Aggressive Behavior of Pigeons: Suppression by Archistriatal Lesions

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The agonistic responses of pigeons to the introduction of a stick and the experimenter's hand into their home cages is described. The effects of lesions of the archistriatum, a presumed homologue of the mammalian amygdala, of lesions of the overlying neostriatum and of control sham operations on this behavior in selected aggressive pigeons are reported. Only archistriatal lesions lead to a persistent depression of the aggressive and a converse increment of the avoidance components of the pigeon's response to both test stimuli. The results are discussed in relation to other evidence on the role of the avian archistriatum and this structure's correspondence with the amygdala.

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Key words: pigeon, archistriatum, intra/interspecific aggression

INTRODUCTION

Ethological studies show that the aggressive behavior of animals serves a variety of functions depending on the socio-ecological niche occupied by each species. Accordingly, it can be expected that the physiological mechanisms controlling aggression will differ from species to species. A common phyletic origin may conversely have caused the retention of similar patterns of control. It is obvious that comparative studies on the physiological basis of aggression are needed to assess the effect

of these opposing evolutionary tendencies. Presently available information derives largely from only a few species, the cat and the rat being the preeminent ones. The pigeon (*Columba livia*), an ecologically and phylogenetically quite different animal, could be a suitable subject for expanding our knowledge about the physiological substrates of aggression across species. It is a convenient laboratory species, it possesses a relatively stereotyped repertoire of agonistic responses that facilitate quantitative observations, and it has been reasonably well investigated with behavioral methods. Little, however, is known about the physiological basis of the pigeon's agonistic behavior. As part of a more extensive project on this theme [Martin Ramirez and Delius, in press; see also Delius, 1973] we have examined the effect of lesioning the pigeon's archistriatum. This avian forebrain structure is generally thought to be homologous to the mammalian amygdala [Ariens Kappers et al, 1936]. It is well documented that the amygdala is profoundly involved in the control of aggression in mammals; some evidence to be reviewed later in the paper indicates that the archistriatum may play a similar role in birds. Concerning specifically the pigeon, however, the information supporting such an inference is slender. Thus an attempt to establish this role in this species seemed to be worthwhile.

METHODS

Seventy five adult homing pigeons of unknown sex were bought from local dealers. All had previous free-ranging experience. In the laboratory they were kept in standard 50 X 40 X 30 cm cages. Blinds between the cages reduced the visual contact among the animals. They were exposed to an artificial 12-hour light—12-hour dark cycle and to a nearly constant temperature of 18 degrees centigrade. About one third of the animals had previously served in operant conditioning experiments for about three months and had been chronically food-deprived to 80% of their normal weight as well as handled nearly daily. The remainder had simply been kept in the laboratory for about one month. During this study all animals were given ad lib food and water.

In order to elicit agonistic responses from them the subjects were exposed to a sequence of stimuli. First the experimenter approached their cage and peered at them for about 15 seconds. Then he introduced a wooden stick into the cage moving it with stabbing motions toward the animal for some 30 seconds before withdrawing it. Afterwards he waved a hand in front of the cage for 15 seconds and then introduced it into the cage through the door approaching and following the animal with a closed fist for about 30 seconds. Finally the experimenter recorded standardized scores and made notes about the behavioral responses the subject had shown. The details of the scoring will be described later. As a rule the subjects were tested once daily at 11 AM excepting weekends.

Preliminary testing served to select 18 pigeons that responded reliably with predominantly aggressive behavior (see below). These animals were then systematically

tested for four weeks before they were submitted to surgery. After a postoperative recovery pause of one week they were tested for a further five weeks. Simultaneously their daily food consumption was determined by giving them a fixed weight of food (40 gm) in a deep trough minimizing grain scattering and weighing the remainder 24 hours later. The subjects were also weighed weekly with a spring balance held in a cloth-jacket.

For the operation the animals were anaesthetized with Equithesin (intramuscular, initial dose 0.25 ml/100 gm bodyweight, additional doses 0.1 ml/100 gm) and their head held in a Stellar-Johnson stereotaxic apparatus modified according to the Karten and Hodos [1967] pigeon stereotaxic atlas. The scalp was retracted and the skull perforated with a dental drill. A brass olive was placed in the cloaca, to serve as indifferent electrode. We attempted to place bilateral lesions in 12 birds at coordinates A 5-6, 5, L 6-7 and V 7-8 using an insulated stainless steel needle with an 0.5 mm exposed tip and by passing a 100 kHz current of approximately 30 mA for 10 seconds. As will be described later there was, however, some variation in the lesions actually obtained. Six control birds were similarly treated except that no coagulation current was applied.

After termination of the observations the animals were sacrificed and their brains perfused with saline and formalin following cannulation of the carotids. After at least one week of fixation in formalin the brains were removed from the skull and sectioned in the stereotaxic frontal plane with a freeze microtome. The 40 μ sections containing lesioned tissue were stained with cresyl violet and examined under the microscope. The extent of the lesions was transferred on to brain section outlines taken from the Karten and Hodos [1967] atlas.

RESULTS

Behavior

Although accounts of the agonistic behavior of pigeons are available [eg, Fabricius and Jansson, 1963; Spiteri, 1975] in the special test situation we used, the responses of the subjects differed somewhat from the extant descriptions. We thus find it necessary to briefly review the behavior shown, conforming as far as possible with the accounts of the above mentioned authors.

The usually initial and least intense response to the testing stimuli is attention. Mostly with a latency of some seconds the subject takes up an erect posture, extending its neck, and begins to make scanning movements with the head, with the eyes wide open. It appears to watch the environment and particularly the experimental stimulus ready to respond with a more active behavior. If the neck remains stretched and the plumage sleeked during this attentive posture then it is likely that the subsequent behavior will be fearful; if the neck is shortened and the plumage fluffed, then the probable

sequel is aggression. Freezing is a fear response that will often develop from the attentive response, the animal simply becoming immobile and remaining so for a period varying between several seconds and minutes before slowly beginning to make small amplitude movements or before suddenly exploding into extreme flight behavior. From attention or such unfreezing pigeons often progress to leaning away, that is bending the body and head away from the stimulus with a sideways orientation without shifting and while observing the stimulus intently. In this position it may hold out the wing closer to the stimulus: wing fending. This may lead to withdrawing, that is walking away mostly with a sideward attitude to the stimulus and attempting frantically to leave the cage, pushing against the wire netting. Attempts to fly away may then be observed, the birds extending and flapping the wings and pushing against the cage walls. This active flight behavior is sometimes, though not often, preceded by alarm calls, harsh notes transcribable as "hinnh." A variant style of avoidance and escape is crouching, when the pigeon presses the body against the floor, the wings drooping slightly and the neck retracted, and sneaking, where it crawls away maintaining this posture.

A distant stimulus often elicits bow-cooing that is walking, tracing a series of reversing semicircles with the plumage fluffed, the tail spread and the throat swollen, with interspersed brief bursts of speed and body and head bows while giving repeated calls "cooo-cooo." If the stimulus approaches, the animal will usually revert to threat. The animal fluffs the plumage, sometimes also spreads the tail and swells the throat maintaining a sideways orientation to the stimulus. The wing opposite to the stimulus is raised above the back, that close to the stimulus is flicked or more rarely also raised. This may lead to attack where the animal approaches the stimulus, sometimes jumping forward and slapping with the wing close to the stimulus, exceptionally with both wings, raising them and bringing them down sharply on it. It will also peck, most short of target, but sometimes gripping the stimulus vigorously, shaking or twisting it with the eyes closed. A deep throated aggressive vocalization may accompany this behavior.

For the final routine scoring the response of a pigeon to a stick or hand test was classed as either attack, threat, retreat or flying away depending on the responses predominantly shown by the subject. In the great majority of the tests there was no difficulty in deciding between the categories. The interobserver agreement was of the order of 95%. Additionally we also noted which of the behavior elements described above were shown during each test component. Later in the text we will also often refer to aggressive and avoidance behavior; these categories simply refer to attack and threat, and retreat and flying away respectively taken together.

We compared the efficacy with which the two stimuli used, stick and hand, elicited aggressive responses from the initial 75 animals not yet selected for predominant aggressive responding. The stick elicited more agonistic responses than the hand in only 5% of the pigeons while the hand did so more than the stick in 84% of the subjects, the remainder of the subjects reacting similarly to both

stimuli. Figure 1 shows that the tests with two stimuli elicited different response profiles. The hand released relatively more attack, retreat and flying away scores than the stick which yielded predominantly threat, while relatively few tests yielded no agonistic responses at all.

Fig. 1. Agonistic behavior shown by pigeons ($N = 75$) in response to a stick and a hand introduced into their home cages.

Lesions

The examination of the histological sections revealed differences in the location and extent of the lesions in the 12 experimental animals. This made it necessary to class them into three groups: three subjects had bilateral lesions in the archistriatum; three others had only unilateral lesions in the same structure (it is possible that very small contralateral lesions might have passed undetected); six subjects had bilateral lesions that largely spared the archistriatum and mainly affected the overlying neostriatum caudale (Fig. 2). Additionally there were six subjects in the control group that had undergone a sham operation; their brains were histologically normal.

Comparing in each case the percentage response scores on both the stick and the hand tests four weeks preoperatively and five weeks postoperatively reveals that both the bilateral and the unilateral archistriatally damaged animals showed reasonably similar decrease in aggressive behavior and increase in avoidance behavior (Fig. 3). This warranted lumping them together into a single group of archistriatals. Due to chance several subjects with preoperatively less marked aggressive and more pronounced avoidance behavior were included in this group. Nevertheless, all the archistriatally lesioned pigeons showed a postoperative decrease in aggression and an increase in avoidance behavior. The animals with neostriatal lesions showed no

Fig. 2. Location of the archistriatal and neostriatal brain lesions. Only a sample of neostriatal lesions is shown; the three remaining pigeons had similar lesions. Numbers identify the subjects.

Fig. 3. Agonistic behavior shown by pigeons during tests before (B) and after (A) lesions of archistriatum. Numbers identify individual subjects.

change in behavior unless it was a slight average increase in aggression (Fig. 4). The control subjects overall similarly did not show changes except that one animal (No. 16) yielded an unexplained delayed and transitory postoperative decrease in aggression and increase in avoidance (Fig. 5).

Figure 6 illustrates the mean results of all three groups. Comparison of the pre-operative with the postoperative behavior separately for the stick and the hand tests reveals that only the archistriatally lesioned animals showed significant changes. The decrease in aggression in the hand test was significant at $P < 0.01$ ($t = 5.43$, $df = 5$). The increase in avoidance was significant for both the stick test ($t = 4.92$, $df = 5$) and the hand test ($t = 5.59$, $df = 5$) at $P < 0.01$.

The nature of the response changes in the archistriatally lesioned animals is shown in more detail in Figure 7. Excepting some of the more rarely occurring patterns for which the evidence is not clear, all other patterns showed changes compatible with the overall conclusion that the lesions produced a decrease in aggressive and an

Fig. 4. Agonistic behavior shown by pigeons during tests before (B) and after (A) lesions of the neostriatum. Numbers identify individual subjects.

increase in avoidance behavior. In particular pecking and wing slapping decreased and leaning away and crouching increased as a consequence of partial ablations of the archistriatum. However the effects of the archistriatal lesions on the agonistic behavior may not be permanent. Figure 8 shows that by the sixth postoperative week the subjects' responses, particularly the aggressive components, returned some way towards preoperative levels. We do not have sufficient data available to decide whether the time until recovery is dependent on the size of the lesion but this seems possible. Since the histology showed that the lesions were filled with glial scar tissue incapable of neural functioning, it must be concluded that other neural tissue must have been responsible for this recovery.

Regarding food consumption there was only a rather slight difference between the archistrially lesioned and the controls (unlesioned and neostrially lesioned). While both groups showed a transitory, about 10% decrease in food intake after the intervention, this decreased intake may have been more prolonged in the archistriatal animals (three weeks) than in the controls (two weeks). This difference did not show up in the body weights, which increased steadily in both groups by about 5% in the course of eight weeks of observation.

Fig. 5. Agonistic behavior shown by pigeons during tests before (B) and after (A) control sham operations. Numbers identify individual subjects.

Fig. 6. Mean agonistic behavior shown by pigeons (N = 6 in each group) during tests before (B) and after (A) archistriatal or neostriatal lesions and sham control operations.

Fig. 7. Comparison of pre- and postoperative agonistic behavior of archistriately lesioned pigeons ($N = 6$).

DISCUSSION

Agonistic behavior is shown by animals in many different functional contexts. It may address members of other species as part of predatory behavior, as an anti-predator response, as a defense against parasites or as a reaction against ecological competitors. As a response to conspecifics it may function to secure or defend resources (including social partners) or to support or prevent intraspecific predation or even to reject diseased individuals. While the behaviors shown in these various situations by a given species may be qualitatively different, they often overlap. The functional context of the agonistic responses elicited by our testing procedures is

Fig. 8. Time course of agonistic behavior changes after archistriatal lesions in pigeons. Mean of six subjects.

probably complex. On the one hand it may be understood as an interspecific anti-predator behavior as indicated by the occurrence of freezing, crouching and sneaking, responses shown in the wild toward predators but rarely against conspecifics [Delius, unpublished observations]; on the other hand there are indications that this domestic species considers man to some extent as a conspecific, much as imprinted geese do their caretaker. This is suggested by the occurrence of bow-cooing, a response that is not shown toward natural predators by pigeons but is very frequent in intraspecific social encounters, both agonistic and sexual. Our tests may thus assay a functionally heterogeneous set of behaviors that conceivably could also involve different control substrates.

These considerations however will provisionally be subordinate in view of the simplicity and relative reliability of the tests. Their usefulness is justified by the results. Lesions located in the archistriatum markedly and significantly depress the aggressive responses in favor of a predominance of avoidance behavior as measured by the tests. Lesions in the neostriatum do not have this effect; rather there may

be a slight, though nonsignificant, increase in aggressive behavior. Note that this group of animals provided a blind control group since only the histology revealed that the intended archistriatal lesion had been misplaced. Control sham operated animals did not show any significant change.

The reduction in aggression and increase in avoidance following archistriatal lesions contrasts somewhat with results obtained on birds by other authors. Phillips [1964] reported taming as the main consequence of ventromedial archistriatum and tractus occipito-mesencephalicus lesions in mallards (*Anas platyrhynchos*), the tract being the main efferent pathway of the archistriatum. The descriptions seem to suggest that taming consisted principally of a reduction of fear responses elicited by man. He also obtained comparable results with similarly lesioned lovebirds (*Agapornis roseicollis*): fear-inducing objects were less effective in suppressing feeding. However there was also reduction in mobbing behavior toward such objects, mobbing being perhaps a partially aggressive response [Phillips, 1968]. Zeier [1968] refers to the taming effect of more lateral archistriatal lesions in pigeons (corresponding more closely to ours) but does not specify of what this taming consisted. Antero-lateral lesions seemed to increase fearfulness, occasionally aggressiveness [Zeier, 1974]. Maser et al [1973] report that archistriatal lesions in chickens (*Gallus gallus*) facilitate the tonic immobility response that we think to be related to freezing behavior, an avoidance response. Dafters [1975, 1976] reports a learning deficit in archistriatally lesioned pigeons when an aversive reinforcer was used [compare also Cohen, 1975]. Wright and Spencer [1976] found that ring doves (*Streptopelia risoria*) with tractus occipito-mesencephalicus transections virtually ceased to show any kind of agonistic behavior to a predator model.

It does indeed not seem possible to ascribe consistently to the archistriatum an aggression-facilitating, avoidance-suppressive function. Several factors may be responsible for the apparent diversity in the results of these various studies: variations in lesion extent and location, species differences, and heterogeneous behavioral assessment. In our case we also wonder whether the selective use of aggressive animals might not have biased the results. Elsewhere one of us has argued that the same neural substrates might have different functions in the control of fear and aggression in individuals with either fearful or aggressive dispositions [Delius, 1973]. Could it be that the same lesion might suppress aggression and facilitate avoidance in an aggressive subject but have the reverse effect in a fearful one?

Collation of information from electrical brain stimulation studies on various avian species suggests that indeed the bird's archistriatum, among other structures, is a control substrate for both aggression and avoidance responses [Akerman, 1966: pigeons; Maley, 1969; Phillips, 1964: mallard; Putkonen, 1966, 1967, 1973; Phillips and Youngren, 1971: chicken; Vowles and Beazley, 1974: ring doves]. Though not decisively, these heterogeneous data seems to indicate that the aggressive responses are obtained predominantly from the ventromedial part of the archistriatum whereas avoidance responses are elicited from more dorsolateral parts of the structure.

Such a differentiation in function might relate to the regional connectivity differentiation that Zeier and Karten [1971] have established for subdivisions of the pigeon's archistriatum [see also Zeier and Karten, 1973; Kondo 1933; chicken]. Our lesion data are insufficient to allow conclusions as to correlations between the intersubject behavior defect differences and the rather small variations in lesion placement. That is an issue that must be pursued in further work. The feasibility of such an analysis is suggested by the fact that small lesions, only affecting reduced portions of the archistriatum, yielded clearcut behavioral effects. A remarkable finding is that unilateral archistriatal lesions, and small ones at that, seem just as effective in reducing aggression as bilateral lesions. As a rule unilateral lesions lead to lesser and sometimes hardly detectable behavioral defects as compared with symmetric lesions. There are cases however in which the effect of such lesions is more marked than that of bilateral ablations. An example is unilateral hemispherectomy in the chaffinch (*Fringilla coelebs*) that leads to a predator mobbing response deficit to stimuli viewed with the contralateral eye. An equivalent deficit is not apparent with symmetric lesions [Strata, 1964]. The phenomenon may apply to the archistriatum since Kalisher [1905] reports a contralateral visual "agnosia" following unilateral lesions of this structure in parrots (*Psittacidae* sp). However, we did not notice such a lateralization effect. Aggressive responses to the test stimuli were reduced seemingly no matter with which eye the animal viewed them but admittedly no detailed attention was given to this point.

It remains to comment on the absence of marked alteration of the feeding behavior of the archistriatally lesioned animals as compared with their controls. Archistriatal lesions in pigeons have been reported to lead to temporary aphagia by Zeigler et al [1969]. This fits with the archistriatum anterior being a projection of the nucleus basalis, a structure that undoubtedly plays a role in controlling food uptake responses [Zeigler, 1976]. Our lesions almost certainly spared the relevant portion of the archistriatum and this may explain the slightness of the feeding deficit we obtained. The homology of the avian archistriatum and the mammalian amygdala is supported in a general way by the results of lesions and stimulation experiments in birds. The behavioral syndromes obtained correspond to those often found in equivalent studies in mammals. Amygdala lesions have variously affected aggressive and avoidance behavior [eg, Kaada, 1972], food intake [eg, Fonberg, 1974; Box and Mogenson, 1975] and predatory behavior [eg, Zagrodzka and Fonberg, 1977; Karli et al, 1977]. Stimulation on the other hand has been shown to elicit or at least facilitate aggression, avoidance [eg, Fernández de Molina and Hunsperger, 1962; Delgado, 1967], predatory aggression [eg, Egger and Flynn, 1963] and feeding [eg, Fonberg and Delgado, 1961; Lewinska, 1968]. A recurring theme in these studies however is the functional differentiation of the amygdala, in some cases coinciding with recognizable anatomical subdivisions. It is premature to relate this to the situation in birds. Zeier and Karten [1971, 1973] have shown that the archistriatum is differentiated anatomically and actually they argue that the more lateral and anterior portions

may not be homologous to the mammalian amygdala at all. The lesion and stimulation work described above contains some indications of a corresponding functional differentiation but the information available does not yet fit into a coherent pattern.

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REFERENCES

- Akerman B (1966): Behavioural effects of electrical stimulation in the forebrain of the pigeon. II. Protective behaviour. *Behaviour* 26: 339–350.
- Areins Kappers CU, Huber GC, Crosby EC (1936): "The Comparative Anatomy of the Nervous System of Vertebrates, Including Man." New York: MacMillan.
- Box BM, Mogenson GJ (1975): Alterations in ingestive behavior after bilateral lesions in the amygdala in the rat. *Physiol Behav* 15: 679–688.
- Cohen DH (1975): Involvement of the avian amygdala homologue (archistriatum posterior and mediale) in defensively conditioned heart rate change. *J Comp Neurol* 160: 13–35.
- Dafters RI (1975): Active avoidance behaviour following archistriatal lesions in pigeons. *J Comp Physiol Psychol* 80: 1169–1179.
- Dafters RI (1976): Effect of medial archistriatal lesions on the conditioned emotional response and on auditory discrimination performance of the pigeon. *Physiol Behav* 17: 659–665.
- Delgado JMR (1967): Aggression and defense under cerebral radio control. In Clemente CD, Lindsley DB (eds): "Aggression and Defense: Neural Mechanisms and Social Patterns." Los Angeles: University of California Press, pp 171–193.
- Delius JD (1973): Agonistic behaviour of juvenile gulls, a neuroethological study. *Anim Behav* 21: 236–246.
- Egger MD, Flynn JP (1963): Effects of electrical stimulation of the amygdala on hypothalamically elicited attack behaviour in cats. *J Neurophysiol* 26: 705–720.
- Fabricius E, Jansson AM (1963): Laboratory observations on the reproductive behavior of the pigeon (*Columba livia*) during the pre-incubation phase of the breeding cycle. *Anim Behav* 11: 534–547.
- Fernández de Molina A, Hunsperger RW (1959): Central representation of affective reactions in forebrain and brain stem: electrical stimulation of amygdala, stria terminalis and adjacent structures. *J Physiol* 145: 251–265.
- Fonberg EL (1974): Amygdala functions within the alimentary system. *Acta Neurobiol Exper* 34: 435–466.
- Fonberg EL, Delgado JMR (1961): Avoidance and alimentary reactions during amygdala stimulation. *J Neurophysiol* 24: 651–664.
- Kaada BR (1972): Stimulation and regional ablation of the amygdaloid complex with reference to functional representations. In Eleftheriou BE (ed): "The Neurobiology of the Amygdala," New York: Plenum, pp 319–342.
- Kalisher E (1905): Das Grosshirn der Papageien in anatomischer und physiologischer Beziehung. *Abhandl Preuss Akad Wiss Physik-Math* 4: 1–105.
- Karli PL, Vergnes M, Eclancher F, Penot C (1977): Involvement of amygdala in inhibitory control over aggression in the rat: a synopsis. *Aggres Behav* 3: 157–162.
- Karten HJ, Hodos WA (1967): A stereotaxic Atlas of the Brain of the Pigeon. Baltimore: Johns Hopkins Press.

- Kondo T (1933): Über die Nervenfasern, die beim Huhn aus dem Epistriatum entspringen oder in ihm endigen. *Okayama IZ* 45: 124–132.
- Lewinska MK (1968): Inhibition and facilitation of alimentary behavior elicited by stimulation of amygdala in the cat. *Acta Biol Exp* 28: 22–34.
- Maley MJ (1969): Electrical stimulation of agonistic behavior in the mallard. *Behaviour* 34: 138–160.
- Martin Ramirez J, Delius JD (in press): Nucleus striae terminalis lesions affect agonistic behavior of pigeons. *Physiol Behav*.
- Maser JD, Klara JW, Gallup GG (1973): Archistriatal lesions enhance tonic immobility in the chicken (*Gallus gallus*). *Physiol Behav* 11: 729–733.
- Phillips RE (1964): "Wildness" in the mallard duck: effects of brain lesions and stimulation on "escape behavior" and reproduction. *J Comp Neurol* 122: 139–155.
- Phillips RE (1968): Approach-withdrawal behavior of peachfaced lovebirds and its modification by brain lesions. *Behaviour* 31: 163–184.
- Phillips RE, Youngren OM (1971): Brain stimulation and species-typical behaviour: activities evoked by electrical stimulation of the brain of chickens. *Anim Behav* 19: 757–779.
- Putkonen PTS (1966): Attack elicited by forebrain and hypothalamic stimulation in the chicken. *Experientia* 22: 405.
- Putkonen PTS (1967): Electrical stimulation of the avian brain. *Ann Acad Sci Fennicae* 130: 1–95.
- Putkonen, PTS, (1973): Sex difference in social aggression and escape elicited by brain stimulation in cocks and in hens. *Brain Res* 59: 432–436.
- Spiteri N (1975): Social, especially agonistic behaviour in the pigeon. M. Sc. thesis, University of Durham, England.
- Strata P (1964): Neurophysiological analysis of the mobbing response in chaffinch (*Fringilla coelebs*) *Arch Ital Biol* 102: 23–35.
- Vowles DM, Beazley LD (1974): The neural substrate of emotional behavior in birds. In Goodman IJ, Schein MW (eds): "Birds: Brain and Behavior." New York: Academic, pp 221–258.
- Wright P, Spencer AM (1976): Changes in emotionality following section of the tractus occipito-mesencephalicus in the barbary dove (*Streptopelia risoria*). *Behavioral Processes* 1: 29–40.
- Zagrodzka J, Fonberg E (1977): Amygdalar area involved in predatory behavior in cats. *Acta Neurobiol Exp* 37: 131–136.
- Zeier HJ (1968): Changes in operant behavior of pigeons following bilateral fore-brain lesions. *J Comp Physiol Psychol* 66: 198–203.
- Zeier HJ (1974): Behavioral adaptation on operant schedules after forebrain lesions in the pigeon. In Goodman IJ, Schein MW (eds): "Birds: Brain and Behavior." New York: Academic, pp 153–164.
- Zeier HJ, Karten HJ (1971): The archistriatum of the pigeon: organization of afferent and efferent connections. *Brain Res* 31: 313–326.
- Zeier HJ, Karten HJ (1973): Connections of the anterior commissure in the pigeon (*Columba livia*). *J Comp Neurol* 150: 201–216.
- Zeigler HP (1976): Feeding behaviour of the pigeon. *Adv Study Behav* 7: 285–389.
- Zeigler HP, Green HL, Karten HJ (1969): Neural control of feeding behavior in the pigeon. *Psychon Sci* 15: 156–157.