salamander, the direction sensitive pretectal cells, whose preferential direction is T-N for the contralateral eye, are inhibited when each eye is simultaneously by stimulated in the T-N direction. This indicates a reciprocal inhibition between both pretecta (Manteuffel, 1985).

In the experimental conditions. it is difficult to relate the OKN asymmetry to the directionality of the pretectal and nBOR neurons. As it was previously shown in other visual cells such as in the retina (Ariel and Daw, 1982) or in the visual cortex (Sillito, 1977), the administration of GABA antagonist suppressed the directionality of these visual neurons. On the contrary, in our study it seems that the directionality is rather strengthened. The lost of OKN asymmetry or its reinforcement is probably because of the fact that each nucleus (nSS or nEM) is uninhibited and seems to respond better to stimulus direction for which it is specialized in normal conditions (T-N for the nSS and N-T for the nEM). Thus, each nucleus is able to generate an optokinetic response with optimal gain, whereas in normal condition, the nEM is more inhibited for the N-T direction than the nSS, which in turn is more inhibited for the T-N direction.

This last point raises the question of functional significance of the OKN asymmetry in birds. Wallman and his collaborators (Burns and Wallman 1981; Wallman and Veloz, 1985) suggest that the optokinetic system, and especially the AOS code the visual signal according to the coordinates corresponding to the vestibular channels. The visuo-vestibular integration would therefore be obtained by a relatively simple mechanism. However this hypothesis must still be thoroughly checked out.

References

Ariel, M. and N.W. Daw, 1982. Pharmacological analysis of directionally sensitive rabbit retinal ganglion cells. *J. Physiol.* **324:** 161-185.

Azevedo, T.A., A. Cukiert, and L.R.G. Britto, 1983. A pretectal projection upon the accessory optic nucleus in the pigeon: an anatomical and eletrophysiological study. *Neurosci. Lett.* **43:** 13-18.

Baldo, M.V.C. and L.R.G. Britto, 1990. Accessory optic-pretectal interactions in the pigeon . *J. Med. Biol. Res.* **23:** 1037-1040.

Bonaventure, N., M.S. Kim, B. Jardon, and Y.H. Yücel, 1992. Pharmacological study of the chicken monocular optokinetic nystagmus. Effects of GABAergic agonist and antagonists. *Vision Res.* **32:** 611-620.

Brecha, N., H.J. Karten, and S.P. Hunt, 1980. Projections of the nucleus of the basal optic root in the pigeon; an autoradiographic, and horseradish peroxydase study. *J. Comp. Neurol.* **189:** 615-670.

Britto, L.R.G., D.E. Hamassaki, K.T. Keyser, and H.J. Karten, 1989. Neurotransmitters, receptors and

neuropeptides in the accessory optic system: an immunocytochemical survery in the pigeon, (Columba livia). *Visual Neurosci.* **3:** 463-475.

Burns, S. and J. Wallman, 1981. Relation of single unit properties to the oculomotor function of the nucleus of the basal optic root(accessory optic system) in chickens. *Exp. Brain Res.* **42:** 171-180.

Chambon, Jp, P. Feltz, M. Heaulme, S. Restle, R. Schlichter, K. Biziere, and C.G. Wermuth, 1985. An aryl-amicopyridazine derivative of GABA is a new selective and competitive antagonist at the $GABA_A$ receptor site. *Proc. Natl. Acad. Sci. USA* **82:** 1832.

Chown, P.J., P. Ramm, B. Morgan, and B.J. Frost, 1984. Functional analysis of LMmc of pigeon accessory optic system. *Soc. Neurosci. Abstr.* **10:** 574.

Fite, K.V., A. Reiner, and S.P. Hunt, 1979. Optokinetic nystagmus and the accessory optic system of Pigeon and Turtle. *Brain Behav. Evol.* **16:** 192- 202.

Frost, B.J., P. Ramm, and B. Morgan, 1980. Selective Activation of Pigeon nBOR with Vertical Whole-filed Movement as Revealed by 14C-2DG Autoradiography. 10 Annual Meeting Society for Neuroscience, Cincinatti, Vol. 6.

Gamlin, P.D.R., 1984. The Organization of Pretectal and Tectal Visual Pathways in the Pigeon (Columba livia), Ph. D. diss Suny Stony Brook.

Gioanni, H., J. Rey, J. Villalobos, J.J. Bouyer, and Y. Gioanni, 1981. Optokinetic nystagmus in the pigeon (Columba livia). I. Study in monocular and binocular vision. *Exp. Brain Res.* **44:** 362-370.

Gioanni, H., J. Rey, J. Villalobos, D. Richard, and A. Dalbera, 1983a. Optokinetic nystagmus in the Pigeon (Columba livia). 2. Role of the pretectal nucleus of the accessory optic system. *Exp. Brain Res.* **50:** 237-247.

Gioanni, H., J. Villalobos, J. Rey, and A. Dalbera, 1983b. Optokinetic nystagmus in the Pigeon (Columba livia). 3. Role of the nucleus ectomamillaris: interactions in the accessory optic system. *Exp. Brain Res.* **50:** 248-258.

Gioanni, H., J. Rey, J. Villalobos, and A. Dalbera, 1984. Single unit activity in the nucleus of the basal optic root (nBOR) during optokinetic vestibular and visuo vestibular stimulations in the alert Pigeon (Columba livia). *Exp. Brain Res.* **57:** 49-60.

Giolli, R.A., G.M. Peterson, C.E. Ribak, H.M. McDonald, R.H.I. Blanks, and J.H. Fallon, 1985. GABAergic neurons comprise a major cell type in rodent visual relay nuclei: an immunocytochemical study of pretectal and accessory optic nuclei. *Exp. Brain Res.* **61:** 194-203.

Karten, H.J. and W. Hodos, 1967. A stereotaxic Atlas of the Brain of the Pigeon (Columba livia) John Hopkins, Press Baltimore.

Manteuffel, G., 1987. Binocular afferents to the salamander pretectum mediate rotation sensitivity of cells selective for visual backgrounds motions. *Brain Res.* **422:** 381-383.

Manteuffel, G., J. Petersen, and W. Himstedt, 1983. Optic nystagmus and nystagmogen centers in the european salamander (Salamandra salamandra). *Zool. J. Physiol.* **87:** 175-184.

McKenna, O.C. and J. Wallman, 1981. Identification of avian brain regions responsive to retinal slip using 2-deoxyglucose. *Brain Res.* **210:** 455-460.

McKenna, O.C. and J. Wallman, 1985a. Accessory optic system and pretectum of birds: comparisons with those of other vertebrates. *Brain Behav. Evol.* **26:** 91-116.

McKenna, O.C. and J. Wallman, 1985b. Functional postnatal changes in avian brain regions responsive to retinal slip: a 2-deoxy-D-glucose study. *J. Neurosci.* **5:** 330-342.

Montgomery, N., K.V. Fite, M. Taylor, and L. Bengston, 1982. Neuronal correlates of optokinetic nystagmus in the mesencephalon of Rana pipiens: functional analysis. *Brain Behav. Evol.* **21:** 137-153.

Montgomery, N., K.V. Fite, and A.M. Grigonis, 1985. The pretectal nucleus lentiformis mesencephali of Rana pipiens. *J. Comp. Neurol.* **234:** 264-275.

Natal, C.L. and L.R.G. Britto, 1987. The pretectal nucleus of the optic tract modulates the direction selectivity of accessory optic neurons in Rat. *Brain Res.* **419:** 320-323.

Naujocks-Manteuffel, C. and G. Manteuffel, 1986. Internuclear connections between the pretectum and the accessory optic system in Salamandra salamandra. *Cell Tissue Res.* **243:** 595-602.

Reperant, J., 1978. Organisation Anatomique du Systeme Visuel des Vertébrés, Approche évolutive. Thése Paris.

Sillito, A.M., 1977. Inhibitory processes underlying the directional secificity of simple, complex and hypercomplex cells in the cat's visual cortex. *J. Physiol.* **271:** 699-721.

Simpson, J.I., R.A. Giolli, and R.H.I. Blanks, 1988. The pretectal nuclear complex and the accessory optic system, in: Neuroanatomy of the oculomotor system (Buettner-Ennever, J.A., ed.). Elsevier Science Publishers, Amsterdam, pp.335-364.

Wallman, J., O.C. McKenna, and J. Velez, 1981b. Lesions in avian accessory optic system severly disrupt optokinetic nystagmus in nonhorizontal directions.

Soc. Neurosci. Abstr. **7:** 299.

Wallman, J. and J. Velez, 1985. Directional asymmetries of optokinetic nystagmus; developmental changes and relation to the accessory optic system and to the vestibular system. *J. Neurosci.* **5:** 317-329.

Winterson, B.J. and S.E. Brauth, 1985. Direction selective simple units in the nucleus lentiformis mesencephali of the Pigeon (Columba livia). *Exp. Brain Res.* **60:** 215-226.

Yücel, Y.H., C. Hindelang, M.E. Stoeckel, and N. Bonaventure, 1988. GAD immunoreactivity in pretectal and accessory optic nuclei of the frog mesencephalon. *Neurosci. Lett.* **84:** 1-6.

Yücel, Y.H., B. Jardon, M.S. Kim, and N. Bonaventure, 1990. Directional asymmetry of the horizontal monocular and eye optokinetic nystagmus: effects of picrotoxin. *Vision Res.* **30:** 549-555.

Yücel, Y.H., B. Jardon, and N. Bonaventure, 1991. Unilateral pretectal microinjections of SR 95531, a GABA antagonist: effects on directional asymmetry of frog monocular OKN. *Exp. Brain Res.* **83:** 527-532.

(Accepted December 5, 1995))

OKN을 유발하는 단측 Mesencephalic 구조에 GABA Antagonist를 미량 주입할 때의 닭의 OKN 방향적 불균형성에 관한 특수효과

김명순(우석대학교 자연과학대학 생물학과)

GABA antagonist인 SR 95531이 닭의 pretectum nucleus(nucleus Superficialis Synancephali nSS) 또는 nBOR(nucleus Ectomammillaris nEM) 속에 미량 주입되었다. 단안의 optokinetic nystagmus는 한쪽 뇌의 내부에 약품을 주입하기 전후에 탐색 코일 테크닉에 의해서 기록되었다. 한쪽 nSS 또는 nEM 속에 SR 95531를 미량 주입하면 자극의 양방향에 대하여 반대쪽 눈에 의해서 유도된 단안의 OKN 속도 게인이 가역적으로 증가하였다. 이때 nSS 속에 주입하면 N-T 성분의 속도 게인보다 T-N 성분의 속도 게인을 더욱 강하게 증가시킴으로써 방향적 불균형성이 더욱 증가되었다. 한편 한쪽 nEM 속에 약품을 주입하게 되면 T-N 성분의 속도 게인보다 N-T 성분의 속도 게인이 더욱 강하게 증가함으로써 방향적 불균형성을 제거했다. 이것으로부터 우리는 nSS가 특히 N-T 자극에 대한 반응에 단안의 OKN이 관련되어 있고, nEM은 N-T 자극에 대한 OKN 반응에 더욱 관련되어 있는 것으로 유추할 수 있다. 이 결과는 그 약품이 중뇌 수준에서 OKN에 관련된 GABAergic 메카니즘의 억제작용을 제거한다는 것을 암시한다. 미량 주입된 핵에 대하여 같은쪽 눈에 의해서 유도된 OKN의 게인의 증가는 수평적 OKN에 관련된 이들 중뇌 구조들 사이에 강한 상호작용이 존재한다는 것으로 설명된다.