

Dopaminergic Nature of Feeding-Induced Behavioral Stereotypies in Stressed Pigeons¹

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GOODMAN, I., J. ZACNY, A. OSMAN, A. AZZARO AND C. DONOVAN. *Dopaminergic nature of feeding-induced behavioral stereotypies in stressed pigeons*. PHARMACOL BIOCHEM BEHAV 18(2) 153-158, 1983.—Dopamine dependence of feeding-induced behavioral stereotypies (FIBS) was demonstrated by FIBS facilitation following chronic treatment with a dopamine (DA) agonist, apomorphine, and by FIBS inhibition following the administration of haloperidol, a DA antagonist. However, individuals that emitted FIBS were differentiated from those not emitting FIBS not by assayed telencephalic DA concentrations alone but by a higher stereotyping index (SI), a score positively related to the ratio of telencephalic DA-norepinephrine (NE) concentrations. These latter findings support the hypothesis of Antelman and Caggiula [3] which indicates that a catecholamine interaction in the brain serves to facilitate or inhibit some behavioral actions associated with stress.

| Catecholamines | Stereotyped behaviors | Avian brain | Dopamine | Stress |
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STEREOTYPED behavior in birds has been observed in a variety of stressful contexts. For example, birds in open, natural settings, under sexual or aggressive social circumstances, may exhibit repeated movements (displacement activities), seemingly unsuitable for the social demands of that context [19]. Caged birds, especially those in smaller cages, tend to exhibit locomotor and pecking responses [21]. Caged birds that are food deprived will emit restricted bouts of stereotyped behavior following food presentations on a schedule of multiple mini-food presentations (schedule-induced or adjunctive behavior) [27,30] or emit prolonged and numerous bouts following a single daily food presentation [24], these latter inducing conditions and effects hereafter referred to as feeding-induced behavioral stereotypies (FIBS). In all of these examples, when the stressful condition is reduced or removed stereotyped behavior tends to disappear; for example, when FIBS-emitting pigeons are restored to their normal body weights, FIBS are absent [24].

Stereotyped behaviors may be induced by certain drugs; drug-induced behavioral stereotypies (DIBS) are observed following the administration of apomorphine (APO) [11, 12, 17], a direct dopamine (DA) agonist [2,14], or amphetamine (AMP) [17], an indirect DA agonist [26,29] and may be reduced by a dopamine antagonist, haloperidol (HAL) [9], in caged pigeons. A comparison of FIBS and DIBS findings reveals some interesting similarities: (a) response topographies that are quite similar, involving head and neck

movements and locomotion [17,24]; (b) increased FIBS and DIBS under greater food deprivation conditions [7,24]; and (c) a marked tendency to peck at high contrast stimuli, e.g., spots or edges [7,24].

The present study attempted to investigate the dopaminergic nature of FIBS in food deprived, caged pigeons with single daily feedings. It was hypothesized, based upon similarities with DIBS, that FIBS would be facilitated by a DA receptor agonist and inhibited by a DA receptor antagonist. It was further hypothesized, if FIBS were found to be DA-dependent, that among FIBS-emitting and non-emitting pigeons, differential brain levels of DA would be found, high in the former group members, relative to those in the latter group. The telencephalic region of the avian brain was viewed as especially relevant to dopaminergic mechanisms, based upon the relatively high concentrations of DA in avian paleostriatum [20], the established relevance of these mammalian brain homologues [5] for stereotyped behavior [15] and the widespread distribution of catecholaminergic projections to other telencephalic areas [22].

EXPERIMENT 1

Dopamine agonists facilitate DA-dependent behaviors in different test circumstances. A single dose of APO temporarily reversed sensory attention deficits in rats, deficits resulting from the destruction of the DA-bearing nigrostriatal

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pathway [23]. Cage climbing in mice, one of the DIBS observed following a single administration of APO, is facilitated by chronic administration of APO or N-n-propylnorapomorphine (another direct DA agonist) [31]. The supersensitizing effect of chronic, intermittent doses of DA agonists, while not well understood, is well documented [25].

The purpose of this experiment was to investigate the hypothesized DA-dependence of FIBS by testing for a facilitating effect of chronically and intermittently administered APO on FIBS.

METHOD

Animals

Sixteen White Carneaux pigeons (*Columba livia*), experimentally naive, served as subjects. They were individually housed in metal cages that measured 46×31×28 cm high. Opaque ceiling, floor and wall panels prevented animals from viewing one another, but sound communication was possible. Barred front doors contained food and water cups. All animals were kept in the same room which served for purposes of housing and experimental observation under temperature (19–23°C) and light (8 hr on/16 hr off) control. Animals were randomly divided into two groups of eight, each group occupying one rack of cages situated next to the other.

Procedure

During the first two weeks of the experiment, animals were allowed to feed for 1 hr per day (1230–1330 hr) and drink ad lib in their homes cages. In the third week birds were further deprived in order to reduce their body weights to approximately 80% of their free-feeding levels by the fourth week. This weight was maintained throughout Experiments 1, 2 and 3 with a limited feeding once a day at 1200 hr.

Treatment. For the entire 10 weeks of this experiment, birds in one group, Group A, were weighed and injected (IP) with apomorphine hydrochloride (APO) (Merck) (3 mg/kg in a vol. of 1 ml saline/kg body wt.) once a week. The injections were given on Wednesdays at 1030 hr with members of Group B only weighed at that time.

Observations. Pigeons were observed six periods a day, Monday–Friday, every hr on the half hr from 0930–1430 hr, three observations before and three observations after feeding. The “scan” method was used for obtaining data [28]. A characteristic of the scan method is that it is maximally sensitive to reliably occurring behavior because short duration observations are made. There is a low probability that sporadic behavior will occur during an observation period [16]. An observation period consisted of one or two observers standing outside the room, in clear view of the birds, observing each bird for approximately 10 sec. If a bird was emitting FIBS, the observer recorded a one, indicating its presence, and described its topography; if a bird did not emit FIBS, a zero was recorded for that bird for that period. Each observation period lasted about 3 min. Interrater reliability checks indicated that agreement was greater than 95%.

RESULTS

General Description of FIBS

This stereotyped behavior was marked by its consistent topography within individuals but by its variability among

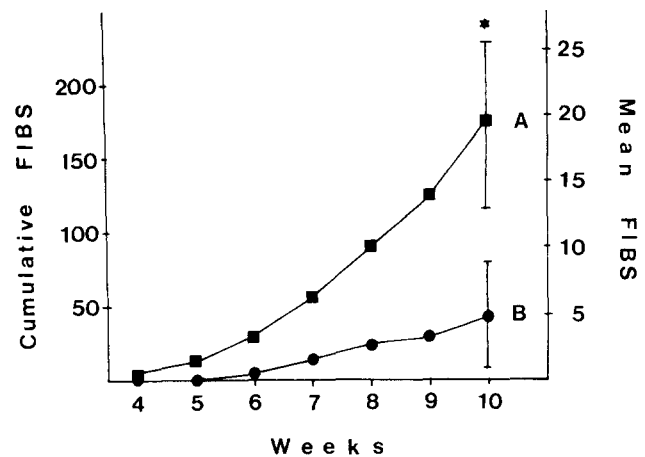


FIG. 1. Cumulative FIBS total and mean episodes observed over a 7 week test period, illustrating a performance separation between Groups A (APO-treated) and B (uninjected). * $p < 0.05$.

them. For example, one pigeon with no tendency to locomote delivered repetitive pecks from a fixed location in the cage to the same location on the edge of the food cup, in many observation periods over days and weeks. Another bird repetitiously exhibited a complex sequence including multiple head bobs, drinking, head shakes, locomotion to the opposite side of the cage over many days and weeks. Observed FIBS involved response repetition (bouts lasting seconds, minutes or hours) of one or more of the following elements: pecking; swallowing; mandibulating; head bobbing; head shaking (all head and neck movements) and locomotion. There was no apparent topography difference based on APO-injection vs. non-injection.

Animals engaged in FIBS were only briefly disrupted by sounds (e.g., loud hand clap) and sights (e.g., appearance of an observer); animals returned to FIBS within a few seconds following a single or occasional disturbance and tended not to stop FIBS with often-repeated or prolonged stimuli (disruptive stimulus adaptation).

FIBS frequency patterns. Data used for comparisons included FIBS observed on 4 days of the week, excluding the APO injection day. Two FIBS measures were used: (a) the number of FIBS-emitting episodes observed for each individual over 7 weeks; (b) the number of birds emitting FIBS in more than three observation periods over 6 weeks.

FIBS were emitted in significantly greater number during post-feeding observation periods than in pre-feeding ones (212 and 10, respectively) among members of both groups over 7 weeks, ($\chi^2(1)=184$, $p < 0.001$). The observation period with the greatest number of FIBS was at 1230 hr with 104, decreasing to 80 FIBS episodes at 1330 hr and 28 episodes at 1430 hr.

Comparison Between APO and Non-APO Groups

The cumulative number of FIBS in each group, plotted over the 7 week period of this experiment shows the behavioral divergence of the two groups (see Fig. 1). A statistically greater number of FIBS was emitted over this period by members of Group A than by those in Group B, $t(14)=2.18$, $p < 0.05$. The number of FIBS birds in Group A was six and

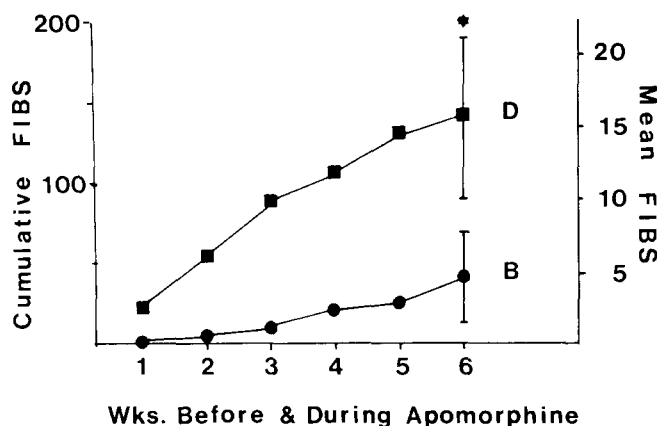


FIG. 2. Cumulative FIBS total and mean episodes observed over two 6 week test periods observed in the same group of animals (B) before and (D) during weekly APO administrations. * $p < 0.05$.

that in Group B was two. This latter difference was not statistically significant (Fisher-Yates Exact Probabilities Test, $p > 0.05$).

DISCUSSION

The experimental findings indicate an enhancing effect of chronically and intermittently administered APO on the number of FIBS emitted. However, the difference between the number of FIBS birds in the two groups failed to be statistically significant at the 95% confidence level, although the difference was in the appropriate direction. The small number of animals used partially accounts for this failure.

It was felt that taking advantage of the opportunity for retesting the hypothesis with another experimental design in Experiment 2 was advisable.

EXPERIMENT 2

The purpose of this study was to test the reliability of the finding of FIBS facilitation by multiple doses of a DA receptor agonist (APO) noted in Experiment 1 by employing a design that used subjects as their own controls.

METHOD

Animals

The eight previously uninjected White Carneaux pigeons in Group B from Experiment 1 were used. The conditions for housing, observation, feeding schedule, and body weight remained the same.

Procedure

FIBS observations were made in the same manner and according to the schedule used in Experiment 1. Unlike their previous "weigh only" treatment, Group B animals over the 6 weeks of this experiment were weighed and injected once a week with APO (3 mg/kg, IP), as Group A members had been in Experiment 1.

RESULTS AND DISCUSSION

For purposes of illustration, weekly FIBS performances

for Group B during the 6 weeks of APO administration and the previous 6 weeks of non-administration (during Experiment 1) are shown in Fig. 2. A statistical comparison of the number of FIBS episodes over each of the two 6 week periods indicated a significantly greater number under APO administration, $t(7) = 3.28$, $p < 0.02$. Also, a significantly greater number of FIBS birds were observed under the APO condition than non-APO condition (seven and two, respectively) (Binomial Test, $p < 0.05$).

These results combined with those in Experiment 1 strongly indicate a behavior-facilitating effect of chronic APO treatment on the number of FIBS birds and the number of FIBS. These findings support the view that FIBS are DA-dependent.

EXPERIMENT 3

The purpose of this experiment was to investigate the hypothesized inhibiting effect of a DA receptor antagonist, haloperidol (HAL) [1,8], on FIBS, serving to further test the hypothesis that FIBS are DA-dependent behaviors.

METHOD

Animals

The sixteen White Carneaux pigeons that participated in Experiment 1 were used. Conditions of diet and housing were the same as in Experiments 1 and 2, except that, due to loss of timing controls, lights remained on daily for 24 hr. This condition began 3 weeks before the start of this experiment and lasted beyond its termination.

Procedure

There was an interval of 5 weeks between the termination of Experiment 2 observations and the beginning of this experiment. All pigeons were observed for 1 day (Tuesday) followed by an injection (IP) of HAL (McNeil) (free base, 1 mg/kg and tartaric acid in saline, adjusted to pH 5.0) on the next day at 1030 hr. Observations were made 1 day prior to injection, the day of injection and post-injection days 1, 2 and 5. Observation periods numbered six on each observation day, three pre- and three post-feeding periods, as in Experiments 1 and 2.

After the passage of four additional weeks, a similar observation-drug treatment sequence was initiated to test the effect of a lower dose of HAL (0.5 mg/kg, IP) on FIBS.

RESULTS AND DISCUSSION

The results of this experiment are graphically shown in Fig. 3. On the days of HAL administration, FIBS were absent. The number of FIBS observed on days following HAL administration was compared to the pre-HAL day number. At 0.5 and 1 mg/kg the number of FIBS was reduced significantly for post-HAL days 1 and 2, t scores (15) > 2.78 , p values < 0.02 , but returned to normal by post-HAL day 5, the next tested day, t scores (15) < 1.4 , p values > 0.05 . The number of FIBS birds also changed significantly for both dosages on post-HAL day 1 (McNemar Tests, p values < 0.05).

Although FIBS were significantly reduced following HAL, pigeons were observed performing normal behaviors such as feeding, drinking, locomotion, preening, sitting, etc. One must conclude that FIBS reduction did not result from a

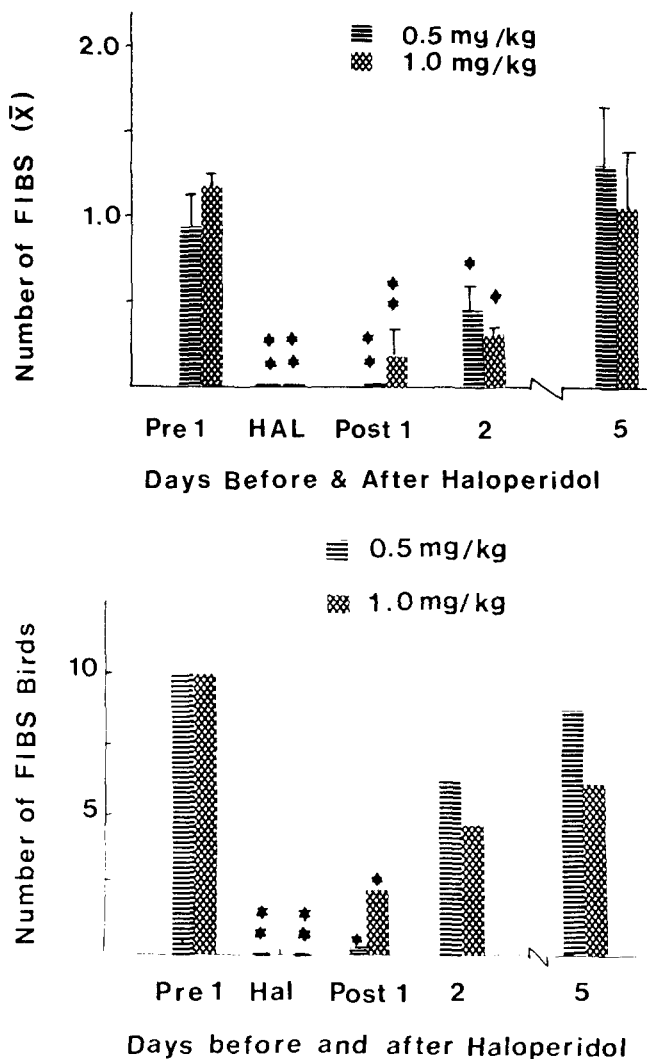


FIG. 3. A. Mean daily FIBS episodes observed before, during and after HAL administration (tested at two different dosages). * $p < 0.05$, ** $p < 0.01$. B. Number of birds emitting at least one FIBS episode before, during and after HAL (tested at two different dosages). * $p < 0.05$.

generalized inability of animals to perform motor acts or assume postures following HAL administration.

EXPERIMENT 4

The findings of the previous experiments in this study support the hypothesis that FIBS are DA-dependent. It is also clear that among the animals used, there was not an equal tendency for FIBS to be exhibited; some pigeons never showed FIBS while others often showed FIBS, a finding previously reported [24]. It appeared that a possible explanation for these individual differences might rest in differences in brain DA levels; FIBS-emitting pigeons might be anticipated to contain higher brain levels of DA than non-emitting pigeons. However, a recent review of findings and a hypothesis presented by Antelman and Caggiula [3] and re-

cent findings in our laboratory [18] suggested that DA-dependent behaviors might not be dependent on brain DA level alone but may be jointly dependent upon brain DA and norepinephrine (NE) concentrations.

This experiment set out to determine if differential concentrations of DA or joint DA-NE in the brain existed in FIBS-emitting and non-emitting pigeons.

METHOD

Animals

Eight White Carneaux pigeons were selected from among those participating in the previous experiments; five were selected from among FIBS-emitting and three from non-emitting birds. Selections were made 4 weeks after the termination of Experiment 3, while animals were still on a single daily feeding/80% body weight regimen.

Catecholamine Assays

Pigeons were decapitated and their brains quickly removed. The telencephalon was dissected away from underlying diencephalon, weighed and placed in ice cold physiological saline. Brain tissue was homogenized in 10 ml of ice cold perchloric acid, containing 0.04% ascorbic acid and 0.03% EDTA. Tissue homogenates were centrifuged at $10,000 \times g$ for 15 min (4°C). The supernatants were saved and each of the pellets suspended in an additional 5 ml of ice cold 0.4 N perchloric acid. Following a second centrifugation, the supernatants were combined and stored at -70°C , until assays were performed. On the day of assay, brain extracts were thawed at room temperature and NE and DA were isolated by cation-exchange chromatography, according to the method of Bertler *et al.* [4]. Briefly, the thawed brain extracts were adjusted to pH=6.5 and passed over a 60×5 mm Dowex 50W, X-4 (200-400 mesh) cation-exchange column that was prepared in Na^+ form, following extensive washings. NE and DA were sequentially eluted in 1 N and 2 N HCl, respectively. An aliquot of the appropriate eluate was assayed for NE or DA by spectrophotofluorometric analysis, using an Amico-Bowman Spectrophotofluorometer. The method of Bertler *et al.* [6] was used to assay NE while the method of Anton and Sayre [4] was used to assay for DA. All values were normalized to respective tissue weights.

RESULTS AND DISCUSSION

The measured concentrations of telencephalic DA and NE for individuals are listed in Table 1. Among the non-emitting animals, two pigeons, 2B and 8B, had higher DA levels than two FIBS-emitting pigeons, 6A and 7B. This outcome does not fit the prediction of higher DA concentration for FIBS animals than non-emitting animals (Mann-Whitney U Test, $p > 0.05$). However, when looking at the stereotyping index (SI), which essentially compares the ratio of DA/NE concentrations, one finds that all five FIBS-emitting animals' SI scores were higher in value than those of non-emitting animals, a statistically significant difference (Mann-Whitney U Test, $p > 0.05$). In the case of pigeons 6A and 7B, each with a low DA level, NE was markedly low, resulting in a relatively large SI score.

These findings support the NE-DA interaction hypothesis [3]; DA appears to facilitate FIBS while NE depresses it. This tentative conclusion regarding telencephalic CA requires further testing in the future.

TABLE 1
TELENCEPHALIC CATECHOLAMINES IN FIBS AND
NON-FIBS PIGEONS

| Bird | NE* | DA* | S.I.† | Behavior |
|------|------|------|-------|----------|
| 2A | 0.22 | 0.85 | 2.42 | FIBS |
| 6A | 0.12 | 0.64 | 2.74 | FIBS |
| 7A | 0.24 | 0.83 | 2.03 | FIBS |
| 7B | 0.10 | 0.64 | 3.38 | FIBS |
| 8A | 0.18 | 1.13 | 5.94 | FIBS |
| 2B | 0.24 | 0.76 | 1.63 | NON-FIBS |
| 4B | 0.21 | 0.36 | 0.26 | NON-FIBS |
| 8B | 0.19 | 0.70 | 1.89 | NON-FIBS |

* $\mu\text{g/g}$ Tissue.

†S.I. = Stereotyping Index.

$$\text{S.I.} = \frac{\text{DA} - \text{NE}}{\text{NE/DA}}$$

GENERAL DISCUSSION

Several findings in this study support the view that FIBS are DA-dependent behaviors. Chronic, intermittent administration of APO facilitated FIBS. This was demonstrated using two independent groups and replicated in a design in which each animal was used as its own control. Behavioral facilitation by a DA agonist has been reported for DA-dependent behaviors following single [23] and multiple or chronic doses [31]. According to a review by Post [25], intermittent DA agonist (direct or indirect) treatment facilitates behavior (drug sensitization) and continuous treatment leads to behavioral depression (drug tolerance). While the former was born out in the present study, the latter case remains to be tested in the context of FIBS performance.

The reduction in the number of FIBS and FIBS birds with HAL, assuming FIBS to be DA-dependent, was expected. Behavioral depression is also produced by HAL with APO-induced pecking [9]. The present results indicate that FIBS inhibition lasts for at least 24 hr after HAL administration by one FIBS measure (number of FIBS birds) and 48 hr or longer by another (number of FIBS). FIBS and DIBS depend upon DA receptor stimulation, it appears.

The nature of DA-dependency might be slightly redefined following the results of Experiment 4, in contrast to that based on findings from the first three experiments alone. Catecholamine assays of FIBS-emitting and non-emitting individuals suggest that FIBS are DA-dependent but that that dependency is tied to the NE level in the telencephalon. The stereotyping index, positively related to DA/NE levels

ratio, was found to be larger in all FIBS-emitting individuals compared to non-emitting ones. These findings support the Antelman and Caggiula NE-DA interaction hypothesis [3].

This hypothesis places an emphasis on the importance of stress in the induction of DA-dependent behaviors. The emphasis on stress or heightened attention [10] is compatible with findings regarding FIBS. Restricted space (caging) and food deprivation are stress conditions present in FIBS and DIBS studies. When food deprivation conditions are reduced or removed, FIBS performance is reduced or absent [24]; APO-induced pecking is also enhanced by food deprivation [7].

The similarity noted in Experiment 1 between FIBS of APO-primed and undrugged animals is apparent not only from a comparison of response topographies but also from a time distribution analysis of FIBS; significantly more FIBS occasions were noted following rather than preceding feeding, which is in accord with findings of Palya and Zacny [24] in undrugged birds. These findings lend confidence in the view that similar behaviors with similar mechanisms were being studied.

While observing FIBS, one is struck by individual differences. We have already suggested a neurochemical basis of differentiating FIBS-emitting and non-emitting animals. However, the variety of FIBS among individuals is remarkable. Interestingly, this is not unlike, for example, the consistent individual styles of APO-induced pecking; some are "wall pecking", some "floor pecking", some "body pecking", some "air pecking", etc. [17]. These differences can, in part, be influenced by environmental stimuli [7]. However when different animals are placed in the same environment, a variety of stereotyped responses are seen [17]. It appears that a finer grain neurochemical analysis will be necessary to account for these differences in stereotyped behaviors; applications and measurements of physical and/or chemical agents will have to be done in more restricted areas and structures within the central nervous system, perhaps something less than the undifferentiated telencephalon. Telencephalic candidate structures like the avian lobus parolfactorius and paleostriatum augmentatum components of the paleostriatal complex, or perhaps the lower lying hypothalamus or restricted mesencephalic areas, also rich in catecholamines [20] may provide good locations for the exploration of the neural basis for these individual differences. It would be of interest to see whether the DA-NE interaction or solely DA correlates best with behavior when assaying CA in these other locations.

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