

## Discrepant effects of unilateral and bilateral forebrain lesions on the visual performance of pigeons

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*Key words:* telencephalon — visual discrimination — hyperstriatum — pigeon

The monocular and binocular performance of pigeons with bilateral, unilateral or sham lesions in the telencephalic Wulst was tested with visual discrimination tasks. Unilateral lesions yielded a marked deficit when the animals could only use the eye contralateral to the lesion. Otherwise the accomplishments of the ablated animals did not differ from that of the controls. The reciprocal inhibition of symmetrical visual brain stem centers is thought to have been unbalanced through the one-sided interruption of a known pathway descending from the Wulst.

Birds possess two main visual projections to the telencephalon: a tectofugal projection ending in the ectostriatum [4, 12], and a thalamofugal one that decussates partially through the supraoptic commissure and ends in a restricted area of the hyperstriatum or Wulst [13, 16, 18, 28]. Bilateral lesions of the ectostriatum apparently cause profound deficits on the performance of even simple visual discrimination tasks [9]. Equivalent ablations of the Wulst yield relatively minor deficits that often can only be demonstrated with sophisticated testing [10, 14, 19, 20, 25, 29]. Incidental observations suggested, however, that under certain circumstances hyperstriatal lesions can, nonetheless, have drastic effects on the visual performance of pigeons. We now report a formal experiment intended to corroborate these preliminary findings.

Twelve adult homing pigeons (*Columba livia*), deprived to 80% of their weight, were used. A conventional two-key Skinner-box (Fig. 1A), controlled by digital programming equipment, was employed. The subjects were first shaped to peck on the keys for 4 sec food access. Then they were taught to discriminate a cross and an outline triangle (white on black background), half of them with the cross, the other half with the triangle defined as positive stimulus. A trial

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began with the discriminanda being back-projected on the keys. When the animal pecked the key bearing the positive stimulus, the stimuli extinguished, food was offered and the next trial began immediately afterwards, the left–right positions of the stimuli being determined by a quasi-random sequence [7]. If the subject responded to the negative stimulus, the stimuli and the houselight extinguished for 10 sec before the next trial began, the stimulus positions being retained, thus instituting a correction procedure. Counters recorded the correct and incorrect responses, correction trials being disregarded. Daily sessions of 40 non-correction trials or 60 min, whichever occurred first, were given until all animals reached the criterion of 80% or more correct responses within a session.

According to their performance in the cross–triangle discrimination the animals were assigned to 3 matched groups of 4 subjects each. One group received unilateral lesions, another bilateral lesions of the Wulst while the third group was sham-operated. Two of the unilaterally ablated pigeons had the right and the two others the left Wulst destroyed. The operations were done under barbiturate–chloral hydrate anesthesia with a radiofrequency coagulator while the subject's head was held in a stereotaxic apparatus. The animals were sacrificed following the behavioral experiments. The perfused brains were sectioned with a freeze microtome and stained with cresyl violet. The lesions were examined under the microscope and their extent transferred onto drawings taken from a stereotaxic atlas [11]. Examples are shown in Fig. 1B.

During the operation a small tapped brass block was fixed to the skull with dental cement. Opaque eye caps could be screwed onto these blocks (Fig. 1C). Testing, using the same discrimination procedure described above, began one week after the operation. First we examined the retention of the previously learned discrimination. The animals had to perform alternately with one or the other eye occluded according to a balanced design. Later we examined the acquisition of a new discrimination (circle against square) in a similar way. Since the results for these two tasks did not differ they were grouped together for the purposes of evaluation. Another discrimination problem (horizontal against vertical rectangles) was interposed between the two to assess the performance of the animals when they had an unimpeded view with both eyes. The subjects were run on each discrimination task until they reached criterion (none took less than two sessions) or completed 4 sessions.

We present the results of these experiments in the form of mean correct responses cumulated over sessions (Fig. 1D–G). It is apparent that the unilaterally lesioned animals performed worse when seeing with the eye contralateral to the lesion than when doing so with the ipsilateral eye (pooled Wilcoxon,  $P < 0.01$ ). In fact two birds, those with the most extensive lesions, appeared to be nearly blind on the contralateral eye and they mostly did not respond at all, while the

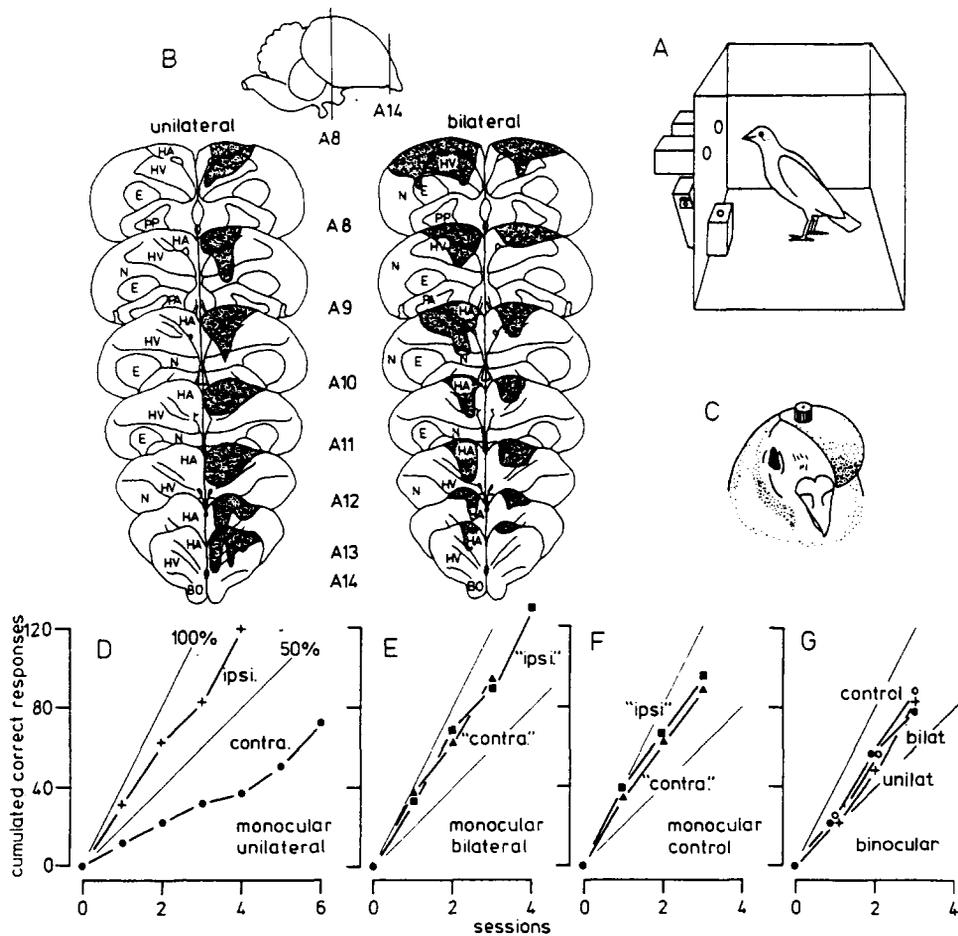


Fig. 1. A: experimental chamber. B: unilateral and bilateral lesions of the birds with the most extensive damage. Drawings based on the atlas of Karten and Hodos [11]. BO, bulbus olfactorius; E, ectostriatum; HA, hyperstriatum accessorium; HV, hyperstriatum ventrale; N, neostriatum; PA, paleostriatum augmentatum; PP, paleostriatum primitivum. C: pigeon with eye cap. D–G: mean cumulative correct responses over sessions. Monocular performance of unilateral (D), bilateral (E) and sham-operated controls (F). Ipsilateral and contralateral: seeing eye with reference to unilateral lesions; arbitrary for bilateral and control subjects. G: binocular performance of all three groups. The slopes corresponding to perfect (100%) and chance (50%) discrimination are indicated. The mean performance of the unilateral subjects with the contralateral eye falls below chance because two animals often did not respond (equivalent to zero correct responses per session).

other two retained enough vision to attempt the task. The performance with the ipsilateral eye, in contrast, did not differ from that of sham-operated controls (pooled Mann–Whitney,  $P > 0.10$ ). The monocular performance of the bilaterally lesioned pigeons also could not be distinguished from that of the controls. When the animals could use both eyes there was no difference among the 3 groups.

It does not seem possible to ascribe the visual deficit of the unilaterally lesioned animals to the loss of the hyperstriatal visual projection area as such. If that were so, the bilaterally lesioned animals should have shown an equivalent, symmetric effect. The unilateral lesion effect must thus be due to some influence that the ablated area exerts upon another brain region processing visual information. The Wulst could do this through either of two efferent pathways. One courses to the periphery of the ectostriatum [13], and the other to a number of brain stem visual centers, among them the tectum opticum and the thalamus opticus via the septomesencephalic tract [1, 13, 17, 18]. The latter pathway is mainly or totally non-decussating and exerts both excitatory and inhibitory effects upon its target neurons [3, 5].

Our finding may relate to older reports describing a contralateral blindness in unilaterally hemispherectomized birds which is relieved by complete detelencephalization or ipsilateral eye excision or contralateral tectum ablation [21, 26]. This would implicate the second of the efferent pathways mentioned above. The working hypothesis is that this projection modulates the action of the intertectal inhibitory pathway [2, 22, 27] so that a unilateral lesion creates an inhibitory imbalance which can be corrected by a suitable additional ablation. We note that Meier et al. [15] found only mild contralateral vision deficits if the unilateral Wulst lesions were accompanied by a supraoptic commissure transection. Their Wulst-only lesions, however, appear to have been less extensive than ours and may well have spared much of the descending hyperstriatofugal pathway [6].

The finding that an additional lesion redresses the deficit caused by another is not exceptional. Sprague (ref. 24, see also ref. 23) has reported a similar effect concerning the superior colliculus and the occipital cortex of cats, and Hodos and Bonbright [8] mention an analogous case with respect to the lateral geniculate nucleus (not homologous to the mammalian structure of the same name!) and the nucleus rotundus of pigeons.

We wish to thank U. Niewendick, J. Emmerton, H. Stankewitz, H. Heinig and A. Lohmann for assistance of various kinds. The research was supported by the Deutsche Forschungsgemeinschaft through its Sonderforschungsbereich 114.

#### REFERENCES

- 1 Adamo, N.J., Connections of efferent fibers from hyperstriatal areas in chicken, raven and African lovebird, *J. comp. Neurol.*, 131 (1967) 337-356.
- 2 Arduini, A., Moruzzi, G. and Zanchetti, A., Soppressione reversibile delle visive di difesa del piccione ottenuta colla stimolazione chimica del tetto ottico ipsilaterale. *Boll. Soc. ital. Biol. sper.*, 24 (1948) 1-2.
- 3 Bagnoli, P., Francesconi, W. and Magni, F., Interaction of optic tract and visual wulst impulses on single units of the pigeon's optic tectum, *Brain Behav. Evol.*, 16 (1979) 19-37.

- 4 Benowitz, L.I. and Karten, H.J., Organization of the tectofugal visual pathway in the pigeon: a retrograde transport study, *J. comp. Neurol.*, 167 (1976) 503–519.
- 5 Britto, L.R.G., Hyperstriatal projections to primary visual relays in pigeons: electrophysiological studies, *Brain Res.*, 153 (1978) 382–386.
- 6 Cuénod, M., Commissural pathways in interhemispheric transfer of visual information in the pigeon. In F.O. Schmitt and F.G. Worden (Eds.), *The Neurosciences, Third Study Program*, MIT Press, Cambridge, Mass., 1974, pp. 21–29.
- 7 Gellermann, L.W., Chance orders of alternating stimuli in visual discrimination learning, *J. genet. Psychol.*, 42 (1933) 206–208.
- 8 Hodos, W. and Bonbright, J.C., Intensity and pattern discrimination after lesions of the pretectal complex, accessory optic nucleus and ventral geniculate in pigeons, *J. comp. Neurol.*, 161 (1975) 1–18.
- 9 Hodos, W. and Karten, H.J., Visual intensity and pattern discrimination deficits after lesions of ectostriatum in pigeons, *J. comp. Neurol.*, 140 (1970) 53–68.
- 10 Hodos, W., Karten, H.J. and Bonbright, J.C., Visual intensity and pattern discrimination after lesions of the thalamofugal visual pathway in pigeons, *J. comp. Neurol.*, 148 (1973) 447–468.
- 11 Karten, H.J. and Hodos, W., *A Stereotaxic Atlas of the Brain of the Pigeon (Columba livia)*, Johns Hopkins, Baltimore, 1967.
- 12 Karten, H.J. and Hodos, W., Telencephalic projections of the nucleus rotundus in the pigeon (*Columba livia*), *J. comp. Neurol.*, 140 (1970) 35–51.
- 13 Karten, H.J., Hodos, W., Nauta, W.H.H. and Revzin, A.M., Neural connections of the visual wulst of the avian telencephalon, experimental studies in the pigeon (*Columba livia*) and owl (*Speotyto cunicularia*), *J. comp. Neurol.*, 150 (1973) 253–278.
- 14 Macphail, E.M., The role of the avian hyperstriatal complex in learning. In P. Wright, P.G. Caryl and D.M. Vowles (Eds.), *Neural and Endocrine Aspects of Behaviour in Birds*, Elsevier, Amsterdam, 1975, pp. 139–204.
- 15 Meier, R.E., Maier, V. and Cuénod, M., Visual learning following unilateral telencephalic lesions in the splitbrain pigeon, *Brain Res.*, 37 (1972) 256.
- 16 Meier, R.E., Mihailovic, J. and Cuénod, M., Thalamic organization of the retino-thalamo-hyperstriatal pathway in the pigeon (*Columba livia*), *Exp. Brain Res.*, 19 (1974) 351–364.
- 17 Mestres, P.P. and Delius, J.D., Origin of the hyperstriatofugal pathway to the optic tectum of pigeons, in preparation.
- 18 Miceli, D., Gioanni, H., Reperant, J. and Peyrichoux, J., The avian wulst: an anatomical and electrophysiological study. In A.M. Granda and J.H. Maxwell (Eds.), *Neural Mechanisms of Behavior in the Pigeon*, Plenum, New York, 1979, pp. 223–254.
- 19 Parker, D.M. and Delius, J.D., The effects of wulst lesions on simple visual discrimination performance in the pigeon, *Behav. Proc.*, 5 (1980) 151–159.
- 20 Pasternak, T. and Hodos, W., Intensity difference thresholds after lesions of the visual wulst in pigeons, *J. comp. physiol. Psychol.*, 91 (1977) 485–497.
- 21 Patay, R. and Tazartez, G., A propos d'une certaine récupération psychique chez le pigeon décérébré en deux temps, *Acta physiol. pharmacol. néerl.*, 6 (1957) 497–498.
- 22 Robert, F. and Cuénod, M., Electrophysiology of the intertectal commissures in the pigeon, *Exp. Brain Res.*, 9 (1969) 116–136.
- 23 Saraiva, R.E.S., Argão, A.S. and Magalhães-Castro, B., Recovery of depressed superior colliculus activity in neodecorticate opossum through the destruction of the contralateral superior colliculus, *Brain Res.*, 112 (1976) 168–175.
- 24 Sprague, J., Interaction of cortex and superior colliculus in mediation of visual guided behavior in the cat, *Science*, 153, 1544–1547.

- 25 Stettner, L.J., The neural basis of avian discrimination and reversal learning. In I.J. Goodman and M.W. Schein (Eds.) *Birds, Brain and Behavior*, Academic, New York, 1974, pp. 165–202.
- 26 Ten Cate, J., Physiologie des Zentralnervensystems der Vögel, *Ergebn. Biol.*, 13 (1936) 93–173.
- 27 Voneida, T.J. and Mello, N.K., Interhemispheric projections of the optic tectum in pigeon, *Brain Behav. Evol.*, 11 (1975) 91–108.
- 28 Webster, K.E., Changing concepts of the organization of the central visual pathways in birds. In R. Bellairs and E.G. Gray (Eds.) *Essays on the Nervous System*, Oxford University Press, Oxford, 1974, pp. 258–298.
- 29 Williams, A.S., *Discrimination Learning and Forebrain Lesions in Pigeons*, Ph.D. Thesis, University of London, Birkbeck College, 1978.