

# Persistence of Approach Response After Decerebration in Newly Hatched Quail Chicks

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KABAI, P. AND J. K. KOVACH. *Persistence of approach response after decerebration in newly hatched quail chicks*. *PHYSIOL BEHAV* 53(4) 699-707, 1993.—The role of telencephalon in controlling the unconditional approach response was studied in newly hatched Japanese quail chicks by lesions. Approach to flickering light and a moving object were not diminished by ablation of various telencephalic areas, ranging from caudal forebrain lesions to complete bilateral hemispherectomy. Open field activity and tonic immobility were likewise unaffected. Results indicated that the neural mediation of unconditional sensory-motor components of imprinting is anatomically separated from the telencephalon, where recognition memory is thought to be formed.

Japanese quail	Chick	Imprinting	Approach	Following response	Open field	Tonic immobility
Telencephalon	Paleostriatum	Basal ganglia	Decerebration			

TELENCEPHALIC areas involved in visual and auditory imprinting have been extensively studied in recent years. Specific telencephalic regions such as the intermediate medial hyperstriatum ventrale (IMHV), and the rostromedial neostriatum/hyperstriatum (MNH), were identified to have a critical role in early learning [(20,34); for a review on lesion studies see (10)]. Although a variety of distinct changes in the anatomy and biochemistry of these regions has been identified and linked to the formation of recognition memory (7,19), little is known about the ways these regions exert their influence on the approach response. Martin and Rich (29) observed that decerebrated domestic chicks ran toward moving objects. Their description of the behavior suggests that this response was actually the now familiar approach response of imprinting. Collias (9) reported that the unconditional following response can be elicited by visual and auditory stimulation in partially decerebrated newly hatched chicks, and that the removal of the basal telencephalon abolished the behavior. Unfortunately, he did not give a quantitative description of the lesioned areas. The issue is important, because precise delineation of forebrain tissue critical for the elicitation of approach and following responses is a necessary first step toward separating the neural representation of early socialization into simpler networks.

The purpose of the present study was to gain better understanding of the role of basal telencephalon in the activation of avian approach and following responses by varying the amount of ablated forebrain tissue. Two conditions were used to elicit approach and following responses (flickering light and moving object) to control for the possibility that the anticipated deficits may be restricted to a particular stimulus situation. Two additional behavior tests were used (open field and tonic immobility)

to control for possible general effects of ablation on motor coordination, or arousal, or both. Surprisingly, the data indicated no losses in these behaviors, even after complete ablation of the telencephalon.

## METHOD

### Animals

Sixty Japanese quail (*Coturnix coturnix japonica*) chicks were drawn from generation 32 of an unselected genetic control line maintained in our laboratory (27). The eggs were incubated and hatched in a dark incubator. The chicks were randomly assigned to four experimental groups and individually tagged in a well-illuminated room. All birds were transferred into a dark incubator within 5 h after hatching.

### Surgery

Chicks were weighed and deeply anesthetized by IM injection of ketamine-xylazine mixture (3 mg-0.02 mg/10 g b.wt.). Circular incision (approx. 0.5 cm in diameter) was made on the soft frontal bone of the skull above the medial portion of the telencephalon. Brain tissue was bilaterally removed by careful suction, by a glass pipette. The amount of tissue ablated was varied among the experimental groups as follows.

1. *Excessive forebrain ablation (FBEX group)*. In this group the telencephalon was completely removed rostrally, and dorsally to the tractus septomesencephalicus.

2. *Complete forebrain ablation (FBCO group)*. Chicks in this group received a lesion similar to the FBEX group, except that a thin layer (about 1 mm thick) of forebrain tissue at the tel-

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encephalon/diencephalo-mesencephalic junction was spared, in order to minimize damage to the underlying hypothalamic/thalamic structures.

3. *Caudal forebrain lesions (FBCA group)*. In this group the volume of the removed forebrain was varied, especially in respect to the paleostriatal complex. However, most of the medial hyperstriatal areas and the caudal telencephalon were ablated in each bird.

4. *No lesion (CONT group)*. These birds received deep anesthesia and no surgery. Otherwise they were kept and treated the same way as the operated birds.

Gelfoam was used to replace the removed tissue and the skin was closed by tissue adhesive. All surgeries were performed within 12 h after hatching. The birds were kept after surgery in a dark hatching incubator overnight. Mortality rate was 13% on the following morning, increasing to almost 20% the second day after surgery (33% in FBEX, 20% in FBCO, 13% in FBCA, and 7% mortality rate in CONT group).

### Behavioral Tests

Four conditions were used to test different behaviors within 24–34 h after the surgery.

1. *Approach response to flickering light*. All quail chicks were tested for response to flickering light in a 7-choice mass screening apparatus (27). The apparatus consisted of 28 choice compartments and eight collection boxes. Each choice compartment was equipped with two optical devices which could be set to present light stimulation with controlled wavelength, pattern, luminance, and intermittence. In the present experiment the stimuli were equal in size and shape (6.45 cm<sup>2</sup>), luminance (10 lux), and intermittence (3 Hz), but differed in color. One of the stimuli in each choice compartment was blue, having a peak wavelength at 481.5 nm, and the other was red at 631.6 nm peak wavelength. The choice compartments were arranged vertically and horizontally in a hierarchical manner, starting with a single compartment on the top, two below in the second row, three in the third row, and so on, until the eight collection boxes on the floor level. Chicks approaching a stimulus within approximately 7.5 cm slid down to the next choice compartment through a trap door built in the floor of the box, until they reached the collection boxes. Arrival in a particular collection box indicated the number of choices made of a particular stimulus. Color preference was estimated as the probability of choosing the blue light over the red light. Persistence of the approach response irrespective to color preference was characterized by the number of completed seven trials: a single run through the apparatus required a travel of approximately 2.5 m.

Chicks were adapted to background light (approximately 1 lux) for 20–40 min, and tested in the apparatus in groups of 9–15. Experimental groups were run separately. Birds completing a single run through the screening apparatus (seven choices) were tested a second time. The whole session was terminated after 45 min. Chicks were kept in dark temperature-controlled boxes until next morning, when response to flickering light was tested again in the same manner as described above. Thus, the maximum number of runs was four, indicating that both runs were completed both days.

Following the test in the mass screening apparatus, birds were tube fed and the groups were put into cardboard boxes in a well illuminated room. At least 3 h were allowed for light adaptation before the final behavioral testing.

2. *Open field test*. Chicks were put individually in the middle of a 36 × 60 × 30 cm tan cardboard box. The floor of the box was divided into eight, 18 × 15 cm squares by white masking

tape. Motor activity as measured by number of squares entered within 2 min was recorded by observer sitting approximately 2 m away from the box. The occurrence of the following easily recognizable behavior categories were also recorded: sleeping (sitting with eyes closed), walking, running, jumping, and distress calls.

3. *Tonic immobility test*. The chicks were individually positioned on their backs on a V-shaped gray foam rubber sheet. The experimenter gently pressed the birds down with hand for 15 s. Elapsed time was recorded until the birds showed the first righting response during the 120 s of the test. Manual restraint was not repeated if the induction of immobility was not successful, in this case birds received a score of 0 s. Chicks remaining immobile during the test period received a score of 120 s. Muscle tension was not examined directly during the test, but relaxed position (head resting on the foam rubber) was recorded. If a bird remained immobile throughout the entire 120 s of the test, its head was gently lifted three times by 3–4 mm to check muscle rigidity. This movement would normally terminate tonic immobility, but not necessarily sleeping.

4. *Response to moving object*. The chicks were individually put on the floor in the middle of a large room. The experimenter approached the chick slowly with one hand close to the floor and fingers moving. After approaching the chick with hand within approximately 15 cm, the experimenter withdrew back to about 2 m. Reactions to the hand were recorded as one of three categories, according to the direction of locomotion of the chick: approach (the chick moved in the direction of the hand of the experimenter), no response (the chick remained stationary, or did not change its course of movement), or escape (the chick moved away from the experimenter). This test was repeated three times, and at least two responses were needed to score approach or escape.

### Histology

Following completion of behavioral testing the subjects were decapitated, their skulls trimmed clean of skin and muscle, glued to cryostat chucks, and embedded in O.C.T. Compound (Tissue Tek). The brains were frozen within the skull in isopentane at –40°C and stored at –35°C until processing within 2 weeks. Twenty micrometer thick frozen sections were cut coronally, one section was saved at least at every 200 μm. Tissue was stained for cells and fibers according to Kluver and Barrera (26). The extent of surgery was indicated by drawing on a standardized quail chick brain atlas (14). In the caudal forebrain lesion group, where the extent of paleostriatal lesions was varied, the damage was estimated as 0, 25, 50, 75, or 100% of the crosssectional area of the paleostriatum augmentatum and p. primitivum at every 200 μm. From these data the volume of missing tissue was approximated by three different measures. Left and right damages were simply averaged (A%), the smaller damage on either the left or right side was used (minimal damage, M%), and a weighted index was calculated to compensate for asymmetry (18),  $W\% = (L\% \times R\%)/100$ , in which L% and R% are percentages of damage to the left and right sides, respectively.

Significant cell losses in deeper structures separated from the lesion site were also recorded. These cell losses, probably caused indirectly by damaging the adjoining fiber pathways, were clearly identifiable as opaque, less intensely stained circular spots with no visible neurons.

### Statistical Analysis

Activity scores and tonic immobility durations were transformed to the 10 based logarithmic scale. Differences among

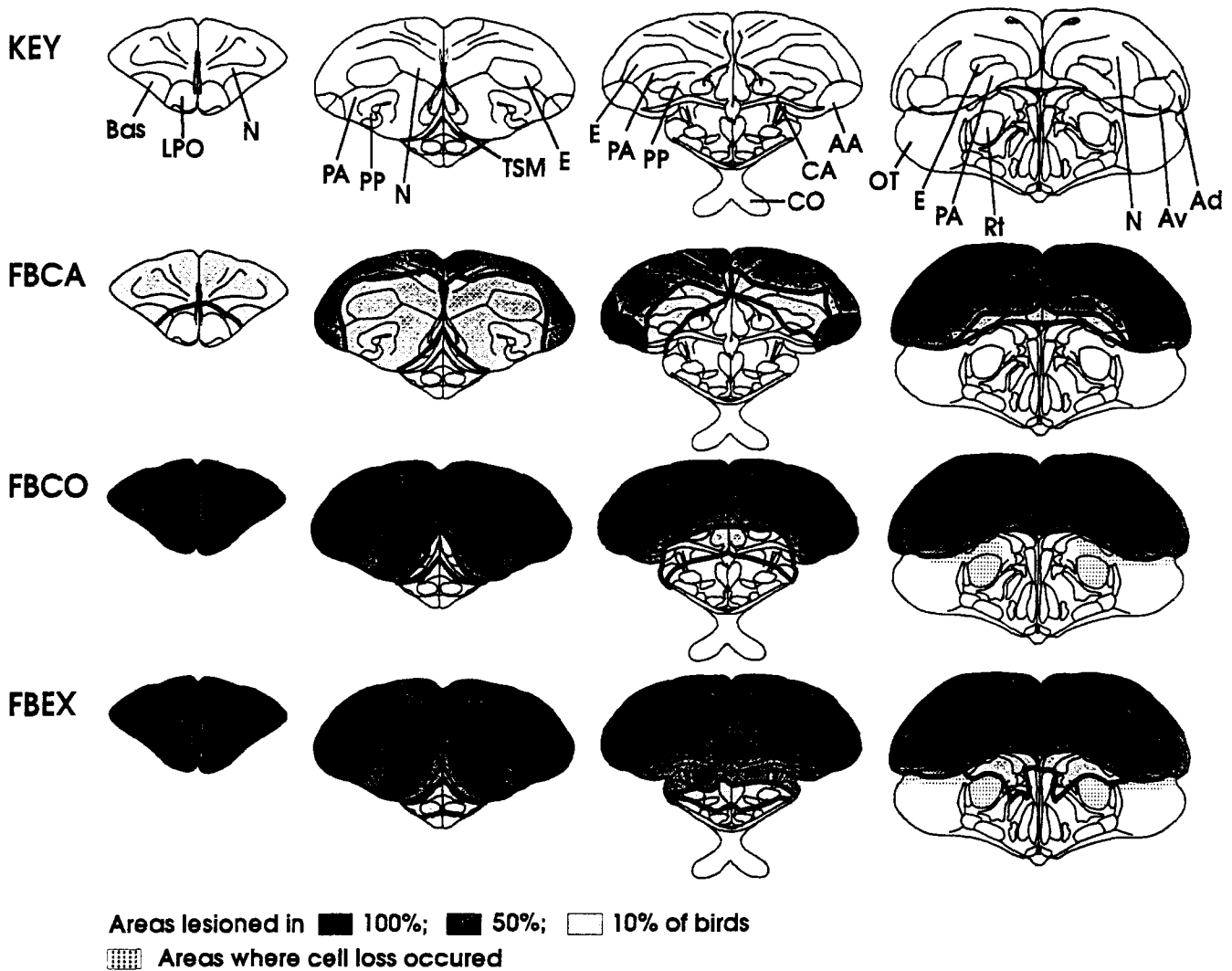


FIG. 1. The extent of forebrain lesions in three experimental groups. FBEX: excessive forebrain ablations; FBCO: complete removal of the cerebral hemispheres; FBCA: caudal portion of the forebrain was ablated. Areas marked with black were ablated in every bird within the group, double shaded areas were damaged in more than 50% of the birds, single shaded areas represent the most extensive lesion within the group. Dotted areas represent regions, where cell loss occurred in at least two individuals in the group.

groups in behavior scores were analyzed by one-way ANOVA, multiple range test, and  $\chi^2$  test. Relationships between different behaviors and between behavior and the extent of lesions in the case of the caudal lesion group were established by rank order correlations.

**RESULTS**

*General Observations*

Brains of chicks which died during the night following surgery could not be processed histologically (FBEX:3, FBCO:3, FBCA: 2, CONT:1). Two of the excessively lesioned birds could not sit or stand up and could not hold upright position when lifted by the experimenter. These two chicks died the following night, and their brains were not processed. The remaining birds walked and vocalized normally on the morning following the surgery. The only unusual reaction observed in FBEX and FBCO chicks was a vigorous headshake and bill wiping upon the first sudden

light exposure. This response was similar in form to the well known taste aversion reaction.

*Histological Data*

1. *FBEX group.* No residual telencephalic tissue was found in any of the excessively decerebrated birds. Some additional damage was caused to the rostral hypothalamus and in some individuals, to the dorsal part of the rostral thalamus (Fig. 2A). Significant tissue losses were observed in some brains in the n. rotundus (Rt) and n. opticus principalis thalami (OPT), especially in the rostral regions. The habenular nuclei were also damaged. In three birds there was additional unilateral postoperative degeneration in the dorsal part of the optic tectum (Fig. 1). All these postoperative damages were variable and scattered throughout the rostral brain stem; therefore, it was not possible to correlate tissue losses with behavioral impairments within the FBEX groups.

2. *FBCO group.* Lesion site was similar in the completely decerebrated birds as in the FBEX group, but the tractus septomesencephalicus (TSM), the lower septal, and preoptic areas were spared in most birds (Fig. 1). However, degeneration of this tissue, as well as of the TSM itself, progressed significantly in every bird, resulting in the loss of the entire telencephalon. Damages in hypothalamic-thalamic regions occurred in some birds, but were minor compared to the FBEX group (Fig. 2B). Restricted cell losses in thalamic relay areas of the ascending visual pathways (Rt and OPT) were also observed, and could represent an initial phase of postoperative degeneration.

3. *FBCA group.* Mean volume of the P. augmentatum ablated in the FBCA group varied between 7 and 98% (Fig. 1). Weighted index for bilateral asymmetry (18) indicated similar range of damage to the P. augmentatum ( $W\% = 0-95\%$ ). Damage was smaller in the P. primitivum ( $A\% = 0-71\%$ ). The lobus parolfactorius was spared and the archistriatum was ablated in most chicks (Fig. 2C).

### Behavioral Data

1. *Approach to flickering light.* (Fig. 3A). There were no significant differences among the groups in color preference in the mass screening apparatus [ANOVA:  $F(2, 32) = 1.80, p > 0.18$ ]. The choice behavior of the operated birds as well as of the controls were consistent with previous findings (28) of a slight blue preference ( $P_{\text{blue/red}} = 0.54$ ). Positive correlation between the individual scores of the first and second series of the seven choice trials [ $r(32) = 0.63, p < 0.001$ ] indicated true discrimination, rather than random walk through the apparatus.

Running performance, as expressed by the number of runs in the choice apparatus, varied significantly among the groups [ANOVA:  $F(3, 44) = 22.46, p < 0.0001$ ]. However, multiple range test (Student-Newman-Keuls procedure) indicated no significant differences among the CONT, FBCO, and FBCA groups. All of these birds ran through the apparatus at least once, and most of them completed the test twice on both days. Approach to flickering light was significantly diminished after excessive forebrain lesions: 33% of the FBEX birds did not complete a single run in the apparatus. Nevertheless, even in this group two of the nine birds completed the test twice both days.

2. *Response to moving object* (Fig. 3B). Treatment effects were highly significant on the responses to moving object [ANOVA:  $F(3, 41) = 13.25, p < 0.0001$ ]. Most birds with excessive forebrain lesion did not respond to the experimenter's hand (66%). Almost all FBCO, FBCA, and CONT birds gave some reaction to the moving object. However, although most FBCO and FBCA chicks approached the experimenter's hand, all nonoperated birds responded with escape.

3. *Open field activity* (Fig. 4B). Significant group effects were indicated by ANOVA for activity scores in the open field,  $F(3, 41) = 4.29, p < 0.01$ . Similarly to the previous tests, FBEX birds were the least active. Despite extensive rostral brain stem damages, however, even these birds showed coordinated motor patterns: they groomed, walked, and vocalized in a normal fashion. Moreover, five of the nine birds ran for some time in the O-F, and one FBEX bird jumped in the corner several times. Interestingly, multiple range test showed no significant difference in activity scores between excessively decerebrated and nonoperated birds. Although nonoperated birds entered few squares in the test, those chicks were not inactive: almost half of them spent time jumping by the wall, or in the corner of the open field. FBCA chicks were significantly more active than FBEX and CONT birds. FBCO birds were statistically not different from any of the experimental groups.

4. *Tonic immobility test* (Fig. 4A). Differences in tonic immobility (TI) durations did not reach statistical significance [ANOVA:  $F(3, 41) = 2.31, p < 0.09$ ]. It should be noted, however, that four of the nine FBCO birds evinced no movement within the 2 min of the TI test, although all birds of the other treatment groups spent less than 1 min motionless. The four FBCO birds with extreme TI durations did not react to touching and lifting their heads. This, and their relaxed posture during the test, indicated that they were more in sleeplike than cataleptic state.

### Correlations Among Behaviors

Relationships among performances in the different behavior tests were examined in each experimental group. In the FBEX group there was a high positive correlation between O-F activity and response to flickering light [ $r(71) = 0.82, p < 0.02$ ], and both these measures had high negative correlations with tonic immobility [ $r(7) = 0.67, p < 0.10$  and  $r(7) = -0.70, p < 0.05$ , respectively].

Performance in the maze was uniformly high in the FBCO, FBCA, and CONT groups; therefore, this behavior was not included in the correlation analyses for these groups. The remaining three scores (response to object, O-F activity, and TI) indicated no significant correlations in any of these groups.

### DISCUSSION

Data of the present study revealed no influence of paleostriatal lesions on the unconditional following response, open field activity, and tonic immobility. Furthermore, these behaviors were well preserved even after complete bilateral ablation of the cerebral hemispheres, provided the underlying diencephalic areas remained undamaged, as in the FBCO group.

Interestingly, nonoperated chicks were no more active than chicks with complete or caudal forebrain lesions (Figs. 2 and 3), and none of these chicks approached the moving object. Inhibition of locomotor activity by novel environment and escape from an unfamiliar moving object in young precocial birds are known to be a result of attachment to a previous stimulus situation [see (6), for example]. The response to a novel object or novel environment thus may depend on prior learning. Areas, such as IMHV and MNH indicated by others as critical in formation of recognition memory (20,34) were ablated from the telencephalon in both of the FBIN and FBCA groups. Prior learning in the nonoperated birds and the absence of such learning in the lesioned birds are the most likely explanation for the reduced open field activity and escape from moving object in the nonoperated birds.

Responses to flickering light and moving object were significantly diminished only after excessive forebrain ablation (FBEX group), and the behavioral deficits in those birds were not specific to the approach response. High positive correlations among the test scores suggested a common underlying factor, probably decrease in arousal. Specific motor deficiency was unlikely, because the excessively decerebrated birds walked, preened, vocalized, etc. in a normal fashion. Histological analysis indicated that, in addition to complete bilateral hemispherectomy, these birds also suffered damage in the rostral areas of the diencephalon. Additionally, Kluver-Barrera (26) staining revealed cell losses in thalamic nuclei of the ascending visual pathways (n. rotundus, OPT) of some chicks. Retrograde degeneration alone, however, did not seem to be responsible for the loss of activity. One bird, for example, which had performance comparable to that of FBIN and FBCA birds in every behavior test, had extensive Rt and OPT degeneration, although other FBEX chicks with no cell

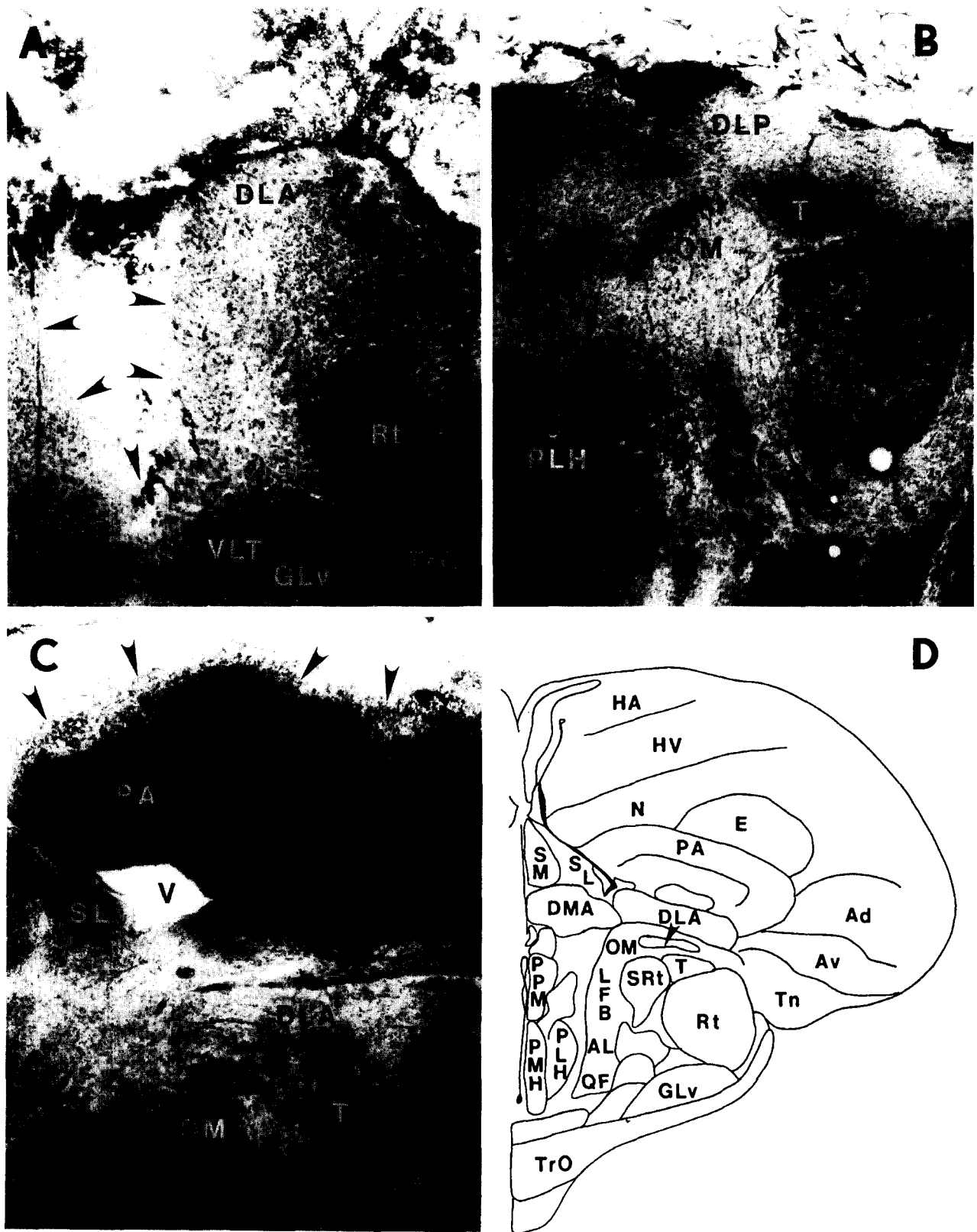


FIG. 2. Photomicrographs of coronal brain sections from chicks of the three experimental groups. The telencephalon was removed both in FBEX (A) and FBCO (B) groups. FBEX birds suffered additional damages in thalamic, hypothalamic, and preoptic areas (one such lesion is marked with arrows in A). Varying portion of the telencephalon was ablated in FBCA birds (lesion indicated by arrowheads in C), sparing some or all of the paleostriatal complex. Scale bars represent 200  $\mu$ m. Abbreviations used: DLA—nucleus dorsolateralis anterior thalami; DLP—nucleus dorsolateralis posterior thalami; DMP—nucleus dorsomedialis posterior thalami; GLV—nucleus geniculatus lateralis, ventralis; E—ectostriatum; OM—tractus occipito-mesencephalicus; PA—paleostriatum augmentatum; PLH—nucleus lateralis hypothalami posterioris; PV—nucleus posteroventralis thalami (Kuhlenbeck); Rt—nucleus rotundus; SL—septum laterale; T—nucleus triangularis; TrO—tractus opticus; TSM—tractus septomesencephalicus.

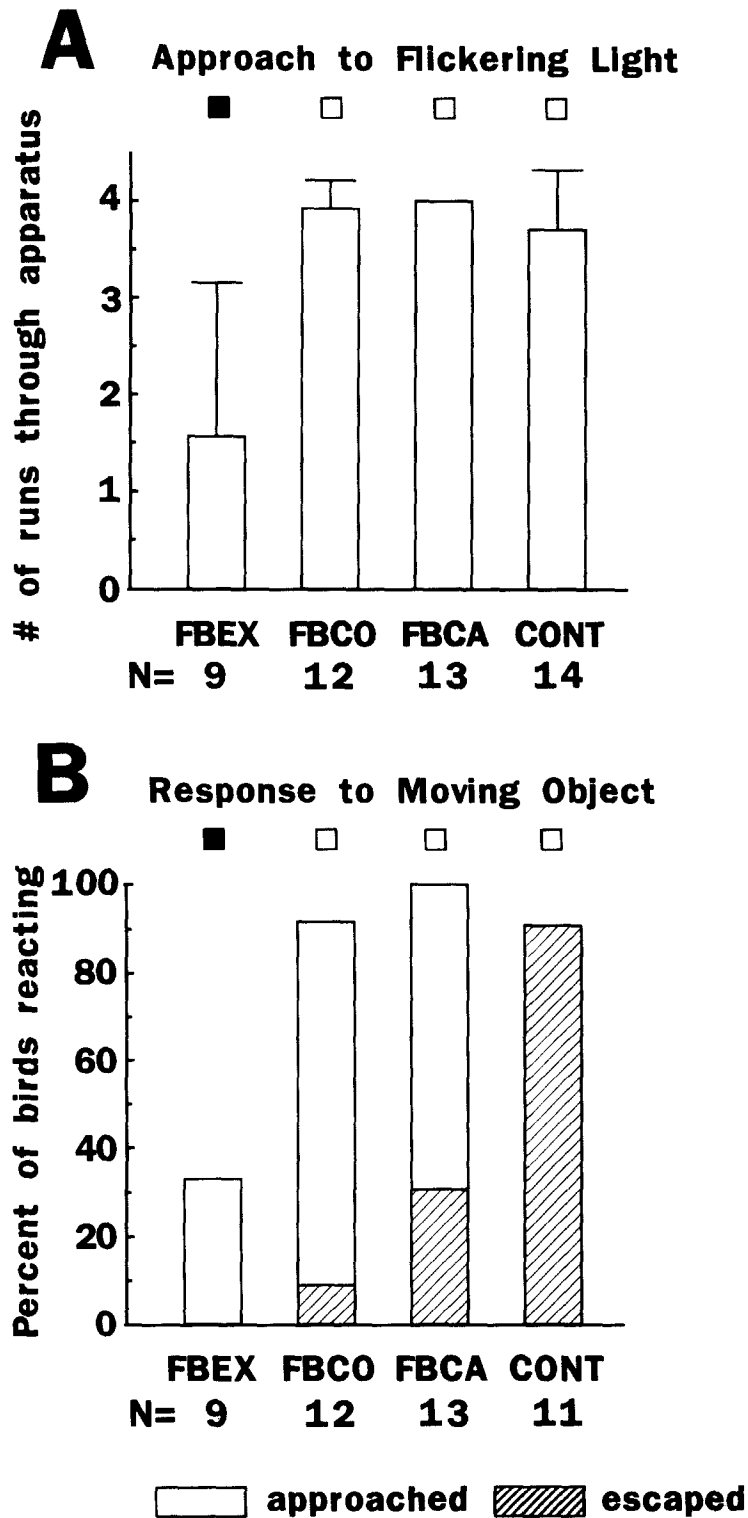


FIG. 3. Response of quail chicks to flickering light (A) and to moving object (B), after various extent of forebrain lesion. FBEX: excessive forebrain ablations, mid-brain was also damaged; FBCO: complete decerebration; FBCA: caudal portion of forebrain was ablated, affecting the paleostriatal complex in varying degree; CONT: birds were only anesthetized. Values marked with different symbols are significantly different at  $p < 0.05$ , values with the same or no symbols are not different statistically.

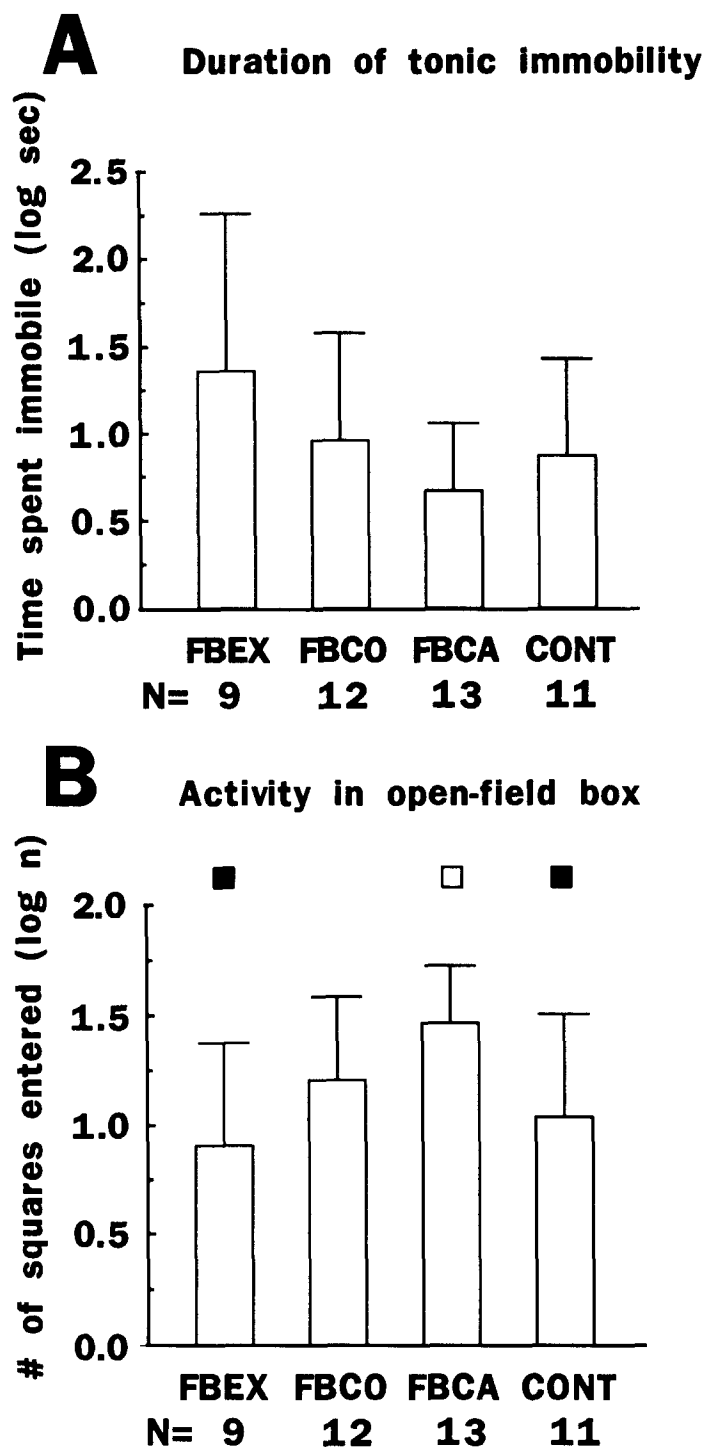


FIG. 4. Performance of lesioned and nonoperated quail chicks in tonic immobility (A) and open field test (B). For abbreviations, see Fig. 2.

loss in the same regions were significantly less active. It is most likely, therefore, that the impairment of following response after removal of all telencephalic tissue in the present study and Collias' previous related study as well, was due to diencephalic damage, rather than to the loss of the basal telencephalon postulated by Collias (9).

There was no correlation between the extent of paleostriatal damage and behavior activity in the group with varying degree of paleostriatal lesions (FBCA group). This was unexpected, because the paleostriatal complex is considered to be a high motor center of the avian brain (4). The paleostriatum augmentatum (PA) corresponds to the caudatoputamen of mammals, and the

paleostriatum primitivum (PP) and n. intrapeduncularis are believed to be anatomically equivalent to the external and internal divisions of the mammalian globus pallidus (4,22). Although there may be considerable organizational differences between the avian and mammalian basal ganglia (25), neurochemical [e.g., (1,2,15)] and behavioral (30,31,39) studies indicate that their roles in motor regulation are comparable. Dopamine receptor agonists facilitate stereotypical behavior in both birds and mammals (11,13,24), though may attenuate the actual consummatory act (12). Striatal lesions, on the other hand, diminish the effects of dopamine receptor antagonists (33). Complete bilateral hemispherectomy involving the paleostriatal complex has been known to depress spontaneous activity [discussed by (5) and (32)].

Though decerebrate birds were observed to exhibit characteristic behavior deficits (pecking without mandibulation, diminished activity in home box), operated chicks had high activity scores in all behavior tests. It has been reported that visual stimulation can elicit motor activity in decerebrate tadpole (35) and domestic chicks [(29,38); though see also (9)], even if spontaneous activity was significantly diminished. In our experiment, the approach response was elicited and guided by conspicuous visual stimuli (flickering light, and moving human hand).

However, decerebrate chicks were active also in the open field and tonic immobility tests. The open field was a cardboard box of uniform tan color, similar to the home boxes, where birds were kept in groups for at least 3 h prior testing. Despite deprivation from companions and, therefore, from moving visual stimuli, all decerebrate chicks walked and vocalized, some of them ran by the walls, and jumped in the corners of the open field box. Moreover, decerebrate chicks terminated tonic immobility as fast as nonoperated birds, though most chicks closed their eyes during immobility. High activity was apparently not activated by specific visual stimulation in the O-F and TI tests.

The open field and tonic immobility tests are thought to induce a combination of escape and exploration tendencies by novel environment, social isolation and the experimenter, as a potential predator (16,37). It appears likely that the decerebrate chicks also reacted to some or all such aspects of the O-F and TI tests.

Little is known about the subtelencephalic neural substrate of the behaviors studied in the present experiment. Ascending visual pathways projecting exclusively to the telencephalon do not seem to be critical for maintaining the unconditional following response, considering that complete removal of the telencephalon did not diminish the behavior. Furthermore, cell losses in certain thalamic relay nuclei (Rt, OPT), did not diminish the following response, even though the same pathways may play an important role in imprinting learning (21). However, a number of diencephalic and mesencephalic areas project to the cerebellum (3,8,23), which can regulate sensory-motor functions in the absence of the basal ganglia [discussed by (17) and (36)].

Whatever the neural mediation of such subtelencephalic sensory-motor association might be, the present data indicated that it can control the unconditional approach behavior even if dissociated from the telencephalon, where recognition memory is thought to be formed. Forebrain ablation can, thus, provide an appropriate preparation in which to study the innate components of the approach response without the interference of recognition memory, and can help to delineate simpler networks within the neural circuitry involved in early socialization.

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