



0031-9384(95)00113-1

Effects of Diencephalic Lesions on Approach Responses and Color Preferences in Quail

A. CSILLAG,*¹ P. KABAI†, AND J. K. KOVACH†

*First Department of Anatomy, Semmelweis University of Medicine, 58 Tűzoltó u., 1450 Budapest, Hungary, E-mail: csillag@anal.sote.hu, and †Menninger Clinic, Research Department P.O. Box 829, Topeka, KS 66601 USA

Received 3 June 1995

CSILLAG, A., P. KABAI AND J. K. KOVACH. *Effects of Diencephalic Lesions on Approach Responses and Color Preferences in Quail*. *PHYSIOL BEHAV* 58(4) 659-667, 1995.—The effects of stereotaxic radio-frequency lesions on artificially selected approach responses and artificially selected or imprinted red or blue preferences were studied in Japanese quail chicks. No effects were found from lesions in anterior preoptic or pretectal areas and only slight attenuation of red preferences by lesions in nucleus rotundus, opticus principalis thalami and geniculatus lateralis pars ventralis. Extensive lesions in medial diencephalic and bordering areas of telencephalon, ansa lenticularis, lateral and medial forebrain bundle diminished approach tendencies and greatly attenuated the genetically influenced red preferences. Medial diencephalic lesions confined to the dorsomedial thalamic complex and lateral hypothalamus left approach tendencies intact but similarly attenuated only red preferences. Imprinted red or blue preferences of a highly imprintable quail line were also attenuated; red preference strongly, blue preference moderately. The data indicate differential diencephalic mediation of the quail's genetically distinct color preferences and suggest diverse subtelen- cephalic channels for mediation of approach responses and stimulus preferences. The results also suggest common neural mediation of genetically determined and acquired stimulus preferences.

Color vision	Approach preference	Avian brain	Neural lesion	Diencephalon
Following response	Imprinting	Japanese quail	Galliformes	

NEWLY hatched quail chicks tend to approach any conspicuous stimulus they first encounter, normally the hen, and exhibit reliable preferences for certain stimulus attributes. Since neither the approach nor the preference is conditional on prior experiences yet both can be modified by artificial selection and/or environmental imprinting, these behaviors are well suited for investigating the neural correlates of gene effects and genotype-environment interactions in behavioral development. The present study is part of our search for such correlates in artificially selected Japanese quail chicks (*C. coturnix japonica*) that exhibit divergent approach preferences for and imprintabilities to particular colors and patterns of otherwise identical visual stimuli (6,12-14,22,23,25). Localized lesions in the tectofugal and thalamofugal projection systems of the avian forebrain are known to impair acquired color and pattern preferences in birds, without damaging the unconditional reflexive capacities for color and pattern discrimination (34). Lesions placed along the ascending visual pathways often leave simple color discrimination unperturbed and, when affected, birds can usually relearn the more complex tasks (2,10,11,31). It is also well documented that complete bilateral hemispherectomy prevents the formation of learned associations (35) and classical conditioning (36) in birds,

yet spares much of unconditional behavioral repertoire (27,35), including genetically variable early stimulus preferences (24). Available data also indicate that the preserved genetically distinct preferences are not attributable to differential sensory mediation at the level of photoreceptors (4). In the present study we set out to investigate what subtelen- cephalic neural structures may be involved with the mediation of approach tendencies and genetically distinct unconditional blue or red preferences in quail chicks.

METHOD

Subjects

Japanese quail (*C. coturnix japonica*) chicks of either sex were used from two genetic lines that were bidirectionally selected for extreme approach preferences for blue and red stimuli (BL and RL) (23), and from a third "high learner" line that was selected for high imprintability (21). They were kept in a dark communal pen, except when tested for color preferences. Prior to preference testing or lesioning experiments the "high learners" were imprinted to red or blue stimuli for 16-18 h (red- or blue-exposed, respectively); such environmental treatments result

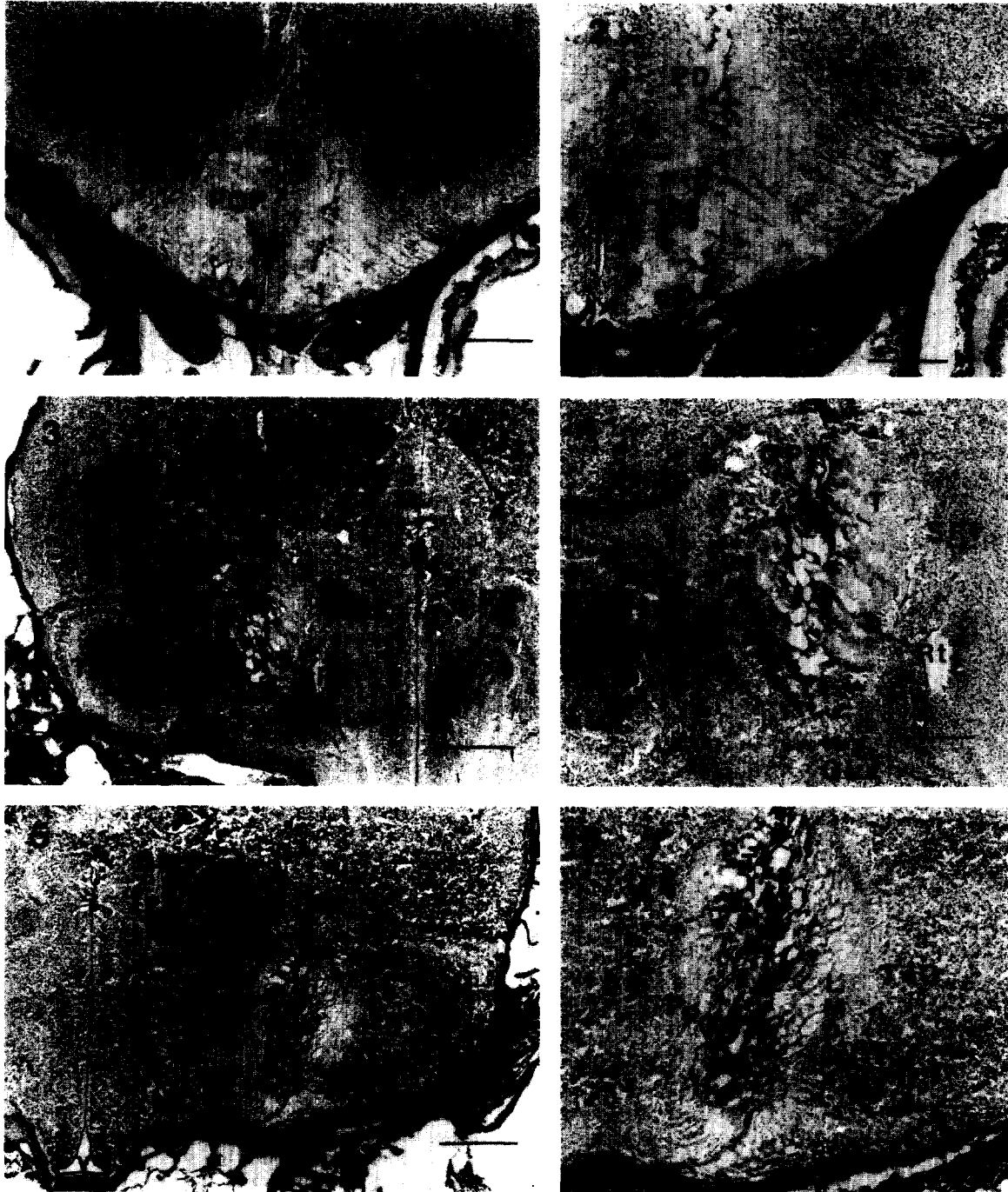
¹ To whom requests for reprints should be addressed.

in strong preferences that match the genetically selected extreme unconditional preferences. Selection and imprinting procedures have been described in detail earlier (21).

Preference Testing

A 7-choice mass screening apparatus similar to a 7-level Galton board was used for testing preferences (21). It consisted

of 28 compartments arranged hierarchically, starting with a single compartment on the top and extending to eight collection boxes on the bottom level. Each compartment offered a choice between the same pair of color stimuli, blue vs. red, set by Wratten gelatin filters No. 45 (480 nm peak wavelength) and No. 29 (631 nm peak wavelength). The shape, size, luminance (10 lx) and intermittence (3 Hz) of the back-lit flickering stimuli were identical.



FIGS. 1-6. Coronal sections of day-old quail brains, demonstrating the position and extent of radio-frequency lesions (common to at least 90% of birds in the experimental group), centered at the anterior preoptic area (Figs. 1,2), the nucleus rotundus (Figs. 3,4) and the pretectum (Figs. 5,6). For explanation of labeling see Nomenclature. Scale bars: 1 mm (Figs. 1,3,5); 0.5 mm (Figs. 2,4,6). Magnifications: Figs. 1,3,5: 12 \times Figs. 2,4,6: 24 \times .

The chicks advanced through the apparatus by approaching one or another of the two stimuli in each compartment to within a distance of 7.5 cm, at which point they would slide into the underlying box through a trap door. Arrival in a particular collection box at the bottom level indicated the number of choices made for one vs. another stimulus in 7 trials. The birds were tested in independent groups of 10–25. Each subject was individually scored on completing the first series of 7 choice trials and returned to the starting box of the apparatus for a second run of seven trials. The running session was terminated after 45 min.

The birds' performance was evaluated in two ways: (i) Preference probability (P_p), calculated as $X/14$, where X is the number of choices for one over another stimulus in 14 trials. (ii) Approach probability (P_a) expressed as $N_r/(N_b \times 2)$, where N_r equals the total number of runs (sequence of seven consecutive choices) completed and N_b is the number of birds tested in the experimental group. The data were statistically evaluated by ANOVA.

Since the birds were tested in groups, it is necessary to say a few words about the implicit social interaction effects. Earlier data indicated statistically identical mean scores and individual variations in quail chicks of similar genetic backgrounds tested individually or by the same mass-screening procedure used in the present study (20). Even in situations when subjects of genetically different stimulus preferences were mixed together and were mass-screened in a single group, only negligible social interaction effects were indicated by their respective approach choices (21). It is reasonable to assume, therefore, that, whatever marginal social interaction may have been involved, its effects were the same across the tested groups of the present study and could not have contributed to the observed statistically reliable differences among the groups.

Surgical Lesions

All surgical operations were performed on hatch day. The birds were kept in a dark incubator at 35°C immediately before surgery and during recovery. They were anaesthetized with a ketamine-xylazine mixture (30 mg and 0.2 mg/100 g body wt., respectively) and placed in a Kopf stereotaxic apparatus, with the beak bar set to 3 mm below ear bar level. Thus, the line connecting the center of ear bars with the beak/beak bar intersect closed an angle of 45° with the base of the instrument. This head angle was chosen to match the coordinates of our stereotaxic atlas of the one-day-old Japanese quail (Péczy et al., in preparation). The scalp was incised and a patch of the (still soft) skull bone with the underlying dura mater was reflected or removed to allow penetration of the lesion electrode (with a 1.5 mm exposed tip length). After inserting the electrode, a radio-frequency wave pulse was delivered (60–70°C peak tip temperature, maintained for 1 min), with the help of a Radionics RFG-4A lesion generator. The electrode was then retracted, the skull wound sealed with Gelfoam (Upjohn, USA) and the scalp closed with the help of Vetbond tissue adhesive. Sham-operated birds were anaesthetized, mounted in the stereotaxic frame and had their skull opened similar to the lesioned birds but without insertion of the lesioning electrode.

Chemical Lesions

Kainic acid was stereotaxically injected as a solution of 2.5 mg/ml in 0.1 M phosphate buffer, (pH 7.25), into the medial diencephalon according to the coordinates used for MT (A) lesions (as defined in Results under the subheading Medial diencephalic lesions), with the help of a Kopf microinjector

attached to a Hamilton syringe. Over a period of 8 min, 0.1–0.2 μ l neurotoxin was injected. Control chicks were injected with vehicle only under identical conditions. Anaesthesia, stereotaxic technique and recovery were as described under surgical lesions.

Histology

The position of lesion sites and the extent of brain damage were examined in each experimental bird by histological procedure. Following completion of behavioral tests, the chicks were rapidly decapitated, the skulls were trimmed clean of skin and glued to cryostat chucks, embedded in O.C.T. Compound (Tissue Tek). The brains were left within the skull, frozen in isopentane at –40°C and stored at this temperature until processing, within 7 days. To ensure cutting the sections in a plane that was close to the plane of electrode penetration, the following procedure was adopted (cf. Péczy et al., in preparation). The severed heads of chicks were remounted in the stereotaxic frame at the same angle that was used for surgery and a guide pin, bent at right angle, was inserted into the rear of the skull horizontally, the short arm of the pin pointing in vertical direction. When the brains were subsequently frozen “nose-down” onto the cryostat chuck, the short arm of the pin was set to lie parallel to the surface of the chuck (i.e. the plane of sectioning). Coronal sections of 20 μ m thickness were cut on a Bright cryostat, every fifth-tenth section was collected, thaw-mounted onto gelatin-coated microscope slides and stained with thionin. In addition to the atlas already noted (Péczy et al. in preparation), we have also consulted further atlases (16,26) for identifying particular brain regions. In the case of the preoptic nuclei, recent studies were used as for guidance (1,30).

RESULTS

Preoptic and Pretectal Areas

Bilateral lesions were placed in a set of six RL birds (Figs. 1,2) into the anterior preoptic region, affecting the nuclei preoptici dorsolateralis, anterior and periventricularis. Stereotaxic coordinates were A1.6 mm (anterior to ear bar), L0.5 mm (lateral from midline) and V4.8 mm (ventral from the pial surface). No effect on the approach response was evident (all birds completed the running task) and the preference probability was not significantly different from sham-operated birds [$P_a = 1.00$; $P_p = 0.893$ with $SE = 0.052$ (6)]. Another set of seven BL birds was exposed to bilateral lesions in the prepectal area (A0, L2.5, V5.5), including the nuclei prepectalis, spiriformis lateralis, lentiformis mesencephali parvocellularis, subprepectalis and the caudal part of the nucleus triangularis (Figs. 5,6). These operations detached a large segment of the optic tectum from the underlying meso-diencephalic regions in all but its ventralmost part. Again, no effects on the approach tendencies and preference probabilities were evident [$P_a = 1.00$; $P_p = 0.960$ with $SE = 0.021$ (7)].

Visual Thalamic Nuclei

We also targeted the major thalamic visual centers by unilateral or bilateral lesions centered at the nucleus rotundus (Rt) (Figs. 3,4), nucleus geniculatus lateralis pars ventralis and the nucleus opticus principalis complex (stereotaxic coordinates: A0.7, 0.4, 0.8; L2.0, 1.5, 2.0; V5.2, 5.9, 4.5, respectively). These lesions did not attenuate the general approach behavior of newly hatched BL or RL quail chicks (all tested birds completed the running task), nor the extreme blue preferences in BL chicks (Fig. 7). The red preference of RL chicks was slightly diminished as indicated by a significant overall difference between the RL

Probability of Choosing Preferred Color

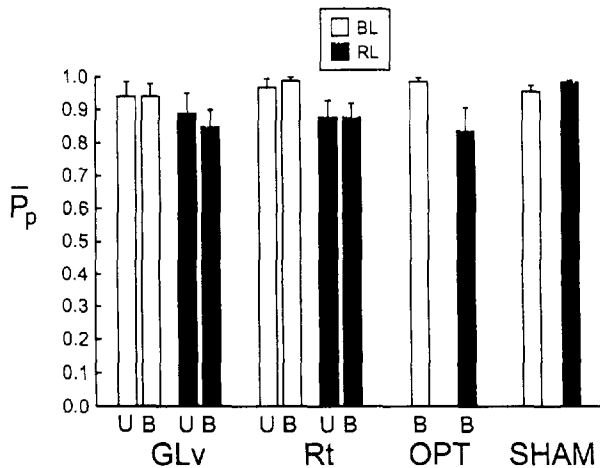


FIG. 7. The effect of radio-frequency lesions on the color preference of day-old Japanese quail chicks from two genetically selected lines: BL (blue preferring line) and RL (red preferring line). Lesions were placed unilaterally (U) or bilaterally (B) in the nucleus geniculatus lateralis pars ventralis (GLv), nucleus rotundus (Rt) and the nucleus opticus principalis thalami (OPT). The data are expressed as the mean \pm S.E., representing 6–16 birds per group.

and BL birds [$p < 0.026$, $F = 5.18$ (1, 75) for the total dataset, and $p < 0.015$, $F = 6.25$ (1, 63) when only bilateral lesions were taken into account]. At the same time, ANOVA revealed no overall differences by the site of surgery [$p < 0.724$, $F = 0.32$ (2, 75)] or type (uni- or bilateral) of surgery [$p < 0.493$, $F = 0.47$ (1, 75)].

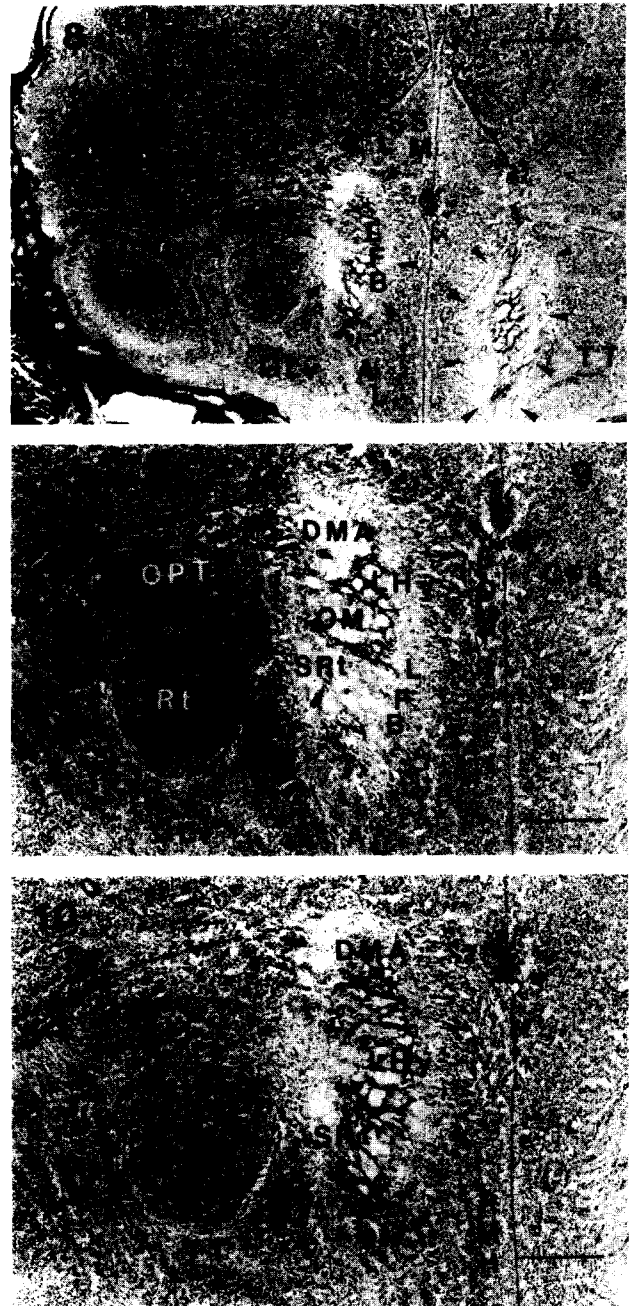
It should be noted that, whereas the destruction of Rt was virtually complete with only minimal damage to surrounding areas, the lesions centered at the nucleus opticus principalis thalami also damaged the dorsal part of Rt, whereas ventral geniculate lesions caused some destruction of medial Rt along the path of the penetrating electrode.

Medial Diencephalic Lesions

By varying the depth and rostral-caudal coordinates of electrode penetration, two major categories of lesions could be distinguished; a dorsomedial thalamic lesion (DMT) and a deeper medial thalamic lesion (MT). Figures 8 and 11 represent both types in a single section for demonstration purpose; usually, however, these bilateral lesions were intended to be placed as symmetrical as possible.

The category termed MT (A0.4–0.8, L1.0, V4.5–5.2) comprised lesions that were larger and deeper than DMT lesions, also encompassing areas lying ventral and rostral to those affected by DMT lesions. The tissue destruction started in the anterior thalamic region, along the diencephalo-telencephalic border, and included the rostral aspect of the nucleus dorsomedialis anterior, while spared the rostral part of the lateral forebrain bundle and the septomesencephalic tract (Figs. 8, 11). These rostrally placed lesions often caused some destruction in the ventral paleostriatum, nucleus accumbens, the lower lateral septum, anterior commissure and the posterior preoptic area. Further caudal they affected the dorsomedial thalamic complex, including the nucl. dorsomedialis anterior, dorsomedialis posterior, part of the dorsointermedius posterior, lateral hypothalamus, nucleus subrotundus, and parts of the occipitomesencephalic tract and the lateral

forebrain bundle. Caudally, MT lesions impaired a segment of the ansa lenticularis, the anterior nucleus of ansa lenticularis, the adjacent medial forebrain bundle and part of the tectothalamic tract. For the analysis of approach probabilities, the MT lesion group (15 RL and 16 BL chicks) was further subdivided into an anterior [MT(A)] (A0.8, L1.0, V4.5) (7 RL and 7 BL chicks) and



FIGS. 8–10. Coronal sections of day-old quail brains, demonstrating the position and extent of radio-frequency lesions (common to at least 90% of birds in the experimental group) in the dorsomedial diencephalon (Fig. 8 left side, Figs. 9,10) and the deep medial diencephalon (Fig. 8 right side). Figures 9 and 10 represent consecutive sections from the brain shown in the low power photograph of Fig. 8. For explanation of labeling see Nomenclature. Scale bars: 1 mm (Fig. 8), 0.5 mm (Figs. 9,10). Magnifications: Fig. 8: 12 \times , Figs. 9,10: 24 \times .

a posterior [MT(P)] (A0.4, L1.0, V5.2) category (8 RL and 9 BL chicks). The extent of the MT(A) lesions is demonstrated in Fig. 11A-B, whereas Fig. 11C shows the extent of MT(P) lesions.

DMT lesions (A0.4, L1.0, V4.5), representing 11 RL and 16 BL birds with a restricted version of the more extensive MT lesions, were confined to the dorsomedial diencephalon with only marginal damage to ventral paleostriatal areas and sparing the nucl. accumbens, septum, and the preoptic area (Figs. 8–11). The ansa lenticularis with its anterior nucleus, the medial forebrain bundle and the tectothalamic tract were also spared with this lesion (Fig. 9). The other structures affected by the DMT lesions were identical to those described under MT lesions (Figs. 8, 11), except that the lesion to the major pathways (occipitomesencephalic tract, lateral forebrain bundle) was less extensive.

Only bilateral lesions, generated with electrode tip temperatures of 65–70°C proved to be effective and are shown here. Smaller, restricted radio-frequency lesions (not shown) failed to affect the studied behaviors.

Effects on Preference Probabilities

Since no significant difference was found between the effects of MT(A) and MT(P) lesions on the preference probabilities (P_p), the MT group contains the pooled dataset from MT(A) and MT(P). These MT lesions strongly attenuated P_p in both genetic lines of birds, with more pronounced effects in the RL where the preferential choice for the genetically favored color was almost completely lost (Fig. 12). DMT lesions significantly diminished P_p in RL birds, but had only negligible effect in BL birds. Two-factor ANOVA of arcsine transformed data revealed a significant overall difference between the RL and BL lines [$p < 0.008$, $F = 7.47$ (1, 60)], between surgery sites [$p < 0.001$, $F = 50.54$ (2, 60)], and indicated reliable line by site interaction [$p < 0.001$, $F = 8.24$ (2, 60)]. To further investigate the latter, the following orthogonal comparisons were performed: (1) MT + DMT vs. SHAM; (2) MT vs. DMT. The results indicated a highly significant line by site interaction when comparing all

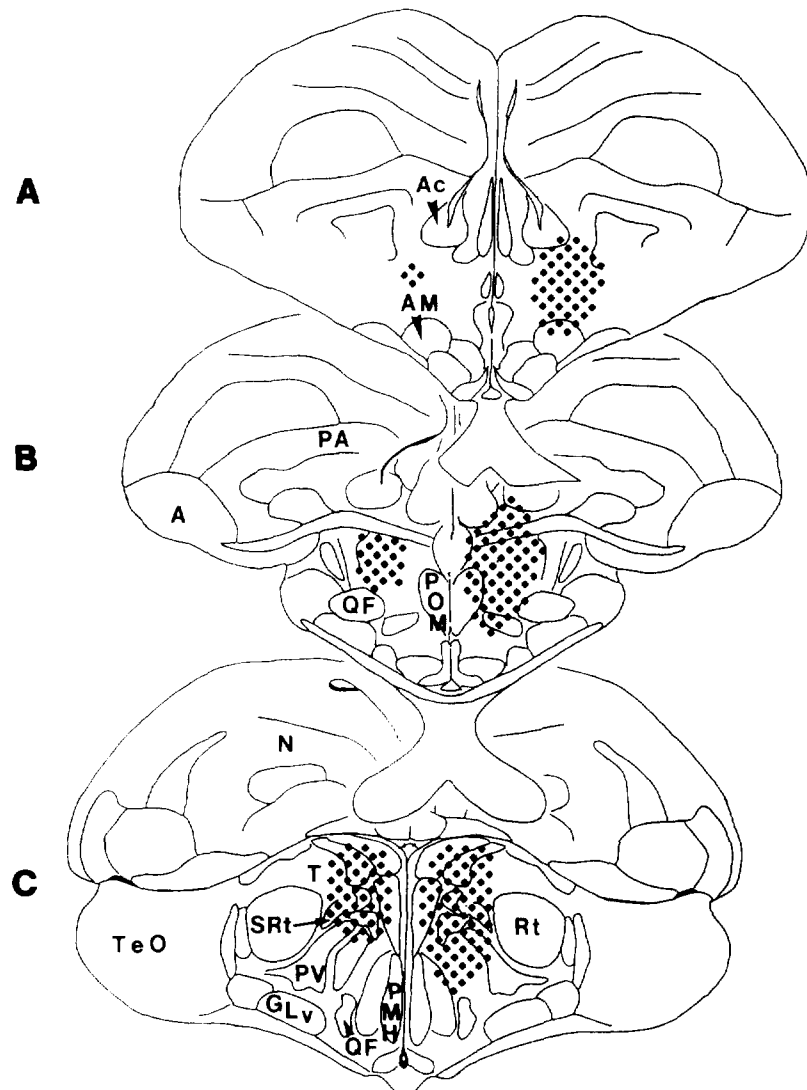


FIG. 11. Schematic drawings of coronal sections from day-old quail at levels A1500 (A), A1250 (B), and A250 (C) as measured from the center of ear bars in μm , to demonstrate the position and extent of two typical diencephalic lesions: dorsomedial (DMT) (left side) and deep medial (MT) (right side). The composite reconstruction drawings show the extent of tissue destruction found in at least 90% of the animals, in the representative section planes. For explanation of labeling see Nomenclature.

TABLE 1
EFFECT OF KAINIC ACID LESIONS TO DORSOMEDIAL DIENCEPHALIC REGION OF RED PREFERENCE SELECTED QUAIL CHICKS (P_p)

	Day 0	Day 1	Day 2	Day 3
Kainic acid	0.979 ± 0.006 (38)	0.907 ± 0.030 (26)	0.875 ± 0.021 (37)	0.921 ± 0.018 (32)
Vehicle	0.980 ± 0.009 (12)	0.923 ± 0.046 (12)	0.974 ± 0.014 (11)	0.941 ± 0.017 (12)

The data are expressed as mean probability of choosing red over blue (mean ± SE (n)) measured before (Day 0) or 1, 2 and 3 days after the administration of kainic acid or vehicle in diencephalic sites termed MT(A): $P_p = 1.00$ indicates errorless red preferences, $P_p = 0.50$ indicates random choices.

lesions (MT + DMT) with sham operates [$p < 0.001$, $F = 13.94$ (1, 60)], but no line by site interaction was indicated when the two lesion types were compared to one another [$p < 0.160$, $F = 2.03$ (1, 60)]. However, the "simple effects" analysis confirmed a significant line difference at lesion site DMT [$p < 0.001$, $F = 19.36$ (1, 60)] and a less pronounced but still significant line difference at lesion site MT [$p < 0.038$, $F = 4.50$ (1, 60)], whereas no line differences were found between the sham groups [$p < 0.146$, $F = 2.17$ (1, 60)]. These indicators corroborated our impression that the restricted thalamic lesions (DMT) affected the RL and BL birds rather more differentially, than did the larger lesions (MT).

In a group of 38 RL chicks we tested the effect of kainic acid lesions, injecting the neurotoxin into locations corresponding to the surgical lesions termed MT(A), which had proved most effective in attenuating P_p in RL birds (Table 1). The behavior was monitored over a period of 3 postoperative days. No consistent impairment of preference was detected in kainic acid treated as compared to vehicle treated birds (12 subjects), except for a slight decrease at day 2, with recovery by day 3.

Effects on Acquired Preferences

MT lesions effects were reproduced in "high-learner" quail chicks that had been imprinted to red (15 subjects) or blue (13

Probability of Choosing Preferred Color

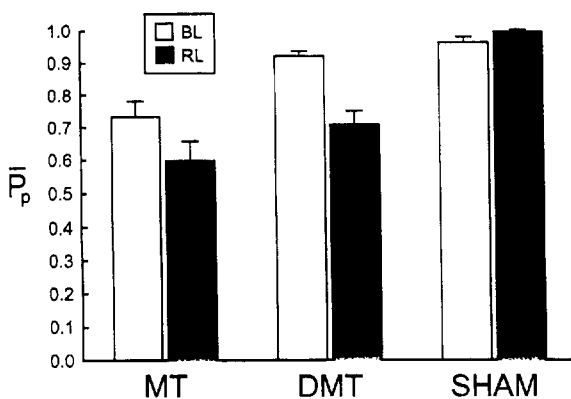


FIG. 12. The effect of radio-frequency lesions on the color preferences of day-old Japanese quail chicks from two genetically selected lines: BL (blue preferring line) and RL (red preferring line). Lesions were placed in the medial diencephalon including anterior and posterior ventromedial regions (MT), or restricted to the dorsomedial diencephalon (DMT). The data are expressed as the mean ± S.E., representing 9–14 birds per group.

subjects) stimuli and expressed near-perfect acquired preferences for the respective colors (Table 2). The red preference was reduced by almost 50% in red-imprinted chicks, whereas the blue preference was diminished by just under 30% in blue-imprinted chicks. Multivariate ANOVA and subsequent step-down analysis revealed a significant overall difference between pre and postoperative runs [$p < 0.021$, $F = 5.734$ (1, 48)]. Further univariate analysis based on this parameter confirmed a highly significant effect of treatment, that is, surgery as compared to sham [$p < 0.0001$, $F = 53.14$ (1, 49)] and also indicated a significant effect of exposure [$p < 0.018$, $F = 5.99$ (1, 49)] and an interaction between treatment and exposure [$p < 0.029$, $F = 5.04$ (1, 49)].

Effects on Approach Tendencies

The deep medial thalamic lesions [MT(A + P)] significantly attenuated the approach tendencies in both red- and blue-selected genetic lines (Table 3). However, when the anterior and posterior lesion groups were evaluated separately, a dramatic decrease of P_a was evident after MT(P) lesions, whereas MT(A) lesions had only moderately attenuated the birds' approach. Even less pronounced was the effect following DMT lesions. ANOVA revealed highly significant differences between the MT and DMT groups [$p < 0.006$, $F = 8.39$ (1, 52)] and also between MT(A) and MT(P) groups [$p < 0.001$, $F = 14.47$ (1, 52)]. However, no line by site interaction was verified in either case [$p < 0.116$, $F = 2.55$ (1, 52) and $p < 0.387$, $F = 0.76$ (1, 52), respectively], suggesting that, unlike the color preferences, the approach tendencies were similarly affected in the two genetic lines. It should be noted that the MT lesioned birds that failed to approach the stimuli in the testing apparatus were able to walk normally in the pen and were similar to nonlesioned subjects in pecking at small objects in their field of vision.

SUMMARY OF OBSERVATIONS

The color preferences of genetically selected quail chicks were unaffected in BL birds and slightly attenuated in RL birds by radio-frequency lesions to the Rt, opticus principalis thalami and nucleus geniculatus lateralis pars ventralis. Lesions to anterior preoptic and pretectal areas failed to affect the color preference of birds from either genetic line. By contrast, lesions to the medial diencephalon attenuated color preference in both lines, with the more pronounced effects in RL birds. Lesions extending to the rostral and caudal ventromedial diencephalon (MT) led to greater deficits in color preferences, affecting both BL and RL birds, whereas lesions confined to the dorsomedial diencephalon

TABLE 2
EFFECT OF RADIO-FREQUENCY (RF) LESIONS TO DORSOMEDIAL DIENCEPHALON ON THE ACQUIRED COLOR PREFERENCE OF "HIGH LEARNER" QUAIL CHICKS

	P_p after RF lesion	P_p after sham operation
Red-exposed	0.438 ± 0.041 (15)	0.864 ± 0.056 (11)
Blue-exposed	0.665 ± 0.042 (13)	0.903 ± 0.032 (14)

The data are expressed as the probability of red over blue preference (red-exposed birds) or blue over red preference (blue-exposed birds), mean ± SE (n). The results represent running scores 24 h after radiofrequency lesions (RF lesion) or sham operations in diencephalic sites termed MT. ($P_p = 1.00$ indicates errorless preferences; $P_p = 0.50$ indicates random choices).

(DMT) were less disruptive in RL and virtually without effects in BL birds. MT lesions attenuated the acquired red or blue preferences in red or blue exposed "high learner" chicks, respectively, the former effect being stronger. The quail's ability to approach the light stimulus was spared after preoptic, pretectal and visual thalamic lesions, but it was reduced after medial diencephalic lesions. However, the approach probability was severely attenuated only when the lesion affected the caudal subregion of the deep medial diencephalon.

DISCUSSION

Implication For the Mediation of Color Preference

The manifestation of color preferences, red preference in particular, required the intact dorsal thalamic and/or lateral hypothalamic region that were affected by the DMT lesions. Some aspects of the color preference may thus be encoded here and matched to the incoming sensory information or, which is more likely, the lesions interfered with the pathways that transmit such information to other areas for processing and conversion into overt behaviors. Since these diencephalic regions appear to have no direct retinal afferentation in the pigeon (9,33), chicken (7) or quail (37), it remains to be clarified where the primary visual processing for the given behavioral task takes place, and how the information from primary visual receptor is transmitted to the dorsomedial diencephalic areas. The finding that lesions to the Rt, the optic principalis complex and the lateral geniculate nucleus fail to attenuate the color preference of BL birds and have very limited effect in RL birds is somewhat puzzling, considering the reported involvement of these centers in color vision (8,28,39). In the light of the present data, the optic tectum appears the most likely candidate for this primary visual processing of the studied color preferences.

The observation that the blue preference is spared in BL but red preference is impaired in RL birds after restricted thalamic (DMT) lesions raises the possibility of an anatomical separation of the blue and red preferences. That such a separation is feasible has been demonstrated by Maximov et al. (29), who has observed that under the photopic conditions, tectal fibers in the frog are driven exclusively by red-sensitive receptors.

Apparently, the behavioral deficit elicited by medial diencephalic lesions is not restricted to the genetically selected color preferences but it is also evident in birds with acquired (imprinted) color preferences. The degree to which red or blue exposed birds were affected is very similar to that seen in genetically red or blue selected lines. This observation is indicative of some common neural mechanism underlying the manifestation of stimulus preference behavior, whether innate or acquired, at least in young posthatch birds. The observed stronger effect in red exposed chicks corroborates a separation of blue and red selective response, because in this case the differences cannot

be ascribed to a differential lesion sensitivity of genetically distinct quail lines.

Implications For the Mediation of Approach Responses

The differential effects of localized neural lesions on the reflexive approach responses (P_a) and the genetically variable stimulus preferences (P_p) suggest an at least partial anatomical separation. The approach tendency might also be represented in the antero-medial thalamus and/or the antero-lateral hypothalamus. This is corroborated by a previous study (13), according to which deficits in early approach preference behavior were observed only after extensive telencephalic ablations that also involved damage to lower septal, rostromedial thalamic, and lateral hypothalamic areas. In the present study, MT, most notably MT(P), lesions were found to attenuate the approach tendency, without rendering the chicks visually defective or physically incapacitated. Therefore, these lesions are likely to have affected some visuomotor coordination center, which is specific for the given task. Damage to such a visuomotor complex itself or to pathways connecting it to tectal or thalamic visual centers would explain the deficit.

Anatomical Implications

The large extent of lesions causing behavioral deficits makes it difficult to ascribe the observed behavioral effects to specific anatomical structures at this stage. Both effective lesion types involved extensive damages to diencephalic tissue and differed by the DMT lesions not extending ventrally beyond the ventral-most border of Rt and rostrally to the diencephalo-telencephalic border areas, affected by the MT lesions. The MT(A) lesions affected the lower septum, nucl. accumbens and ventral paleostriatum (equivalent to the ventral pallidum of mammals). The anterior and posterior dorsomedial thalamic nuclei affected by medial diencephalic lesions, are known to form limbic connections (3,17,18,38).

The observed behavioral deficit following these lesions may have been caused by the severance of the ascending or descending diencephalo-telencephalic pathways. This is so because while sparing statistically reliable portions of genetically distinct preferences in BL and RL subjects, the total ablation of telencephalon resulted in preference alternatives that appear to be similar to the presently observed attenuation; including the differential effects on blue and red preferences (14). The most parsimonious explanation for this coincidence seems to be that our diencephalic lesions impaired some connecting telencephalic pathways that travel through the region. The lack of effects of kainic acid injections in the medial diencephalon supports this explanation. However, our findings do not exclude the possibility that a diencephalic center is involved in the representation of these studied preferences.

TABLE 3
THE EFFECT OF RADIO-FREQUENCY LESIONS ON THE APPROACH PROBABILITY (P_a) OF DAY-OLD JAPANESE QUAIL CHICKS FROM TWO GENETICALLY SELECTED LINES: B (BLUE PREFERRING LINE) AND R (RED PREFERRING LINE)

Surgery Line	MT(A)		MT(P)		MT(A + P)		DMT		Sham	
	R	B	R	B	R	B	R	B	R	B
P_a	0.857	0.750	0.281	0.389	0.550	0.547	0.977	0.688	1.00	1.00
S.E.	0.143	0.109	0.129	0.157	0.120	0.108	0.023	0.090	—	—
n	7	7	8	9	15	16	11	16	9	11

Lesions were placed in the medial diencephalon including anterior [MT(A)] and posterior [MT(P)] ventromedial regions, the combination of those MT(A + P), or in the dorsomedial diencephalon (DMT). P_a = percentage of completed series of seven choices. The data are expressed as the mean \pm SE (n = number of birds in experimental group).

If the observed behavioral deficits were indeed due to pathway destruction it remains to be investigated what specific projections might be involved. The DMT and MT(A) lesions both impaired the occipitomesencephalic tract and lateral forebrain bundle (main projecting pathways of the archistriatum and basal ganglia, respectively) whereas MT(P) lesions reached the ansa lenticularis and medial forebrain bundle. The latter two pathways represent important ascending and descending connections with the paleostriatum, lobus parolfactorius, nucleus accumbens, septal nuclei and the midbrain tegmentum. The ascending pathways include catecholaminergic fibers from the avian substantia nigra (5,15,19,32), which are likely to be involved in the motivation (reinforcement) of behavior. Descending pathways comprise striotegmental fibers terminating in the substantia nigra and ventral tegmentum. The anterior nucleus of ansa lenticularis has been suggested to be equivalent to the mammalian subthalamic nucleus (5) and may be a candidate for visuomotor pattern processing. The ventralmost extension of the MT lesions is likely to have impaired the tectothalamic tract, fanning out from the ventral optic tectum in a near-horizontal plane. This might have, disrupted some connections between the optic tectum and the medial diencephalon.

In conclusion, identifying the localized or possible multiple representation of the studied functions will require follow-up investigation. Nonetheless, the present data provide an important point of departure for the study of gene effects and genotype-environment interactions in the neural representation of variable stimulus information. Specifically, as suggested by our preliminary observation in "high learner" birds, we may now examine, whether the subtelencephalic lesions that influence genetically variable unconditional stimulus preferences also affect the expression of overtly identical but acquired (imprinted instead of genetically determined) stimulus information, and whether or not the observed deficits in unconditional response tendencies may interfere with the quail chicks' capacities for learning from imprinting.

ACKNOWLEDGEMENTS

This study was supported by grant 5-ROI-HD06770 from the National Institute of Child Health and Human Development, by the Menninger Clinic and by a Fogarty-NIH CEESFN Research Fellowship No. 5 F05 TW/NS04645-03 NSS to A.C. We thank Mr. G. Wilson and Dr. L. Coyne for help in the analysis of data, and Ms K. Herl, Ms M. Young and Mrs E. Roit for skilled technical assistance.

NOMENCLATURE

A—archistriatum
Ac—nucleus accumbens

AHP—area hypothalamica posterior
AL—ansa lenticularis
AM—nucleus anterior medialis hypothalami
ANOVA—analysis of variance
BL—blue preferring line
CPa—commissura pallii
DLP—nucleus dorsolateralis posterior thalami
DMA—nucleus dorsomedialis anterior thalami
DMP—nucleus dorsomedialis posterior thalami
DMT—dorsomedial diencephalic lesion
GLv—nucleus geniculate lateralis pars ventralis
IPS—nucleus interstitio-pretecto-subpretectalis
LFB—lateral forebrain bundle
LHy—nucleus lateralis hypothalami
LM—nucleus lentiformis mesencephali
LMmc—nucleus lentiformis mesencephali pars magnocellularis
LMpc—nucleus lentiformis mesencephali pars parvocellularis
LPO—lobus parolfactorius
ML—nucleus mamillaris lateralis
MT—medial diencephalic lesion
MT(A)—anterior medial diencephalic lesion
MT(P)—posterior medial diencephalic lesion
N—neostriatum
OM—occipitomesencephalic tract
OPT—nucleus opticus principalis thalami
Ov—nucleus ovoidalis
P_a—probability of approach
PA—paleostriatum augmentatum
PD—nucleus preopticus dorsolateralis
PMH—nucleus medialis hypothalami posterioris
POA—nucleus preopticus anterior
POM—nucleus preopticus medialis
POP—nucleus preopticus periventricularis
P_p—probability of preference
PPC—nucleus principalis precommissuralis
PT—nucleus pretectalis
PV—nucleus posteroventralis thalami
RL—red preferring line
QF—quintofrontal tract
Rt—nucleus rotundus
SL—nucleus septalis lateralis
SM—nucleus septalis medialis
SPL—nucleus spiriformis lateralis
SRt—nucleus subrotundus
T—nucleus triangularis
TeO—tectum opticum
TSM—tractus septomesencephalicus
TT—tectothalamic tract
v—ventricle

REFERENCES

- Bailhache, T.; Balthazart, J. The catecholaminergic system of the quail brain: Immunocytochemical studies of dopamine β -hydroxylase and tyrosine hydroxylase. *J. Comp. Neurol.* 329:230–256; 1993.
- Bessette, B.B.; Hodos, W. Intensity, color and pattern discrimination deficits after lesions of the core and belt regions of the ectostriatum. *Vis. Neurosci.* 2:27–34; 1989.
- Bons, N.; Oliver, J. Origin of the afferent connections to the parolfactory lobe in quail shown by retrograde labelling with a fluorescent neuron tracer. *Exp. Brain Res.* 63:125–134; 1986.
- Bowmaker, J. K.; Kovach, J. K.; Whitmore, A. V.; Loew, E. R. Visual pigments and oil droplets in genetically manipulated and carotenoid deprived quail. A microspectrophotometric study. *Vis. Res.* 33:571–578; 1993.
- Brauth, S. E.; Ferguson, J. L.; Kitt, C. A. Prosencephalic pathways related to the paleostriatum of the pigeon (*Columba livia*). *Brain Res.* 147:205–221; 1978.
- Csillag, A.; Kabai, P.; Kovach, J. K. Unconditional approach preferences in the quail: Effects of thalamic and midbrain lesions. *Soc. Neurosci. Abs.* 19:1612. 1993.
- Ehrlich, D.; Mark, R. An atlas of the primary visual projections in the brain of the chick *Gallus gallus*. *J. Comp. Neurol.* 223:592–610; 1984.
- Granda, A. M.; Yazulla, S. The spectral sensitivity of single units in the nucleus rotundus of pigeon, *Columba livia*. *J. Gen. Physiol.* 57:363–381; 1971.
- Güntürkün, O.; Karten, H. J. An immunocytochemical analysis of the lateral geniculate complex in the pigeon (*Columba livia*). *J. Comp. Neurol.* 314:721–749; 1991.

10. Hodos, W. Color discrimination deficits after lesions of the nucleus rotundus in pigeons. *Brain Behav. Evol.* 2:185–200; 1969.
11. Hodos, W.; Karten, H. J.; Bonbright, J. C. Jr. Visual intensity and pattern discrimination after lesions of the thalamofugal visual pathway in pigeons. *J. Comp. Neurol.* 148:447–468; 1973.
12. Kabai, P.; Kovach, J. K.; Vadász, C. Neural correlates of genetically determined and acquired color preferences in quail chicks. *Brain Res.* 573:260–266; 1992.
13. Kabai, P.; Kovach, J. K. Persistence of approach response after decerebration in newly hatched quail chicks. *Physiol. Behav.* 53:699–707; 1993.
14. Kabai, P.; Kovach, J. K. Subtelencephalic visual discrimination in selected lines of Japanese quail. *NeuroReport* 4:255–258; 1993.
15. Karten, H.J.; Dubbeldam, J. L. The organization and projections of the paleostriatal complex in the pigeon (*Columba livia*). *J. Comp. Neurol.* 148:69–90; 1973.
16. Karten, H.J.; Hodos, W. A stereotaxic atlas of the brain of the pigeon (*Columba livia*). Baltimore, Maryland: Johns Hopkins Press; 1967.
17. Kitt, C. A.; Brauth, S. E. Projections of the paleostriatum upon the midbrain tegmentum in the pigeon. *Neuroscience* 6:1551–1566; 1981.
18. Kitt, C. A.; Brauth, S. E. A paleostriatal-thalamic-telencephalic path in pigeons. *Neuroscience* 7:2735–2751; 1982.
19. Kitt, C. A.; Brauth, S. E. Telencephalic projections from midbrain and isthmal cell groups in the pigeon. II. The nigral complex. *J. Comp. Neurol.* 247:92–110; 1986.
20. Kovach, J. K. Binomial assessment of behavioral phenotypic variations: Constancy of choices, trial effects and social interaction effects in mass-screened color preferences in quail chicks (*Coturnix coturnix japonica*). *J. Comp. Physiol. Psychol.* 91:851–857; 1977.
21. Kovach, J. K. Toward the genetics of an engram: The role of heredity in visual preferences and perceptual imprinting. In: Fuller, J. L.; Simmel E. C., eds. *Perspectives in behavior genetics*. Hillsdale, N. J.: Lawrence Erlbaum Assoc.; 1986:95–153.
22. Kovach, J. K. Nonspecific imprintability of quail to colors: Response to artificial selection. *Behav. Genet.* 20:91–96; 1990.
23. Kovach, J. K. Constitution-environment interaction modeled by artificially selected colour preferences and imprinting in quail. *Neth. J. Zool.* 43:46–67; 1993.
24. Kovach, J. K.; Kabai, P. Effects of bilateral hemispherectomy on genetically variable stimulus preferences and imprinting in quail chicks. *Brain Res.* 629:181–186; 1993.
25. Kovach, J. K.; Wilson, G. Early approach preferences of patterns and colours in quail: Responses to artificial selection and imprinting. *Anim. Behav.* 46:95–109; 1993.
26. Kuenzel, W. J.; Masson, M. A stereotaxic atlas of the brain of the chick (*Gallus domesticus*). Baltimore and London: The Johns Hopkins University Press; 1988.
27. Martin, E. G.; Rich, W. H. The activities of decerebrate and decerebellate chicks. *Am. J. Physiol.* 46:396–411; 1918.
28. Maturana, H. R.; Varela, F. J. Color-opponent responses in the avian lateral geniculate: A study in the quail (*Coturnix coturnix japonica*). *Brain Res.* 247:227–241; 1982.
29. Maximov, V. V.; Orlov, O. Yu.; Reuter, T. Chromatic properties of the retinal afferents in the thalamus and the tectum of the frog (*Rana temporaria*). *Vis. Res.* 25:1037–1049; 1985.
30. Panzica, G.; Viglietti-Panzica, C.; Sanchez, F.; Sante, P.; Balthazart, J. Effects of testosterone on a selected neuronal population within the preoptic sexually dimorphic nucleus of the Japanese quail. *J. Comp. Neurol.* 303:443–456; 1991.
31. Pritz, M. B.; Mead, W. R.; Northcutt, R. G. The effects of Wulst ablations on color, brightness and pattern discrimination in pigeons (*Columba livia*). *J. Comp. Neurol.* 140:81–100; 1970.
32. Reiner, A.; Karten, H. J.; Solina, A. R. Substance P: Localization within paleostriatal-tegmental pathways in the pigeon. *Neuroscience* 9:61–85; 1983.
33. Repérant, J. Nouvelles données sur les projections visuelles chez le pigeon (*Columba livia*). *J. Hirnforsch.* 14:151–187; 1973.
34. Riley, N. M.; Hodos, W.; Pasternak, T. Effects of serial lesions of telencephalic components of the visual system in pigeons. *Vis. Neurosci.* 1:387–394; 1988.
35. Rogers, F. T. Studies of the brain stem. VI. An experimental study of the corpus striatum of the pigeon as related to various instinctive types of behavior. *J. Comp. Neurol.* 35:21–65; 1922.
36. Tuge, H.; Yueh, C. H. Functional compensation of the somatic and visceral components of defensive conditioned reflexes after decerebration in young pigeons. *Activitas Nervosa Superior* 4:275; 1962.
37. Weidner, C.; Repérant, J.; Miceli, D.; Haby, M.; Rio, J. P. An anatomical study of ipsilateral retinal projections in the quail using radioautographic, horseradish peroxidase, fluorescence and degeneration techniques. *Brain Res.* 340:99–108; 1985.
38. Wild, J. M. Thalamic projections to the paleostriatum and neostriatum in the pigeon (*Columba livia*). *Neuroscience* 20:305–327; 1987.
39. Yazulla, S.; Granda, A. M. Opponent-color units in the thalamus of the pigeon (*Columba livia*). *Vis. Res.* 13:1555–1563; 1973.