Title	Effects of unilateral spreading depression upon monocularly trained operant behavior in Pigeons
Sub Title	
Author	渡辺, 茂(Watanabe, Shigeru)
Publisher	三田哲學會
Publication year	1978
Jtitle	哲學 No.68 (1978. 10) ,p.133- 143
JaLC DOI	
Abstract	Pigeons were monocularly trained on FR 40. Then, unilateral spreading depression was produced by a micro-injection of Kcl solution into the hyperstriatum. Spreading depression on the trained hemisphere (contralateral to the trained eye) completely suppressed the responding of the subjects, but spreading depression on the untrained hemisphere (ipsilateral to the trained eye) did not cause complete suppression. However, the depression on the untrained hemisphere had a transient decreasing effect on the responding of the subjects. The present results demonstrate the lateralization of monocular FR training in that the intact trained hemisphere is necessary to maintain a high rate responding. EEG was continuously monitored during the experiment, but the duration of EEG depression, did not agree well with the duration of behavioral suppression.
Notes	
Genre	Journal Article
URL	https://koara.lib.keio.ac.jp/xoonips/modules/xoonips/detail.php?koara_id=AN00150430-00000068-0133

Effects of Unilateral Spreading Depression upon Monocularly Trained Operant Behavior in Pigeons[1)]

Shigeru Watanabe[2)]

Pigeons were monocularly trained on FR 40. Then, unilateral spreading depression was produced by a micro-injection of Kcl solution into the hyperstriatum. Spreading depression on the trained hemisphere (contralateral to the trained eye) completely suppressed the responding of the subjects, but spreading depression on the untrained hemisphere (ipsilateral to the trained eye) did not cause complete suppression. However, the depression on the untrained hemisphere had a transient decreasing effect on the responding of the subjects. The present results demonstrate the lateralization of monocular FR training in that the intact trained hemisphere is necessary to maintain a high rate responding.

EEG was continuously monitored during the experiment, but the duration of EEG depression did not agree well with the duration of behavioral suppression.

One of the most interesting topics in the study of the interhemispheric relation of learning is the lateralization of effects of monocular training. Research combining unilateral cortical spreading depression and monocular training was attempted in rats and rabbits[1, 2, 3, 12, 13, 16, 17)]. Burešovà and Nadel[1)] trained hooded rats monocularly on brightness and pattern discrimination and found that the saving of relearning was 30 percent when the trained hemisphere

1) The author wishes to express his gratitude to Dr. Bureš for his valuable comments and criticism.

2) Department of Psychology, Keio University.

(hemisphere contralateral to the open eye during the original monocular training) was depressed and 70 percent when the untrained hemisphere (hemisphere ipsilateral to the open eye during the original monocular training) was depressed. These results show that relative lateralization of memory trace is formed during the original monocular training. Burešovà, Bureš, and Rustova[3] obtained savings of 0 percent and 90 percent with the trained and the untrained hemisphere depression respectively in similar situation. These results are compatible to those obtained from commissure section and lesion studies[6,14,15].

Birds are convenient subjects for research on interhemispheric relation of learning because of their completely crossed optic chiasm[21,23,24,25]. Catania[5] and Watanabe[23] reported that pigeons could learn conflict discrimination in which S^D and S^Δ were reversed depending on which eye was used. For example, pigeons learned to peck a key illuminated with a green light and not to peck the key illuminated with a red light when they used their left eye, and to peck the key illuminated with a red light and not to peck the key illuminated with a green light when they used their right eye. Successful learning of the conflict discrimination task by intact pigeons suggests that contradicted memory trace was formed in each hemisphere. In other words, each memory trace was considered to be lateralized in this case.

These behavioral studies with pigeons are suggestive but a study combining spreading depression and monocular training has not yet been attempted in birds. In our preliminary report, we trained pigeons monocularly on VI 50″ and tested their responding under the following four monocular conditions with unilateral spreading depression[10]: 1) the trained eye open and the trained hemisphere depressed, 2) the trained eye open and the untrained hemisphere depressed, 3) the untrained eye open and the trained hemisphere depressed, 4) the untrained eye open and the untrained hemi-

sphere depressed. In general, the pecking response was severely suppressed when the trained hemisphere was depressed, but the suppression was weak when the untrained hemisphere was depressed. These results suggest that the effects of monocular VI training are lateralized. But the fluctuation of the data was great and the results seemed to be inconclusive.

In the present expriment, the author focused on the first and the second test conditions mentioned above. If the response was suppressed in the test with the depression of the trained hemisphere but not in the test with the depression of the untrained hemisphere, the effects of monocular training will be shown to be confined to the trained hemisphere. The schedule of reinforcement was changed to FR. Pigeons respond with constant high rate under FR schedule. Therefore the suppression effect of spreading depression is considered to be more sensitively detected by FR than by VI.

Method

Subjects: Six experimentally naive pigeons (Columba livia) were used. They were maintained at about 80 percent of their free feeding weights throughout the behavioral experiment sessions.

Apparatus: EEG was amplified and recorded by a multipurpose poligraph (Nihon-koden RM 85). The behavioral experimental chamber was a Skinner-box (30 cm×17 cm×30 cm) with a single key. Diameter of the key was 30 mm. A grain feeder for reinforcement was attached 15 cm below the key. The Skinner-box and a projector to illuminate the key were set up in a shielded room. The presentation of the lighted key and the schedule of reinforcement were controlled by a logic module controller (Unitec UP-1000) located outside the shielded room. The pecking response of the subject was counted by an electromagnetic counter and was recorded by a comulative recorder. The behavior of the subject was monitored by a TV set and white noise was continuously present.

Procedure: A surgery to implant chronically electrodes and canulae for Kcl solution injection was performed under anesthesia by Nembutahl (4.0 mg/kg). The subject was placed in a stereotaxic apparatus modified in accordance with Karten and Hodos[11]. Six silver ball electrodes, diameter 1.00 mm, were bilaterally placed over the dura of the hyperstriatum. Monopolar recording was obtained from these sites with reference to a silver ball implanted in the bone above the cerebellum. These electrodes were connected to a miniature socket fastened to the skull with dental cement. Two poli-tubes, outer diameter 1.00 mm, were bilaterally implanted over the dura of the hyperstriatum (anterior 7.00~10.00, lateral 2.00~4.00). An injection needle connected to an injector by a flexible vinule tube can be inserted in these poli-tubes. Spreading depression was produced by a micro-injection of 0.75 mcc of 30 percent Kcl solution into the hyperstriatum in accordance with the method developed by Shima[18].

After a few day recovery period, the elicltation of spreading depression was tested. EEG was amplified with a time constant of 0.3 sec and a high frequency cut at 15 Hz. Subjects failing to produce spreading depression were discarded.

Each subject was binocularly shaped up to peck the key by the method of successive approximation. Then, plastic goggles were placed over both eyes of the pigeons with collodion. After one day of continuous monocular reinforcement schedule, they were trained on Fixed Ratio (FR) 40 schedule. One daily session consisted of 100 reinforcements. No blakout period was employed. This schedule continued until the performance of the subject seemed to have attained a steady state on the comulative record. Then two tests with spreading depression were administered: 1) test with the trained eye under depression of the hemisphere contralateral to the trained eye, and 2) test with the trained eye under depression of the hemisphere ipsilateral to the trained eye. During the test EEG was continuously monitored and data without EEG depression were

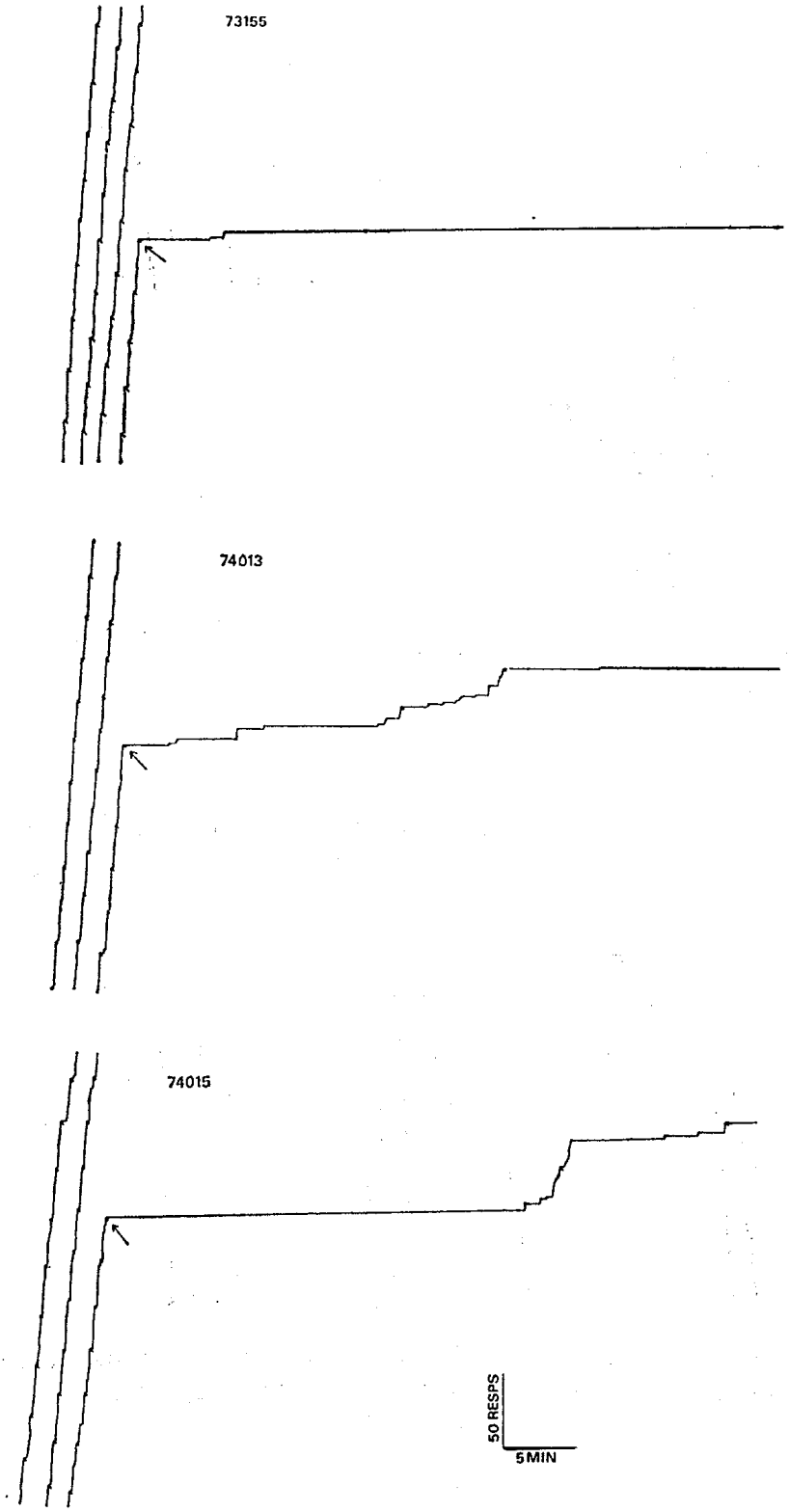

Fig. 1. Cumulative records in the test with the trained hemisphere depression. Arrows indicate injection of Kcl solution.

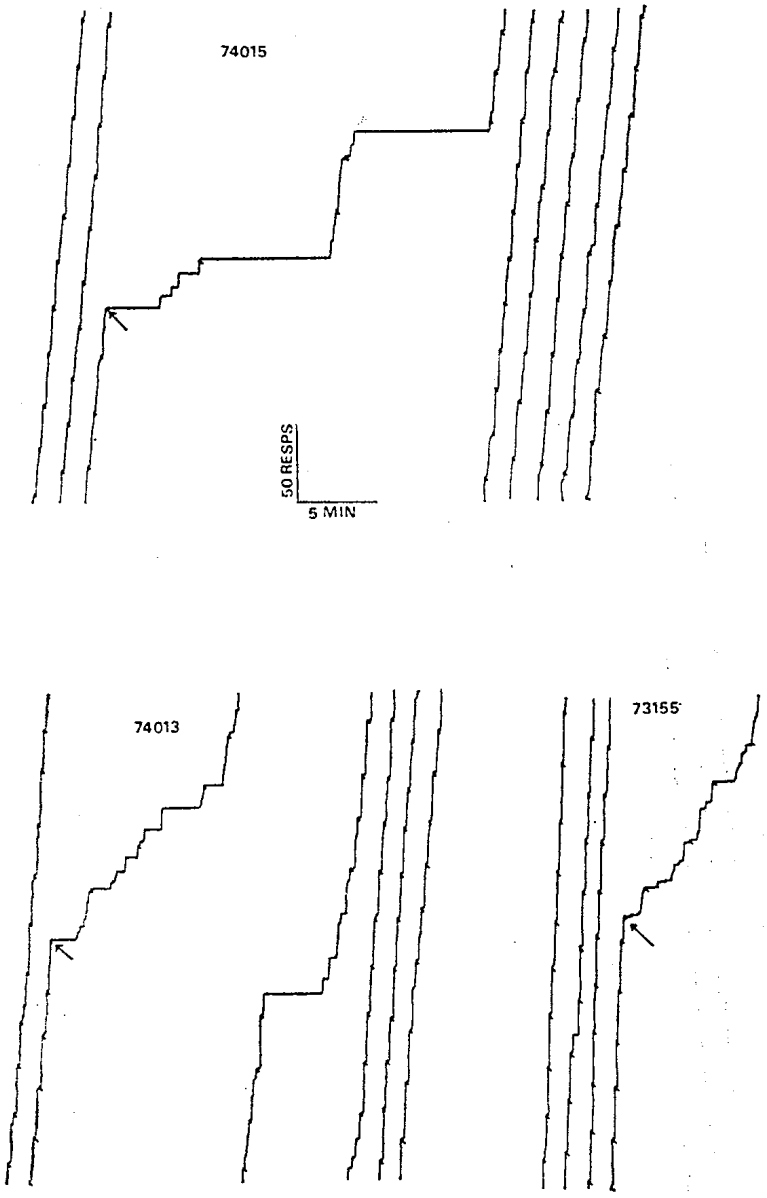

Fig. 2. Cumulative records in the test with the untrained hemisphere depression. Arrows indicate injection of KCl solution.

discarded. Reinforcement was available throughout the sessions.

Results

Subjects were monocularly trained on FR 40 for 10~12 sessions. All of them showed constant high rate of responding. Because three of the six subjects were discarded, results of tests with the application of spreading depression were obtained from the remaining three subjects. Results of the first test are shown in Fig. 1. When spreading depression was produced in the trained hemisphere, responding decreased remarkably or was completely suppressed. A complete suppression of responding was observed in pigeon 73155 and the response did not recover even 100 min after a Kcl injection in this case. Pigeon 74015 also showed a sudden suppression of responding but emitted several responses irregularly until 14 min after a Kcl ingection. Then, it stopped responding completely. A repeated test of this subject showed a 10 min delay of suppression after a Kcl injection. A low rate of responding was observed after a Kcl injection in pigeon 74013, but a complete suppression began 26 min after the injection and continued for 40 min. In a repeated test with this subject, complete suppression continued for 70 min and no recovery was observed.

Results of the second test are shown in Fig. 2. When the untrained hemisphere was depressed, transient decrease of responding was observed but responding did not disappear completely and soon recovered. 74013 showed a decrease of responding for 17 min then exhibited a high rate of responding. A decrease of responding continued for 16 min in pigeon 74015 but the recovery was complete. A repeated test of this subject showed a low rate of responding for 21 min and a 1 min delay of suppression. 73155 also exhibited a decrease of responding but it did not show a clear recovery.

Fig. 3 shows the control test with distilled water injection. In these cases, 0.75 mcc of distilled water was injected into the trained

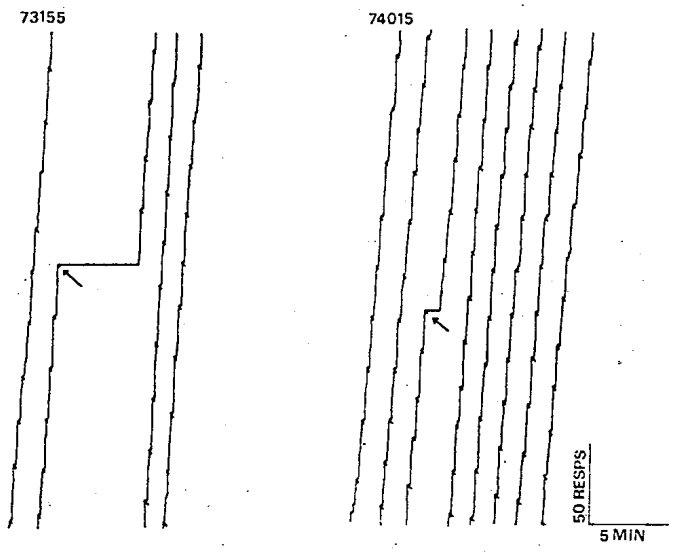

Fig. 3. Cumulative records in the test with distilled water injection. Arrows indicate injection of distilled water into the trained hemisphere.

hemisphere. Some transient decreasing effect was observed but responding reappeared rapidly and recovery was remarkably abrupt.

Discussion

Little information is available on the effect of spreading depression upon conditioned behavior in birds. Shima[18] reported that the key pecking of the pigeon was suppressed by bilateral spreading depression produced by a micro-injection of Kcl solution. He found a good correlation between the duration of behavioral suppression and the time course of EEG depression. In the present experiment, a clear correlation between the duration of behavioral suppression and that of EEG depression was not obtained. The subjects, which did not emit pecking response after recovery from EEG depression, showed no movement and seemed to be drawsy. Carew and Petrinovich[4] reported that the duration of behavioral suppression was longer than that of EEG depression in hooded rats. But their behavioral measure was hyperthesia and not conditioned operant

behavior with positive reinforcement. Suzuki and Uneoka[19] found longer latency of suppression of bar pressing than that of DC or EGG depression in rabbits. In the study of active avoidance in rats, a good correlation between behavioral performance and slow potential shift by spreading depression was reported[8,9]. Physiological index of spreading depression in the present experiment was only the amplitude of EEG, and it will be necessary to record slow potential shift for analysis of phasic relation of spreading depression and behavioral change in pigeons.

In the present experiment, spreading depression on the trained hemisphere completely suppressed the monocularly trained FR schedule controlled behavior. On the other hand, spreading depression on the untrained hemisphere did not severely suppress that behavior. These results can be explained in terms of lateralization of the effects of monocular training or in terms of blindness caused by unilateral spreading depression. Visually evoked potentials are recorded from both ipsilateral and contralateral hyperstriatum of the pigeon by a photic stimulation to one eye[7,20]. Thus, it is not plausible to assume that unilateral spreading depression caused complete blindness in the pigeon. Therefore, the present results are considered to demonstrate the lateralization of the effects of the monocular FR training.

One point to be discussed is the effect of spreading depression on the untrained hemisphere. Spreading depression on this side did not completely suppress the responding but decreased its rate, and a high rate of responding soon reappeared. A decrease of responding rate may mean that the lateralization in the experiment was not absolute but a relative one. However, as shown in the test with spreading depression on the trained hemisphere, an intact trained hemisphere is necessary to maintain a high rate of responding. In other words, the untrained hemisphere could not maintain a high rate responding by itself even if it participates in monocular responding. A rapid recovery of high rate responding may mean that

the trained hemisphere compensates for the lack of function of the untrained hemisphere. These explanations are only speculative and the function of the untrained hemisphere in monocular training is not yet clear.

In summary, it is concluded that the effects of monocular FR training was lateralized to the hemisphere contralateral to the trained eye in the sense that the trained hemisphere must be intact to maintain a high rate of responding.

References

1) Burešová, O. and Bureš, J. The siginificance of crossed and uncrossed projections for the acquisition and retrieval of visual engrams in hooded and albino rats. *Psychol. Forsch.*, **35**: 46–56, 1971.
2) Burešová, O. and Nadel, L. Interhemispheric transfer in the rat. *Physiol. Behav.*, **5**: 849–853, 1970.
3) Burešová, O., Bureš, J. and Rustová, M. Conditions for interhemispheric transfer of initially lateralized visual engrams in hooded rats. *J. comp. physiol. Psychol.*, **75**: 200–205, 1971.
4) Carew, T., Crow, T. and Petrinovich, L. F. Lack of coincidence between neural and behavioral manifestations of cortical spreading depression. *Science*, **169**: 1339–1341, 1970.
5) Catania, A. C. Interocular transfer of discrimination in the pigeon. *J. exp. Anal. Behav.*, 8: 147–155, 1969.
6) Creel, D. J. and Sheridan, C. L. Monocular acquisition and interocular transfer in albino rats with unilateral striate ablations. *Psychon. Sci.*, **6**: 89–90, 1966.
7) Cuénod, M. Commissural pathway in the interhemispheric transfer of visual information in the pigeon. In: *Neuroscience*, edited by Schmitt, F. O. and Worden, F. G. London: MIT Press., 1973, pp. 21–29.
8) Freedman, N. L. Recurrent behavioral recovery during spreading depression. *J. comp. physiol. Psychol.*, **68**: 210–214, 1969.
9) Freedman, N. L. and Bureš, J. Conditions of phasic impairment of avoidance responding during bilateral spreading depression. *J. comp. physiol. Psychol.*, **78**: 433–441, 1972.
10) Ito, M., Watanabe, S., Yokoyama, K. and Sato, M. The effects of spreading depression upon operant responses in pigeons. *Proc. 36 th Congr. J. P. A.*, 410–411, 1972.

11) Karten, H. J. and Hodos, W. *Stereotaxic atlas of the brain of the pigeon.* Baltimore: John Hopkins, 1967.
12) Lishman, W. A. and Eayrs, J. T. Localization of a memory trace in the intact rat. *Physiol. Behav.*, **1**: 161–166, 1966.
13) Megirian, D. and Bureš, J. Unilateral cortical spreading depression and conditioned eyeblink responses in the rabbit. *Exp. Neurol.*, **27**: 34–45, 1970.
14) Myers, R. E. Corpus callosum and interhemispheric communication: Enduring memory effect. *Fed. Proc.*, **16**: 92, 1957.
15) Myers, R.E. and Sperry, R.W. Interhemispheric communication through the corpus callosum. *Arch. Neurl. Psychiat.*, **80**: 298–302, 1958.
16) Nadel, L. and Burešovà, O. Monocular input and interhemispheric transfer in the reversible split-brain. *Nature*, **220**: 914–915, 1968.
17) Nadel, L. and Burešovà, O. Interocular transfer in the hooded rat. *Physiol. Behav.*, **4**: 613–619, 1969.
18) Shima, I. Behavioral consequences of striatal spreading depression in pigeons. *J. comp. physiol. Psychol.*, **57**: 37–41, 1964.
19) Suzuki, H. and Uneoka, K. Effect of cortical spreading depression on operant behavior in the rabbit. *Physiol. Behav.*, **1**: 301–304, 1966.
20) Takada, K., Watanabe, S., Omino, T. and Yokoyama, K. Visual evoked potentials in the hyperstriatum of the pigeon. (in Japanese) *Studies in Sociology, Education and Psychology*, **13**: 79–83, 1973.
21) Watanabe, S. Interocular transfer of stimulus control in pigeons. *Ann. Anim. Psychol.*, **24**: 1–14, 1974.
22) Watanabe, S. Interocular transfer of generalization along line-tilt dimension in pigeons: A separation of three types of symmetric stimuli. *Jap. psychol. Res.*, **17**: 133–140, 1975.
23) Watanabe, S. Reversal discrimination learning with each eye in pigeons. (in Japanese) *Proc. 39 th Congr. J. P. A.*, **168**: 1975.
24) Watanabe, S. An experimental analysis of the mirror image reversal effect during learning with each eye in pigeons. *Proc. 21 th internl. Congr. Psychol.*, **168** (abstr.), 1976.
25) Watanabe, S. and Ogawa, T. An experimental analysis of mirror image reversal effects in pigeons. *Ann. Anim. Psychol.*, **23**: 1–13, 1973.