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# Methamphetamine-Induced Stereotypies in Newly-Hatched Decerebrated Domestic Chicks

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Metamphetamine in high dose has been reported to induce stereotypic behavior of abnormal form in the pigeon and domestic chick. A number of reports suggested that the target of metamphetamine was the paleostriatal complex, the highest motor center of the avian brain. The present study tested this hypothesis by treating newly-hatched domestic chicks with high dose of metamphetamine (10 mg/kg b.w.) after complete decerebration or sham operation. Stereotypic mandibulations were observed both in sham-operated and in decerebrated birds in similar form following methamphetamine treatment. The results suggested that brainstem pattern generators remain responsive to dopaminergic stimuli in the absence of the main telencephalic (striatal) targets.

**KEY WORDS:** Domestic chick; methamphetamine; dopamine; basal ganglia; paleostriatum; stereotypic behavior.

## INTRODUCTION

Catecholaminergic systems known to be involved in attention and arousal are highly conserved in vertebral evolution. Of these, the dopaminergic system predominantly controls motor activities including highly stereotypic movements. Particular attention has been paid to the ascending pathways arising from the substantia nigra and ventral tegmentum and terminating in the striatum and nucleus accumbens, respectively. Birds have been demonstrated to possess dopaminergic perikarya and fibers (1–5) and dopamine D1 and D2 receptors, highly enriched in the striatal regions. D1 receptor binding in the medial striatal region, lobus parolfactorius (LPO), was altered as a result of passive avoidance learning (6). In most studies stimulation of dopaminergic activity was achieved by agents which block the reuptake of dopamine and, to some extent, other catecholamines. Such agents (amphetamine derivates, apomorphine) have been shown to enhance attention to stimuli (7) and motor activity (8) of domestic chickens. Dopamine was also implicated in various forms of stereotyped behavior of birds (9,10,11,12). Kainic acid lesions of the paleostriatum in pigeon resulted in similar behavior deficiencies (circling, postural disturbances etc.) as in mammals (13). Young domestic chicks failed to perform imprinting related approach response following the removal of the paleostriatal complex (14). Such behavioral and anatomical evidence confirmed the notion that the paleostriatal complex is the highest motor center of the avian brain (15) and is critical in controlling behavior patterns mediated by dopaminergic systems.

On the other hand, Kabai and Kovach demonstrated, that contrary to previous findings (14), complete decerebration, including the removal of the paleostriatal complex did not diminish imprinting related approach response nor affected open-field activity or

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tonic immobility (16), and even color and pattern discrimination was spared (17) in Japanese quail chicks, when thalamic/hypothalamic structures were not damaged by the operation. Moreover, at least in one study, the predominantly dopaminergic agent amphetamine was effective in increasing forced locomotion, head shakes and wing drooping though not pecking in decerebrated domestic chicks (18).

The question rises whether these observed dopamine related effects are dependent on the integrity of tegmentostriatal pathways or else dopaminergic effects on avian behavior may be elicited also in the absence of striatum. One possible approach to this problem, overcoming the difficulty in achieving isolated yet complete striatal lesions, is total telecephalic ablation, which in contrary to mammals, leaves the majority of sensory and locomotor functions intact, at least in young nidifugous birds (16–18). Should a considerable portion of dopaminergic response persist in decerebrated birds, it could be concluded that dopamine fibers terminating in subtelencephalic areas are instrumental in that particular task. Decerebration is technically feasible in chicks at a very early age, survival rates being considerably greater than in adults. Dopamine receptors are present in post-hatch chicks (6,19,20), and D2 sites did not show significant changes within the first four posthatch days (21). For a relevant comparison with previous experiments performed on young birds, in the present study, we investigated the effect of the predominantly dopaminergic stimulant methamphetamine on simple behavioral events of normal and decerebrated domestic chicks at the age of 3 days.

## EXPERIMENTAL PROCEDURE

*Animals.* One day old Hunnia broiler chicks were purchased from a commercial hatchery. The chicks were kept in groups of 15 under warm lamps and were provided with water and pelleted food ad libitum. Fourty chicks were randomly assigned to two groups one of which was sham operated and the other one was decerebrated. Twenty chicks were anesthetized by IM injection of ketamine-xylazine mixture (3 mg-0.02 mg/10 g. b.wt), and a circular incision (approx. 5 mm in diameter) was made on the frontal bone of the skull above the ventral portion of the telencephalon. In the sham operated group the cutaneous incision was closed by tissue adhesive and chicks were allowed to recover from anesthesia.

*Surgery.* For decerebration the telencephalic brain tissue was completely removed rostral and dorsal to the tractus septomesencephalicus except for an approx. 1 mm thick layer of forebrain tissue spared at the telencephalon/diencephalo-mesencephalic junction to prevent damage to the underlying hypothalamic/thalamic structures. Our previous studies showed, that the spared tissue layer as well as the tractus septomesencephalicus degenerates rapidly after such surgery (16). The extent of the lesions was checked with post-mortem craniotomy and macroscopic inspection (Fig. 1). Following perfusion with 4% buffered paraformaldehyde, horizontal sections of 10 μm were cut with a freezing microtome and stained with cresyl-violet (Fig. 2 and 3). The telencephalic hemispheres including the striatum and pallidum were absent after the lesions, only part of the septum remaining intact. The diencephalon and brainstem were macroscopically intact, however, considerable retrograde degeneration in some subtelencephalic areas following such ablations was reported in a previous study (16).

*Behavioral* Test. Open-field test was performed one day after the surgery. The open-field arena was a 40 × 40 × 30 cm tan cardboard box. The floor of the box was divided into nine, 13 × 13 cm squares by white masking tape. Chicks were put individually in the middle of the box, and behavioral measurements started 20 sec. after the placement of the chick. Occurrence of 15 behavior elements and motor activity were recorded for 20 min. by an observer sitting 2 m away from the box. The observer were blind to the drug treatment.

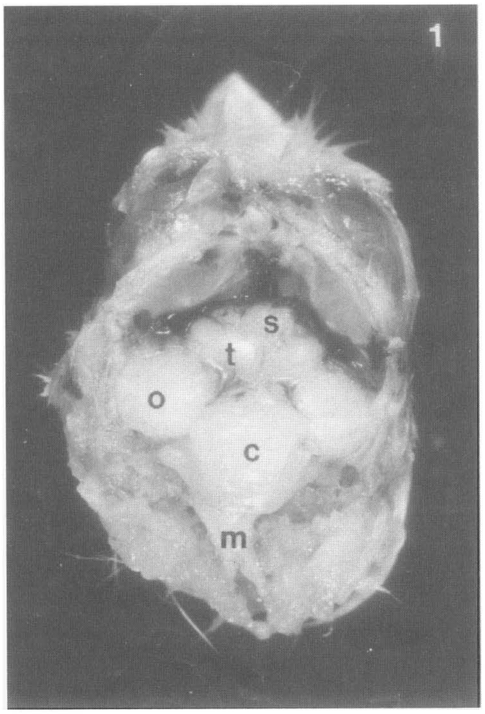
Behavioral categories to be recorded and the dose of drug to be applied were established during a preliminary experiment using different doses of metamphetamine (0.1, 1, and 10 mg/kg body weight) in 5-5 unoperated chicks. Methamphetamine in lower doses resulted in some increase in locomotion and pecking, but caused no alteration of the form of any behavior. Following the injection of 10 mg/kg b.w. methamphetamine behaviors of abnormal form appeared (open-pecking, upward movement of body, etc.). Since our aim was to test any specific effects of the dopaminergic drug on telencephalectomized birds we used methamphetamine only in the higher dose (10 mg/kg b.w.) in the main experiment.

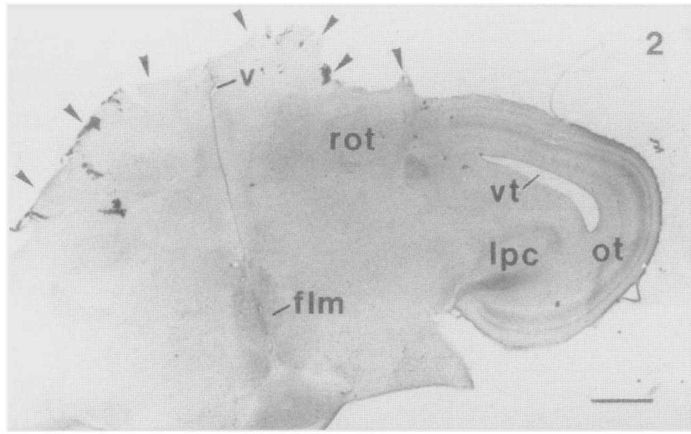
Some of the behaviors such as "preening or wiping the beak", "body or wing shaking", "scratching", "pecking wall or floor", "defecation", "eye closure" and "head shaking" occurred in a regular pattern and were identical to categories traditionaly used open-field studies in chicks (9,16).

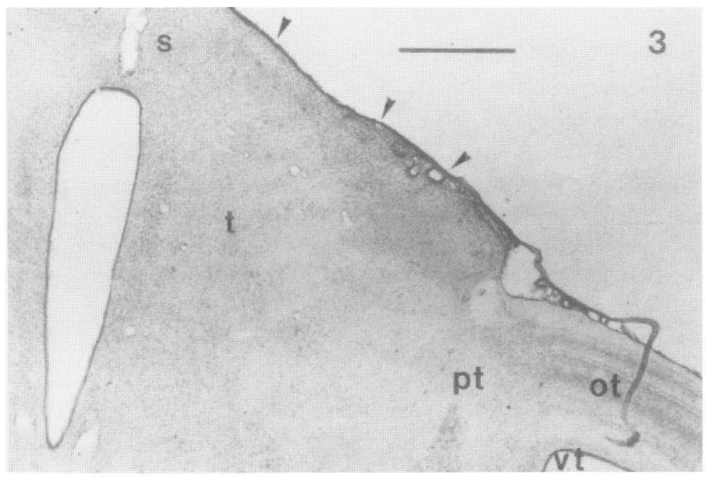
However, followig metamphetamine treatment, behaviors of abnormal forms similar to drug induced orofacial movements in mammals also occured, which need further explanation. "Yawning" was defined as opening the beaks wide. "Vacuum preening" occurred in form similar to normal preening but without the beaks touching the body. "Upward movement of the body" was scored when the birds stretched their body vertically. This movement sometimes ended with quick steps to one side ("loosing balance"). Methamphetamine treated birds often made movements which started similar to pecking but without the beaks closing ("open-pecking"). Such open-pecking was either oriented to the wall or floor ("oriented open-pecking") or happened in the air without touching any surface ("unoriented open-pecking"). One behavior characterized by quick, alternative opening and closing the beaks without head movement ("chewing") was omitted from analyses because it occurred only in a few birds with low frequency. Emittance of any sound was scored as "vocalization", because we did not categorize peeps, trills etc. into different classes. Locomotor activity was measured by the number of squares entered.

*Drug treatment.* Decerebrated and unoperated birds (D and U treatment, respectively) were injected with methamphetamine (10 mg/kg b.w.) or saline intraperitoneously (M and S treatment, respectively) 1 min. before the open-field test (10 chicks in each treatment groups, DS, DM, US, UM).

*Statistical Analysis.* Treatment effects were analyzed statistically by comparing frequencies of each behavior category among the experimental groups. Nonparametric tests were used because the distribution of behavior variables violated the normality assumption of parametric tests (22). We tested for overall differences among




**Figs. 1-3.** Representative photographs demonstrating the extent of brain tissue lesion following telencephalic ablation in day-old domestic chicks. **Fig. 1.** Macroscopic photograph showing the anatomical lesion site one day after surgery. s - septum, t - thalamus, o - optic lobe, c - cerebellum, m - medulla oblongata. **Fig. 2.** Microphotograph of Nissl stained horizontal section showing the lesion one day after surgery. The surface of lesion is marked by arrowheads. v - third ventricle, rot - nucleus rotundus, Ipc - nucleus isthmi parvocellularis, vt - tectal ventricle, ot- optic tectum, flm - fasciculus longitudinalis medialis. Bar: 1 mm. **Fig. 3.** Microphotograph of Nissl stained horizontal section showing the lesion five days after surgery. The surface of lesion is marked by arrowheads. Note the prominent distension of the ventricles. s - septum, v - third ventricle, t - thalamus, pt - pretectum, vt - tectal ventricle, ot - optic tectum. Bar: 1 mm

treatment groups by Kruskal-Wallis one-way ANOVA. If a significant overall effect was found we conducted Mann-Whitney U-test for 4 combinations of the groups (US/DS, UM/DM, US/UM and DS/DM) to detect significant differences related to surgery or drug treatment. As "familywise" error may inflate the true level of significance in such post-hoc multiple comparisons (23), we identified $\alpha$ (c = 4) = 0.0127 as a critical level of significance for the pairwise comparisons. One chick represents one data point in each test. Mean ± SE and two-tailed probabilities are given.

## RESULTS

We found significant differences among treatment groups in all behaviors (Kruskal-Wallis tests: $\chi^2 = 7.909 - 27.098$, df = 3, $P < 0.05$) except in the frequency of yawning ($\chi^2 = 4.194$, df = 3, $P > 0.2$). Although there were significant differences among the groups in the frequency of vacuum preening ($\chi^2 = 12.955$, $P < 0.01$), loosing balance ($\chi^2 = 16.619$, $P < 0.001$) and pecking ($\chi^2 = 12.223$, $P < 0.01$), no significant differences were revealed by pairwise post-hoc comparisons (Table I).

Decerebration itself affected many behaviors significantly as revealed by comparison of the unoperated and decerebrated saline treated groups (US/DS). Frequency of behavior categories related to self-cleaning in decerebrated birds was significantly higher than in unoperated chicks (preening: z = 2.956, $P < 0.004$; scratching: z = 3.106, $P < 0.002$; head shaking: z =

**Table I.** Behaviour of Chicks in the Four Treatment Groups

| | Treatment | | | | |
|---|---|---|---|---|---|
| | Unoperated | | Decerebrated | | |
| Behaviour | Saline (US) | MET (UM) | Saline (DS) | MET (DM) | Comparison |
| Preening | 0.6 ± 0.6 | 0.0 | 7.8 ± 4.8 | 0.8 ± 0.5 | a (2.956)<br>d (2.685) |
| Scratching | 0.0 | 0.0 | 4.6 ± 2.3 | 0.7 ± 0.4 | a (3.106) |
| Wing shaking | 0.2 ± 0.2 | 0.0 | 3.5 ± 0.8 | 0.1 ± 0.1 | a (3.397)<br>d (3.521) |
| Body upward | 0.0 | 14.5 ± 8.8 | 0.0 | 0.0 | b (3.105)<br>c (3.105) |
| Loosing balance | 0.0 | 7.3 ± 3.2 | 0.0 | 0.0 | |
| Yawning | 0.1 ± 0.1 | 4.9 ± 4.0 | 1.1 ± 0.4 | 1.2 ± 0.5 | |
| Chewing | 3.8 ± 1.3 | 4.7 ± 1.2 | 0.2 ± 0.1 | 6.7 ± 2.1 | a (2.999)<br>d (3.701) |
| Vacuum preening | 0.0 | 0.0 | 0.0 | 3.1 ± 1.6 | |
| Defecation | 1.3 ± 0.3 | 0.3 ± 0.2 | 1.3 ± 0.2 | 0.1 ± 0.1 | c (3.095)<br>d (3.460) |
| Eye closure | 7.7 ± 2.0 | 1.9 ± 1.3 | 0.0 | 0.4 ± 0.3 | a (3.727)<br>c (2.780) |

Mean ± SE frequency of each behaviour component is shown as observed during 20-min trials (n = 10 chicks in each group).
Letters in the Comparison column indicate significant pair-wise differences: a: US/DS, b:UM/DM, c: US/UM, d: DS/DM (Mann-Whitney U tests, z values are given in parenthesis, $\alpha = 0.0127$ was accepted as a corrected significance level for the four post-hoc comparisions)

3.609, $P < 0.001$; wing shaking: $z = 3.397$, $P < 0.001$), whereas eye-closing and vocalization decreased after surgery in the saline reared groups ($z = 3.727$, $P < 0.001$ and $z = 2.725$, $P < 0.007$, respectively). Even though locomotor activity and frequency of pecking was considerably higher in the decerebrated group than in the unoperated group (6 and 9 times difference, respectively), these differences did not reach the level of significance when corrected for family-wise errors (locomotor activity, US/DS: $z = 2.209$, $P < 0.0272$; pecking, US/DS: $z = 2.422$, $P < 0.0154$). Overall, in the saline treated groups the frequency of behavior elements reflecting motor activity was higher following decerebration.

Methamphetamine affected many of the behavioral components in intact or decerebrated chicks, or both. Although locomotor activity of decerebrated saline treated birds was at least 8 times higher than in the other groups, pairwise comparison revealed significant difference only with respect to the operated methamphetamine treated group (DS/DM, $z = 2.506$, $P > 0.012$, Fig. 4). Unoriented open-pecking was exclusively performed by chicks injected with the drug, and such drug effect was significant both in the unoperated and decerebrated groups (US/UM: $z = 2.798$, $P < 0.005$; DS/DM: $z = 2.798$, $P < 0.005$). In oriented open-pecking at the wall or floor the difference between methamphetamine and saline treated groups was significant in decerebrated birds and slightly below the level of significance in intact chicks (DS/DM: $z = 3.413$, $P < 0.0006$; US/UM: $z = 2.484$, $P < 0.0130$, respectively).

Methamphetamine increased the frequency of head shaking in decerebrated but not in unoperated chicks (DS/DM: $z = 2.950$, $P < 0.003$;US/UM: $z = 2.236$, $P < 0.025$). Frequency of preening, wing shaking and vocalization decreased after methamphetamine injection in decerebrated chicks, although it was unaffected by the drug in the intact individuals (see Table I and Fig. 4 for statistics). Scratching frequency was also unrelated to drug treatment both in intact and in operated chicks (Table I). This behavior was performed only by decerebrated individuals, that performed scratching significantly more often than the intact individuals if no drug was provided (US/DS: $z = 3.106$, $P < 0.002$). Upward movements of the body occurred only in intact chicks treated with drug, and the differences between this and the other treatment groups were significant (Table I). Methamphetamine decreased the frequency of eye closure in unoperated individuals (Table I). Frequency of defecation was diminished following methamphetamine treatment and that effect was significant in all comparisons except between groups of unoperated chicks (Table I).

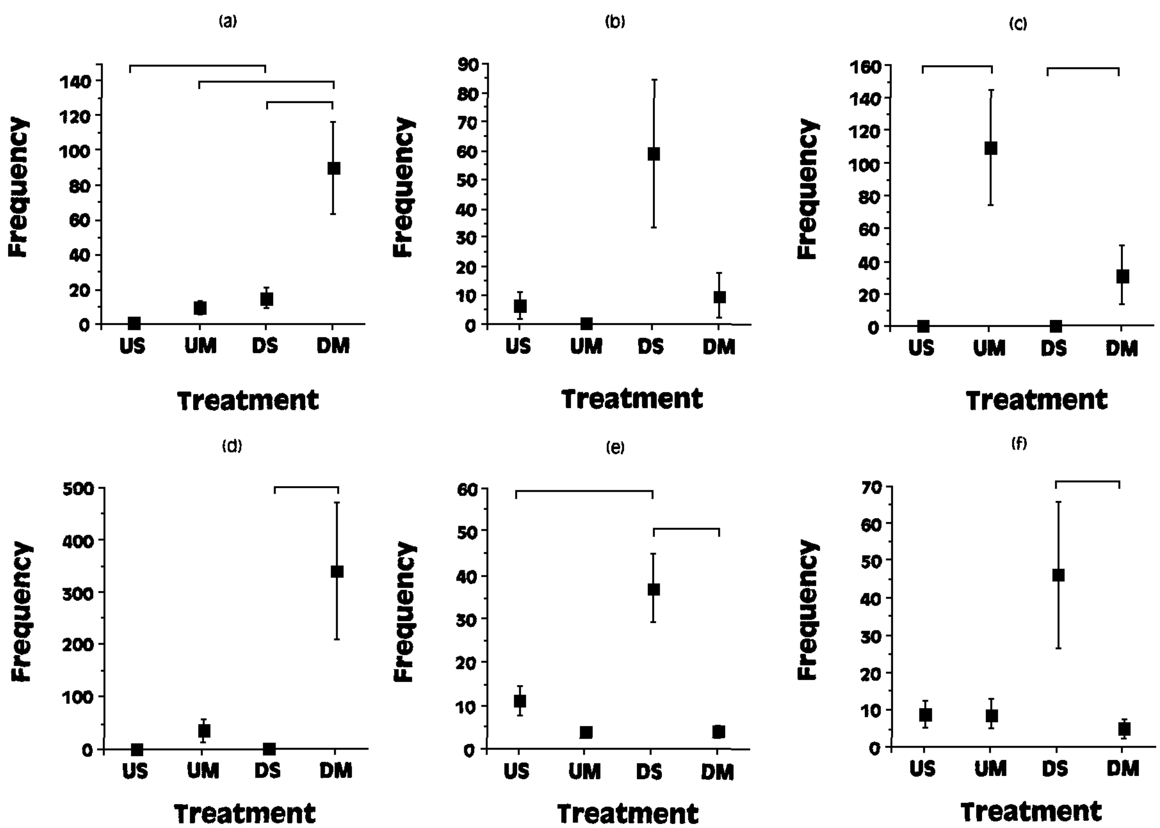



**Fig 4.** Behaviour of chicks in the four treatment groups: (**a**) head shaking, (**b**) pecking wall or floor, (**c**) unoriented open pecking, (**d**) oriented open pecking, (**e**) vocalization, (**f**) locomotor activity (mean ± SE frequencies, n = 10 in each group). Horizontal lines indicate significant pair-wise differences (Mann-Whitney U tests, $\alpha = 0.0127$ was accepted as a corrected significance level for the four post-hoc comparisions, see Methods). US: unoperated, saline, UM: unoperated, metamphetamine, DS: decebrated, saline, DM: decebrated, metamphetamine.

Methamphetamine treatment had statistically differential effect in the unoperated and decerebrated chicks only on the frequency of upward movement of the body and head shaking. Even though the frequency of non-oriented open-pecking following methamphetamine treatment was three times higher in unoperated chicks than in decerebrated birds, and DM birds performed 9 times more oriented open-pecking then UM, these differences did not reach the level of significance (UM/DM: $z = 1.172$ ,$P > 0.241$ and UM/DM: $z = 2.234$ ,$P > 0.025$, respectively, Table I), because of large individual variations and the inflation of significance after correction for pairwise comparison.

## DISCUSSIONS

A variety of dopaminergic responses have been reported in birds, including an increase of locomotion, pecking and vocalization (7), as well as initiation of stereotyped behaviors (9). Some of these effects are likely to depend on the birds' attention to stimuli (7). Similarly, an impairment of mesotelencephalic dopamine input resulted in a sensory inattention in rats (24). The dopaminergic stimulant apomorphine was found to enhance motor activity and to decrease the duration of tonic immobility in 3 to 5-week-old chickens (8).

The present findings indicate that the methamphetamine administered ip. is able to elicit marked changes of stereotyped behavior even in the absence of telencephalic, in particular striatal structures. This observation is in agreement with one previous study (18) according to which amphetamine-induced forced locomotion and head shakes were still present after ablation of the cerebral hemispheres. At the concentration of methamphetamine applied in our study we found typical drug induced mandibulations, such as open pecking, both in the nonoperated and decerebrated birds.

Although some areas controlling elementary behavioural responses, such as gaze stabilisation have been localised (Burns, wallman 261. old.,) in the brainstem, areas organising pecking have not yet been anatomically identified. Our finding that a functional tegmento-striatal pathway is not essential for metamphetamine induced stereotypies, might focus the attention on catecholaminoceptive, more specifically dopaminoceptive subtelencephalic regions. There is considerable projection from nigral and ventral tegmental areas to subtelencephalic targets in birds. In the pigeon, efferent fibers from AVT neurons reach the central gray, pretectal areas, the lateral habenular nucleus, dorsomedial and dorsolateral thalamus as well as the lateral hypothalamus, whereas those from the nigra (TPc) innervate, among others, the central gray, nucleus intercollicularis, reticular formation, dorsal thalamus, lateral hypothalamus and pretectum (25). The presence of TH-positive fibers in subtelencephalic regions has also been reported in pigeon (26), in zebra finch (3), in quail (2), and in domestic fowl (27). Both D1 and D2 receptors are detectable at the subtelencephalic level, in particular in the tegmentum of the midbrain (Stewart, Kabai and Csillag, unpublished), although the studies known to us have focused attention on the forebrain (19,28,6,20). Thus, available anatomical and functional evidences seem to support that the metamphetamine sensitive pattern generators are operational independent of the striatal system, in the mesodiencephalic region.

It should be noted that the different repetitive behavioral elements were differentially affected both by ablation and by methamphetamine in the present study. Stereotypies occurring in regular form such as preening, wing shaking, scratching, vocalization or pecking were enhanced only by detelencephalization and not by drug treatment. Conversely, typical "orofacial" and postural methamphetamine induced behaviors, such as open-pecking or upward movement of the body were increased by methamphetamine but not by surgery itself. Thus methamphetamine had an unquestionable effect on both intact and decerebrated birds, however, the results are inconsistent as to whether such effects were quantitatively different in the two groups. Our findings, that following methamphetamine treatment, decerebrated birds tended to target their pecking, whereas intact birds performed more non-directed beak movements is ambiguous, because this difference did not reach the level of statistical significance in the four way comparisons. However, this question is of some importance, because cholinergic stimulation of the ventrolateral striatum in rodents has been shown to elicit non-directed mouth movements, quite distinguishable from stimulus-directed, amphetamine-induced biting (29). The possible difference between intact and decerebrated birds in their response to methamphetamine treatment could be ascribed to the fact, that methamphetamine also affects muscarinic cholinergic receptors, abundant in the avian striatum (28,30) in the non-operated birds. However, this does not invalidate the basic finding that certain brainstem pattern generators remain responsive to cat cholaminergic, predominantly dopaminergic, stimuli in the absence of the main telencephalic (striatal) targets of these ascending activator systems. This may be a transient phenomenon typical for the young bird and superseded later by the activity of the fully mature tegmentostriatal pathway. In contrast with newborn mammals, however, most neural sytems of nidifugous birds are anatomically and functionaly mature already at the time of hatching. Thus, an alternative hypothesis is that the findings reflect a more lasting but normally latent feature of motor organization.

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