

Pigeons Consistently Prefer Easy Over Harder Access to Food: No Reversal After Direct Dopaminergic Stimulation

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Many studies show that animals may prefer earned over free food—a phenomenon referred to as “contrafreeloading.” In rodents, dopamine—which is involved in incentive motivation and effort—facilitates the occurrence of such a preference. Here, we investigated the behavioral effects of pramipexole (PPX), a dopamine D2/3 receptor agonist, on contrafreeloading in pigeons. In Experiment 1, 2 groups of pigeons (PPX and SAL) were simultaneously exposed to a bowl that contained grains only (easy food option) and a bowl that contained grains covered with sawdust (harder food option) for 6 sessions. They were tested in two treatment conditions (high vs. low amount of food available). In Experiment 2, the two groups of pigeons were first repeatedly presented with the harder food option (training phase, 6 sessions) and then with the two options at the same time (test phase, 3 sessions). In order to potentially increase the physiological effects of PPX, the dose was tripled, and there was a 2-week incubation of the drug between Sessions 3 and 4 at training. The results indicate that the pigeons from both groups preferred to forage on the easy food option, and PPX did not alter this preference. Despite indications that PPX was effective, its action consisted of reducing—rather than magnifying—the attractiveness of the harder food option. It is suggested that pigeons are less motivated to deploy foraging effort than rodents in similar tasks.

Keywords: contrafreeloading, dopamine, pigeons, pramipexole, preference

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When animals are allowed to freely choose between one option in which food is easy and one in which it is harder to access, they sometimes decide to spend more time seeking and to consume more food items from the latter rather than the former option. For example, gerbils prefer to eat from a bowl containing 200 sunflowers mixed with sand while another bowl containing 1,000 sunflowers without sand is also present (Forkman, 1991, 1993). This propensity to prefer earned over free food has been identified in many animal species, including birds, and is referred to as “contrafreeloading” (Inglis, Forkman, & Lazarus, 1997). A number of factors may influence the expression of contrafreeloading, which optimally occurs when deprivation level is low, the required effort remains moderate, and the food items are not too scarce. This literature connects to studies showing that, under some circumstances, rodents come to prefer a cue that ambiguously predicts food or no food to a cue that unambiguously predicts food on each trial (Cocker, Dinelle, Kornelson, Sossi, & Winstanley, 2012;

Tremblay et al., 2017). Contrafreeloading is also perhaps related to studies revealing that animals and humans can make suboptimal choices, preferring a less valuable alternative when a more profitable one—in terms of reward rate or effort—is available (Belke & Spetch, 1994; Johnson, Madden, Brewer, Pinkston, & Fowler, 2011; Johnson, Madden, & Stein, 2012; Laude, Stagner, & Zentall, 2014; Madden, Dake, Mael, & Rowe, 2005; Stagner & Zentall, 2010; Zald et al., 2004).

Neurobiological investigations show that striatal dopamine is involved in suboptimal choices. In rats, contrafreeloading is enhanced after repeated injection of pramipexole (PPX)—a dopamine D2/3 receptor agonist (Schepisi, De Carolis, & Nencini, 2013; Schepisi et al., 2016). Also, rats given a choice between a variable ratio and a fixed ratio of responses to levers have a natural preference for variability, and this preference is increased after receiving an acute injection of PPX (Johnson et al., 2011, 2012). Indeed, this drug, often used to alleviate parkinsonian symptoms in humans, is a recognized cause of several addictions, including pathological gambling in some patients (Dodd et al., 2005; Voon et al., 2011). The role of dopamine in favoring suboptimal choices is clearly demonstrated in a study by Beeler, Daw, Frazier, and Zhuang (2010). They allowed mice to press a lever for cheap food (20 presses required) or another lever for expensive food (presses required were incrementally increased by 20 presses every day, from 40 to 200). So, compared to the low-cost lever, the high-cost lever represented a harsher option—and also perhaps a form of uncertainty because the required number of presses for that lever was more difficult to estimate (although always predictably

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harder) than that of the low-cost lever. In this free-choice task, Beeler and colleagues examined the role of dopamine—a neurotransmitter known to magnify incentive motivation and the willingness to work for reward (Berridge, 2007; Salamone & Correa, 2002). For that, they compared the preference for each option of normal wild-type (C57BL/6) mice with that of dopamine-transporter knockdown (DATkd) mice. These animals are characterized by more elevated extracellular dopamine levels and were shown to approach and contact cues predictive of food more avidly than normal mice (Peciña, Cagniard, Berridge, Aldridge, & Zhuang, 2003). The results indicated that DATkd mice not only spent more effort on pressing the high-cost lever but also earned more food pellets per day per gram of body weight. This laboratory study suggests that high dopamine levels prepare organisms to work harder and to get more food than organisms with lower dopamine levels, despite choosing the less profitable option more often.

The common ancestor of birds and mammals lived more than 300 million years ago. So, despite a number of anatomical and functional homologies between their respective brains, some differences in neural connectivity have occurred in regions controlling motivation and decision making (Durstewitz, Kröner, & Güntürkün, 1999; Herold, Joshi, Hollmann, & Güntürkün, 2012; Husband, 2004; Waldmann & Güntürkün, 1993; Yamamoto & Vernier, 2011). Such differences suggest that trying to infer the behavior of birds based on what we know about mammals can be rash. For example, we showed that apomorphine, a nonselective dopamine agonist, does not elicit any preference for variability over constancy in reward delay or for 50% over 100% chance of reward in pigeons (Anselme, Edeş, Tabrik, & Güntürkün, 2018). Yet, some findings in mammals indicate that those decision processes should be sensitive to dopaminergic activity (Hariri et al., 2006; Johnson et al., 2011, 2012; Kobayashi & Schultz, 2008; Roesch, Calu, & Schoenbaum, 2007; Zald et al., 2004; but see Day, Jones, Wightman, & Carelli, 2010). Thus, based on some homologies in brain connectivity between birds and mammals, we could expect them to behave similarly in contrafreeloading tasks. However, some neurobehavioral data indicate that such a prediction might be incorrect. In particular, birds and mammals were certainly not exposed to the same selective pressures for food, which may have led to distinct foraging strategies. In the present study, our goal was twofold: (a) determining whether pigeons show a spontaneous preference for hard over easy access to food, as often reported with rodents, and (b) determining whether PPX can induce/enhance preference for hard over easy food access, as also observed with rodents. Homing pigeons could freely choose between a bowl in which grains were directly accessible (easy food option) and a bowl in which the same grains were less directly accessible because covered with sawdust (harder food option). In Experiment 1, the effects of a relatively low dose of PPX (0.1 mg/kg) were tested with higher (Treatment 1) or lower (Treatment 2) amounts of food in each bowl. There were six choice sessions per treatment. In Experiment 2, the effects of a higher dose of PPX (0.3 mg/kg) were assessed with only one bowl (the harder food option) for six training sessions, and then the pigeons were tested with the two-bowl options, like in Treatment 1 of Experiment 1, for three choice sessions. In order to potentially increase the physiological effects of PPX, a 2-week incubation period was introduced between Sessions 3 and 4 at training. These tasks were partly inspired by the work of Forkman (1991, 1993) in gerbils.

We aimed to determine whether similar effects could be observed with pigeons (the sand was replaced by sawdust, which is easier to remove for animals that do not dig the soil) and added a pharmacological approach that was absent in Forkman's studies.

Experiment 1

Materials and Method

Animals and housing conditions. Sixteen unsexed naïve pigeons (*Columba livia*) were used. They were food deprived for 24 hr in their home cages before each 6-day experimental treatment and received no extra food after a session. Water was available ad libitum in home cages but not during the sessions. Half of the birds were housed together in an aviary, and the other half were housed in standard individual cages because of space limitation. The pigeons differently housed were fairly distributed in the two groups tested (see further). Housing was carried out under a 12-hr light/dark cycle (lights on at 7:00 a.m.). The pigeons had been accustomed to their home environment for several weeks before the experiment began. All procedures followed the German guidelines for the care and use of animals in science and were in accordance with the European Communities Council Directive 86/609/EEC concerning the care and use of animals for experimentation.

Apparatus. The pigeons were tested in an individual chamber (34 cm × 34 cm × 50 cm). The front panel consisted of a transparent Plexiglas window, through which the pigeons could be video recorded by means of an external camera (Sony Hybrid HDD) placed at approximately 70 cm in front of this panel. The other panels were gray colored and opaque. One pigeon was placed in the chamber via the back panel, which opened vertically from its upper part. The chamber contained LED lights on the ceiling, allowing optimal recording of the pigeon's activity. The chamber also contained two white squared bowls (14 cm aside and 5.5 cm in height), one on each corner formed by the transparent front panel and the adjacent side panel. In order to avoid pigeons climbing the bowls and spilling them, we built a simple wood-made system that maintained the bowls in their initial position. This system did not impede accessibility to the contents of the bowls. The floor of the chamber consisted of a grid covering an empty space of 4 cm in height, in which the grains and sawdust removed from the bowls by the pigeons could fall down. This prevented the pigeons from foraging on grains that were not in the bowls. An external white noise system was turned on during an experimental session in order to camouflage any possible disturbing noises from the lab. Figure 1 is a picture of the apparatus, as revealed by the camera.

Drug. PPX hydrochloride is a potent dopamine D2/3 receptor agonist, typically used to treat Parkinson's disease in humans. PPX was obtained from BioMol (Hamburg, Germany; purity > 98%), diluted in a Ringer saline solution. We used a concentration of 0.1 mg/kg, injected with a volume of 1 ml/kg, a dose shown to be effective in altering behavior in rats (Collins et al., 2007; Johnson et al., 2011).

Groups and behaviors analyzed. Two groups of eight individuals were tested. In Group PPX, the pigeons received a PPX injection 10 min prior to their placement in the test chamber. In Group SAL, the pigeons received a saline injection 10 min prior to

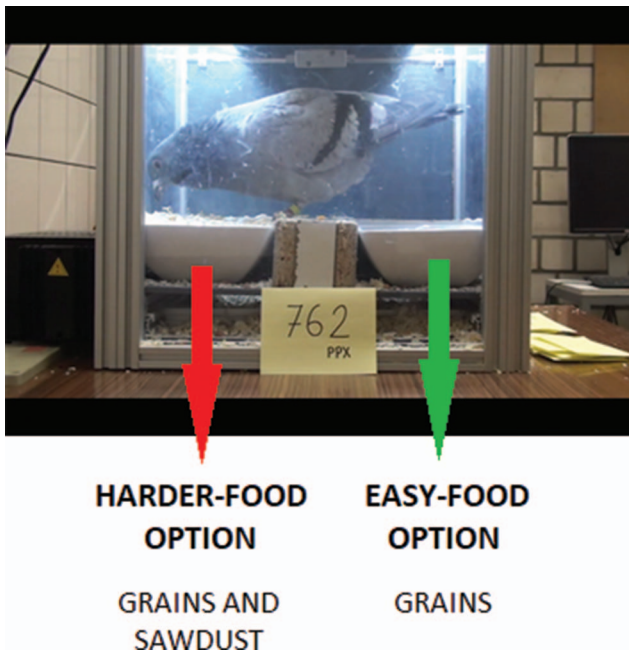


Figure 1. Experimental setup such as recorded by the camera. The two bowls were fixed just behind the transparent front panel. See the online article for the color version of this figure.

their placement in the test chamber. Three behaviors were analyzed:

- Time latency before giving the first peck: time elapsed between the closure of the back door—after introducing a pigeon into the chamber—and the first vertical movement of the head directed to the content of a bowl.
- Number of pecks: number of times a pigeon displayed a vertical movement of the head, directed to the content of a bowl. A peck did not necessarily mean that a grain was swallowed, or even grasped.
- Number of sweeping head movements: number of times a pigeon displayed a horizontal movement of the head, whose function was to get rid of uninteresting materials such as sawdust and grain husks.

Time was measured by means of a stopwatch, while the number of behaviors was counted by means of a clicker. The videos were carefully analyzed one by one. These behaviors were assumed to reflect the strength of foraging motivation, which should decrease time latencies and increase both the number of pecks and the number of head sweeps.

Procedure. The experiment started with a 3-day habituation to the experimental setup, following 24 hr of food deprivation in the home cage. For the first habituation session, 4 cm sawdust was placed in each bowl and 20 grains (a mixture of sunflowers, corns, and peas) were placed on top of it in each bowl, in order to be visible. During the next two habituation sessions, the 20 grains per bowl were covered with a 2-cm layer of sawdust; the pigeons had to remove some sawdust to see and to consume the grains. The habituation sessions aimed to allow the pigeons to learn that the sawdust was predictive of food delivery. Each habituation session lasted 15 min and was not video recorded, but the number of grains

eaten was counted. No injection was administered during the habituation phase.

The individuals were then randomly attributed to Group PPX or to Group SAL. Half of the pigeons from the two groups were assigned to Treatment 1 and the other half to Treatment 2 for 6 days or sessions. The pigeons were tested every second day in order to maintain their weight constant over treatments, each treatment starting with a 24-hr deprivation period. Note that the bowl containing only grains is thereafter referred to as the “easy food” option and the bowl containing gains and sawdust as the “hard food” option. In Treatment 1 (easy-abundant vs. little-hard), one bowl was 60% filled with a grain mixture without sawdust, and the other bowl was 60% filled with the same grain mixture covered by sawdust extending to the upper rim of the bowl. In Treatment 2 (easy-scarce vs. very hard), one bowl was only 10% filled with the grain mixture without sawdust, and the other bowl was 10% filled with the grain mixture covered with sawdust extending to the upper rim of the bowl. Thus, the two treatments differed in the guarantee that the daily amount of food was sufficient—it was in Treatment 1 but perhaps not in Treatment 2. At the end of this first 6-day phase, the pigeons were refed and then again deprived of food for 24 hr before a second 6-day phase started. Here, the subgroups that initially received Treatment 1 were exposed to Treatment 2 and vice versa. They received no extra food after the experimental sessions. The location of the bowls was counterbalanced across pigeons in each group but was always the same—within a treatment and between the two treatments—for a given individual. Each test day, the pigeons were weighed and then received their injection (PPX or SAL). They were injected in the pectoral muscle, half of the volume on each side. They remained out of the test chamber and out of their home cage during the 10 min that followed the injection before being placed in the test chamber. The camera recorded their activity for 15 min. Each test day, all the pigeons were run within the same session and in the same order. When a session was finished, the pigeons were returned to their home cage.

Statistical analyses. All the data were computed by means of mixed analyses of variance, which combine group comparisons with repeated measures. As appropriate, planned comparisons allowed us to examine the differences between two data sets. Statistica 13 was used to process the data.

Results

Habituation phase. Overall, the pigeons ate the grains, whether they were covered with sawdust or not. This indicated that the task could be carried out by pigeons, even for a low amount of food. Two pigeons (one in each group) did not eat most of the grains. Nevertheless, we decided to keep these two animals in the experiment—subsequently, their responses did not differ from those of the other individuals anymore.

Treatment 1: easy-abundant versus little-hard. In Treatment 1, 60% of each bowl contained grains, surmounted by 40% sawdust or nothing. Figure 2A shows that the pigeons strongly preferred to peck in the easy-abundant over the little-hard food bowl, irrespective of the injection received (PPX: $F(1, 14) = 19.904, p = .0005, \eta_p^2 = 0.76$; SAL: $F(1, 14) = 11.365, p = .004, \eta_p^2 = 0.41$). This pattern of responses was similar in the two groups, indicating that the drug was ineffective in altering both the

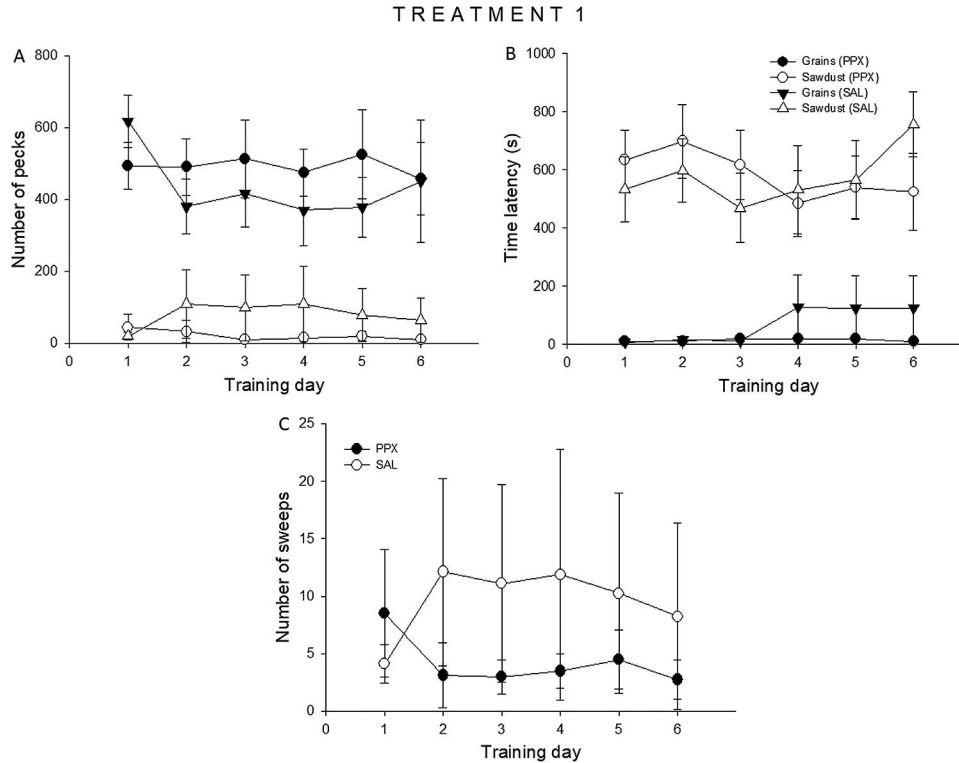


Figure 2. Treatment 1 of Experiment 1: easy-abundant versus little-hard food options (bowls 60% filled with grains) over 6 days. (A) Number of pecks. (B) Time latencies before the first peck. (C) Number of head sweeps (counted only in the bowl containing sawdust).

performance and the preference of the pigeons (easy-abundant: $F(1, 14) = 0.254, p = .622, \eta_p^2 = 0.02$; little-hard: $F(1, 14) = 0.645, p = .435, \eta_p^2 = 0.06$). The changes in the number of pecks every 3-min period within the 15-min daily sessions are presented in [online supplemental Table S1A](#). As shown, the number of pecks between the first and the last 3-min periods for each day decreased significantly for the easy-abundant food option (satiety effect), while it remained nonsignificantly different throughout for the little-hard food option—even though, on average, the exploration of the sawdust increased over time during the first 2 days.

The preference for the easy-abundant food option was confirmed by the analysis of the time latencies required to reach each option within a session. As depicted in [Figure 2B](#), time latencies were shorter for the easy-abundant food option compared to the little-hard food option, independently of the injection received (PPX: $F(1, 14) = 23.461, p = .0003, \eta_p^2 = 0.75$; SAL: $F(1, 14) = 18.638, p = .0007, \eta_p^2 = 0.53$). Here also, the drug had no effect on time latencies before reaching one or the other bowl (easy-abundant: $F(1, 14) = 0.954, p = .345, \eta_p^2 = 0.06$; little-hard: $F(1, 14) = 0.003, p = .953, \eta_p^2 = 0.00$). In [Figure 2C](#), the number of head sweeps in the bowl containing sawdust was counted. There was no significant effect of group ($F(1, 14) = 0.495, p = .493, \eta_p^2 = 0.03$), of day ($F(5, 70) = 0.144, p = .981, \eta_p^2 = 0.01$), and no interaction ($F(5, 70) = 1.216, p = .310, \eta_p^2 = 0.08$). This result also indicates that the drug was ineffective in altering food-seeking behavior.

Treatment 2: easy-scarce versus very-hard. In Treatment 2, where only 10% of each bowl contained grains (one without

and the other with 90% sawdust), results similar to those of Treatment 1 were obtained. The number of pecks was significantly greater for the easy-scarce food option compared to the very hard food option ([Figure 3A](#); PPX: $F(1, 14) = 29.818, p = .00008, \eta_p^2 = 0.73$; SAL: $F(1, 14) = 24.881, p = .0002, \eta_p^2 = 0.52$). Between the two groups, similar amounts of pecks were recorded in the bowl with grains only and in the bowl containing also sawdust (easy-scarce: $F(1, 14) = 0.046, p = .833, \eta_p^2 = 0.00$; very hard: $F(1, 14) = 0.969, p = .341, \eta_p^2 = 0.06$). [Online supplemental Table S1B](#) shows that the number of pecks decreased significantly between the first and the last 3-min periods for each day in the easy-scarce food option, while no significant differences were observed in the very hard food option—despite a noticeable average increase in the exploration of the sawdust on Day 1.

Accordingly, the time latencies to reach the bowls were shorter for the easy-scarce food option compared to the very hard food option ([Figure 3B](#); PPX: $F(1, 14) = 71.102, p = .000, \eta_p^2 = 0.88$; SAL: $F(1, 14) = 51.063, p = .000, \eta_p^2 = 0.62$). Here also, the pigeons responded similarly to each bowl, irrespective of the injection received (easy-scarce: $F(1, 14) = 0.617, p = .455, \eta_p^2 = 0.04$; very hard: $F(1, 14) = 0.659, p = .430, \eta_p^2 = 0.02$). [Figure 3C](#) shows that the number of head sweeps was independent of group ($F(1, 14) = 0.968, p = .342, \eta_p^2 = 0.06$) and of day ($F(5, 70) = 0.718, p = .612, \eta_p^2 = 0.05$), and there was no interaction ($F(5, 70) = 0.476, p = .793, \eta_p^2 = 0.03$).

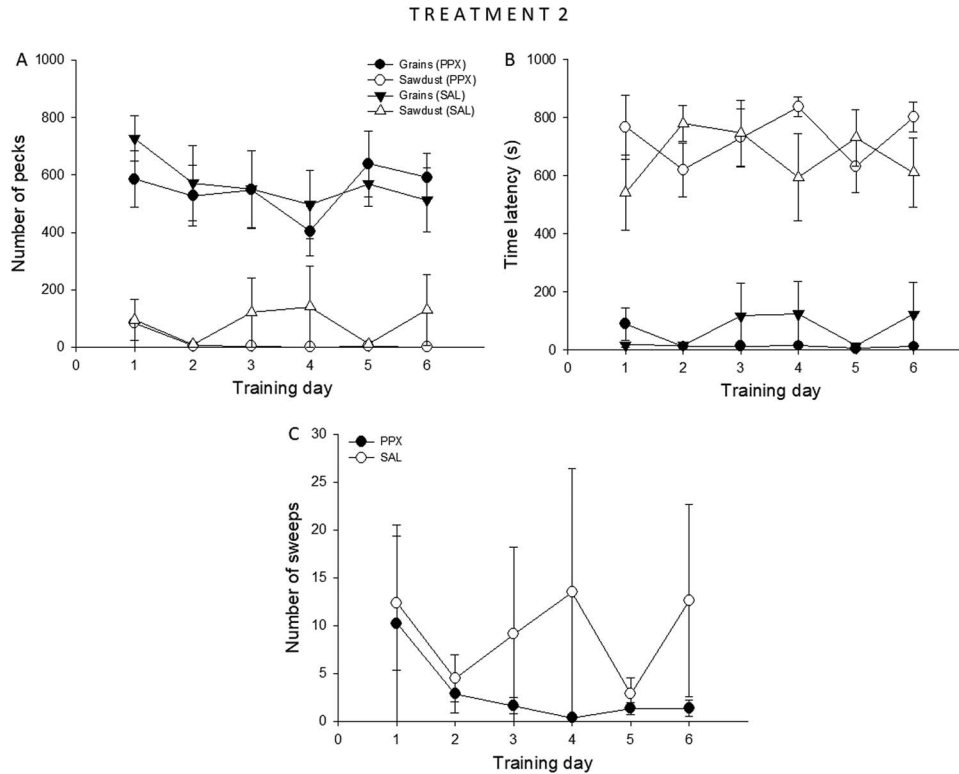


Figure 3. Treatment 2 of Experiment 1: easy-scarce versus very hard food options (bowls 10% filled with grains) over 6 days. (A) Number of pecks. (B) Time latencies before the first peck. (C) Number of head sweeps (counted only in the bowl containing sawdust).

Experiment 2

Experiment 1 revealed that pigeons strongly prefer an easy over a harder access to food, independently of the amount of food available and of dopaminergic stimulation. This is a clear-cut difference with the data reported in the introduction about rodents (e.g., Beeler et al., 2010; Forkman, 1993). In Experiment 2, animals were trained in a way that should increase the chance of obtaining a reversal of preference in the dual-choice task.

Materials and Method

Animals and housing conditions. The eight saline animals used in Experiment 1 were reused and redistributed within two groups, along with 7 naive animals (Group PPX: $n = 8$; Group SAL: $n = 7$). They were housed as previously.

Apparatus. The apparatus was that used in Experiment 1. The wood-made system that guaranteed the stability of the two bowls was, in a first step, replaced by another wood-made system to stabilize only one bowl appearing in the middle of the transparent front panel.

Procedure. Following a 4-day habituation phase similar to that of Experiment 1, the pigeons were trained with only one bowl containing grains (60%) and sawdust (40%) for 6 days in order to increase the chance that the sawdust acquired the properties of a conditioned stimulus (conditional stimulus [CS]). During this training phase with the little-hard food option, the PPX pigeons were injected daily with a higher dose of PPX (0.3 instead of 0.1

mg/kg) and subjected to a drug incubation phase of 2 weeks (without injection) in their home cage between the first 3 and the last 3 training days. Incubation aimed to sensitize responding to the potential CS properties of sawdust. Indeed, the addictive consequences of repeated use of PPX indicate that this drug has long-term brain effects, which could be magnified by an incubation period. In parallel, the SAL pigeons received saline injections and had a 2-week break in their home cage. After these 6 training days with only one bowl, the pigeons were given a choice between an easy-abundant food option (60% grains without sawdust) and a little-hard food option (60% grains and 40% sawdust), like in Treatment 1 of Experiment 1, for 3 days. During the choice phase, the pigeons received the same injection as during the one-bowl training. Each session took place every second day. The same behaviors as in Experiment 1 were analyzed by means of the same statistical methods.

Results

During the 6-day phase of training with only one bowl containing grains and sawdust, there was a nonsignificant trend for the difference in the number of pecks between the Groups PPX and SAL (Figure 4A; $F(1, 13) = 4.038, p = .066, \eta_p^2 = 0.24$). The two groups only differed significantly on Day 3, $F(1, 13) = 8.351, p = .013$, and Day 5, $F(1, 13) = 5.034, p = .043$. Interestingly, the number of pecks increased between Days 1 and 6 in Group PPX, $F(1, 13) = 8.244, p = .013$, but remained stable in Group SAL, $F(1, 13) = 1.354, p = .265$. Figure 4B presents the number of

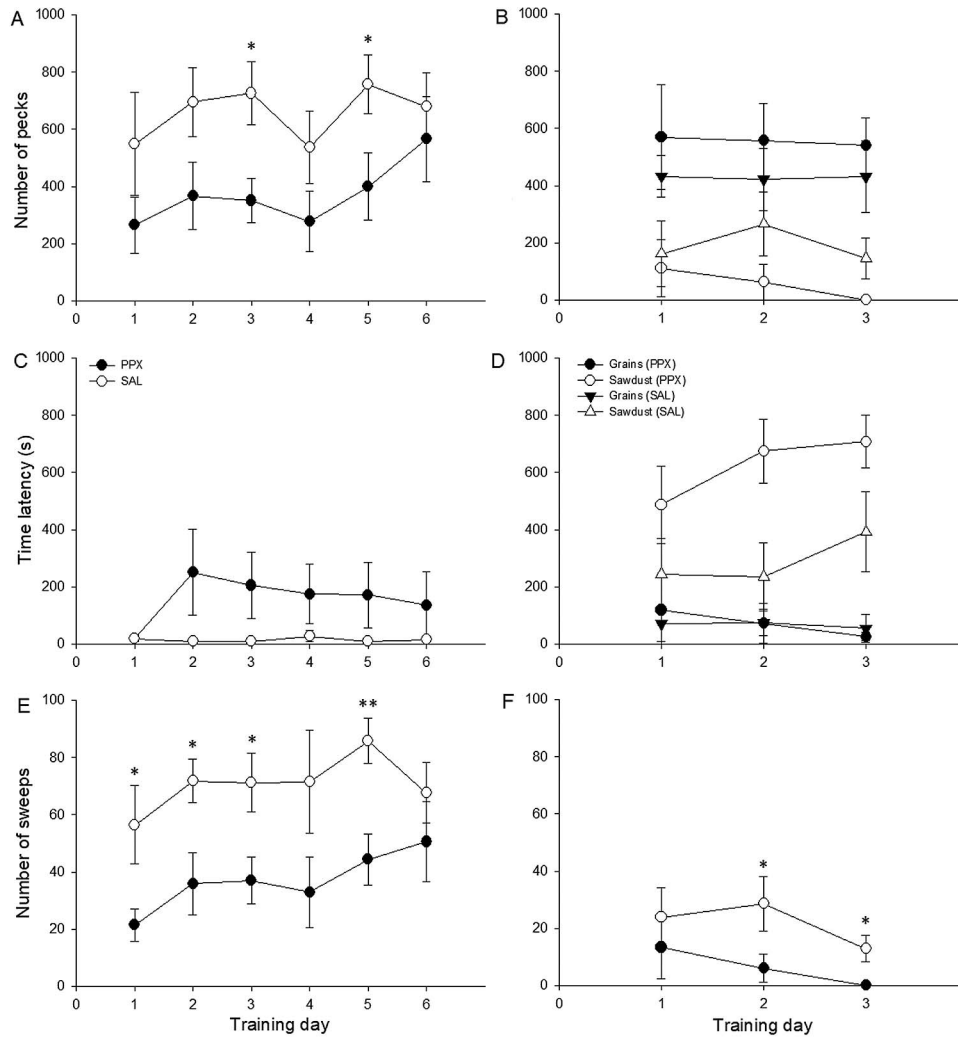


Figure 4. Experiment 2: Training and choice phases over time (bowls 60% filled with grains). At training (A, C, E), the pigeons were only exposed to one bowl (grains with sawdust), while at test, they had to choose between two bowls (one with grains and sawdust, the other with grains only). Note that the number of pecks (B) and time latency (D) were measured in the two bowls, but the number of sweeps (F) was only measured in the bowl with sawdust. (A) Number of pecks at training (no choice). (B) Number of pecks at test (choice). (C) Time latencies before the first peck at training (no choice). (D) Time latencies before the first peck at test (choice). (E) Number of head sweeps at training (no choice). (F) Number of head sweeps at test (choice; counted only in the bowl containing sawdust). * $p < 0.05$. ** $p < 0.01$.

pecks displayed during the 3-day phase of free choice. In Group PPX, there was an overall preference for the easy-abundant food option over the little-hard food option ($F(1, 13) = 24.296$, $p = .000$, $\eta_p^2 = 0.57$), and this preference was significant for the 3 days (Day 1: $F(1, 13) = 6.302$, $p = .026$; Day 2: $F(1, 13) = 9.639$, $p = .008$; Day 3: $F(1, 13) = 18.902$, $p = .001$). In Group SAL, the overall preference for the easy-abundant food option was significant ($F(1, 13) = 4.834$, $p = .047$, $\eta_p^2 = 0.26$), but preference was nonsignificant for all days (Day 1: $F(1, 13) = 1.915$, $p = .190$; Day 2: $F(1, 13) = 0.836$, $p = .377$; Day 3: $F(1, 13) = 4.641$, $p = .050$). **Online supplemental Table S2A** indicates that, at training, the number of pecks decreased significantly between the first and the last 3-min periods for each day in both groups (except on Day

3 in Group PPX). **Table 2B**, which refers to the free-choice task, shows that the number of pecks at the easy-abundant food option significantly decreased in both groups (except on Day 2 in Group SAL), while they remained stable—and lower in comparison—relative to the little-hard food option (except on Day 2 in Group SAL).

The analysis of time latencies before the first peck at training revealed no group differences (**Figure 4C**; $F(1, 13) = 3.016$, $p = .106$, $\eta_p^2 = 0.19$), no effect of day ($F(5, 65) = 0.873$, $p = .504$, $\eta_p^2 = 0.06$), and no interaction ($F(5, 65) = 1.021$, $p = .412$, $\eta_p^2 = 0.07$). Time latencies in each group did not change significantly between Days 1 and 6 (PPX: $F(1, 13) = 2.033$, $p = .177$; SAL: $F(1, 13) = 0.001$, $p = .971$). During the 3 days of free choice, a

significant group difference was observed (Figure 4D; $F(1, 13) = 5.318, p = .038, \eta_p^2 = 0.29$). In fact, the pigeons in Group PPX showed longer overall time latencies to reach the little-hard food option than the pigeons in Group SAL ($F(1, 13) = 6.897, p = .021, \eta_p^2 = 0.39$), while the two groups performed similarly with respect to the easy-abundant food option ($F(1, 13) = 0.005, p = .942, \eta_p^2 = 0.00$). In Group PPX, overall time latencies were shorter for the easy-abundant than for the little-hard food option ($F(1, 13) = 31.860, p = .000, \eta_p^2 = 0.75$), and this preference was observable for each day (Day 1: $F(1, 13) = 7.478, p = .017$; Day 2: $F(1, 13) = 23.906, p = .000$; Day 3: $F(1, 13) = 28.734, p = .000$). In Group SAL, the difference in overall time latencies for each option showed a nonsignificant trend ($F(1, 13) = 4.581, p = .052, \eta_p^2 = 0.24$).

As reported in Figure 4E, the number of head sweeps at training was higher in Group SAL than in Group PPX ($F(1, 13) = 7.514, p = .017, \eta_p^2 = 0.37$). In Group PPX, an increase in the number of head sweeps was noted between Days 1 and 6, $F(1, 13) = 7.148, p = .019$, but performance remained stable in Group SAL, $F(1, 13) = 0.939, p = .350$. During the 3 days of free choice (Figure 4F), there was no effect of group ($F(1, 13) = 3.665, p = .078, \eta_p^2 = 0.22$), of day ($F(2, 26) = 2.431, p = .108, \eta_p^2 = 0.16$), and no interaction ($F(2, 26) = 0.568, p = .573, \eta_p^2 = 0.04$). However, the number of head sweeps was higher in Group SAL than in Group PPX on the last 2 days (Day 2: $F(1, 13) = 4.961, p = .044$; Day 3: $F(1, 13) = 8.764, p = .011$).

Discussion

Our results suggest that pigeons consistently preferred to consume food items whose access was easy, compared to the same food items whose access was harder. This preference occurred independently of food density and of dopaminergic stimulation by means of PPX. Pretraining with the harder food option alone, including a 2-week incubation of a higher dosage of PPX, did not alter preference. Such a pattern of responses is in accordance with optimal foraging theory, which predicts that animals should always prefer a food option that maximizes reward rate intake (Stephens & Krebs, 1986). Although the pigeons also inspected the harder food option, especially at the beginning of an experimental phase, the present results represent a sharp contrast with those observed with rodents exposed to similar experimental conditions (Forkman, 1991, 1993, 1996) or exposed to dopaminergic stimulation in dual-choice tasks involving one food option harder than the other (Beeler et al., 2010; Johnson et al., 2011; Schepisi et al., 2013).

This means that pigeons and rodents—but perhaps not birds and mammals in general—seem to use distinct criteria to make choices and that their decisions may (partly) depend on different neurotransmitters. In Experiment 1, no effect of PPX on choice was observed, whether the pigeons were exposed to a large or a smaller amount of food. Was the dose of 0.1 mg/kg too low? Or is this an indication that dopamine does not play any role in choice behavior? Telencephalic D2-receptor distributions in birds mostly overlap with the mammalian pattern, although the relative striatal concentrations of D2/D1-like receptors are even higher in birds relative to mammals (Durstewitz et al., 1999; Kubikova, Wada, & Jarvis, 2010). Day et al. (2010) showed higher dopamine release for a short delay and a low ratio of responses (relative to their longer/higher counterparts) when rats did not have to choose

between the two options, but similar dopamine levels were observed when they had to choose between them. Accordingly, in pigeons, we failed to induce a preference for a variable over a constant delay after repeated administration of apomorphine (Anselme et al., 2018). Although the reasons for those results are unclear, the idea that dopamine is not involved in choice behavior is relatively implausible regarding other studies (Hariri et al., 2006; Johnson et al., 2011, 2012; Kobayashi & Schultz, 2008; Roesch et al., 2007; Zald et al., 2004). Indeed, the use of a higher dose of PPX (0.3 mg/kg) in Experiment 2 revealed that the drug was effective, in the training (no choice) phase as well as in the test (choice) phase. At training, the PPX pigeons pecked less (Figure 4A) and swept less (Figure 4E) than the SAL pigeons. At test, the PPX pigeons showed longer time latencies (Figure 4D) and fewer head sweep movements (Figure 4F) than the SAL pigeons. Thus, we have to conclude that a PPX dose of 0.1 mg/kg has no noticeable behavioral effects in pigeons.

At this stage, it is not possible to determine whether the differences between the PPX and the SAL pigeons in Experiment 2 reflected motivational effects, motoric effects, or both. However, some information can reasonably be deduced from current data. In rodents, PPX results in an increase in foraging activity on the harder food option (e.g., Johnson et al., 2011, 2012; Schepisi et al., 2013, 2016). Effort facilitation is compatible with the view that dopamine agonists enhance incentive motivational processes (Salamone & Correa, 2002). In pigeons exposed to a choice, PPX reduces foraging activity on the harder food option (Figure 4D and 4F) but does not alter it on the easy food option (Figure 4B and 4D). This suggests that in pigeons, as well as in rodents, the effects of PPX were motivational rather than motoric. But in pigeons, contrary to rodents, PPX seems to cause a stronger aversion—not a stronger attraction—of the harder food option.

Why does PPX reduce the willingness to deploy effort for hidden food in pigeons? Rodents and pigeons are opportunistic species, consuming a wide variety of foods—such as seeds, fruits, and insects—depending on their availability. Rodents deploy a lot of effort in exploring new locations, digging, climbing, stealing, hoarding, gnawing, and manipulating objects in the search of edible items. Also, it is a well-documented fact that dopamine facilitates motivated and effort-related behaviors in rodents (Berridge, 2007; Salamone & Correa, 2002). In contrast, pigeons consume edible items accidentally found on the ground, flying from one location to another, a strategy that does not require much time and energy. Interestingly, microinfusions of the neurotoxin 6-OHDA to bilateral medial striatum in domestic chicks does not alter foraging effort (Ogura, Izumi, Yoshioka, & Matsushima, 2015), suggesting that dopamine is not a facilitator of foraging effort here. Another indication that rodents are more prepared to make effort in the search of food than pigeons is the gentler temporal discounting curve observed in rats compared with pigeons; rats tolerate delayed food more than pigeons (Mazur & Biondi, 2009; Tobin & Logue, 1994). Thus, a demanding foraging task does not motivate pigeons as it can motivate rats. If correct, this means that pigeons are unlikely to prefer to seek grains covered with sawdust when the same grains are directly accessible.

There is evidence that pigeons may show faint preferences for earned over free food under some conditions. Two important parameters are the presentation of a CS associated with the earned food only (Alferink, Crossman, & Cheney, 1973; Neuringer, 1969;

Podlesnik & Jimenez-Gomez, 2016; Wallace, Osborne, Norborg, & Fantino, 1973) and the strength of the habit to consume the earned food during a training phase that precedes the choice phase (Lentz & Cohen, 1980). In our experiments, no specific CS was used (apart from sawdust), but the training of the pigeons with the harder food option failed to reverse the initial preference for the easy food option. The use of sawdust—instead of key pecking—to render access to food harder might contribute to explain why pigeons did not exhibit contrafreeloading here. Pecking is practically uncultured and self-reinforcing for pigeons, so that this activity may have contributed to the attractiveness of the harder/earned food option in the studies mentioned above. In contrast, although head sweep movements belong to the behavioral repertoire of pigeons, this action is not often performed to find their food in nature. Thus, there was no advantage associated with the harder food option for pigeons in our experiments. More thorough investigation is needed to determine how different types of CSs may alter motivation and preference (e.g., Meyer, Cogan, & Robinson, 2014).

It is unlikely that the absence of contrafreeloading resulted from too strong food deprivation or too demanding effort. Concerning food deprivation, it must be noted that pigeons are relatively large birds, for which one day of food deprivation cannot cause nutritional deficits. In fact, because they had the possibility to consume a lot of food every second day, their weight remained quite stable over the experimental sessions and similar to their initial baseline level. With respect to the effort required, it is a fact that pigeons show much less curiosity than rats—for example, in Skinner boxes, pigeons may easily fall asleep while rats avidly explore this new environment (personal observation in other experiments). Thus, removing 90% sawdust to get grains (Treatment 2 of Experiment 1) may have been too demanding for the pigeons. But the task demand was not so high in the other conditions tested (40% sawdust), even though the pigeons remained significantly more attracted by the easy food option. Finally, it could be argued that the two bowls contained the same amount of grains, while in Forkman's (1991, 1993) studies, the bowl with sand contained a smaller amount of seeds than the bowl with seeds only. This is worth being investigated with pigeons. However, given the consistent contrast between the two options over repeated exposure, it is unlikely to observe a reversal of preference if fewer grains were placed in the harder than in the easy food option.

Conclusion

Although contrafreeloading in pigeons has been reported (Inglis et al., 1997), the present study demonstrates that the conditions for its occurrence are narrower than in rodents, especially gerbils. Until now, this had not been shown. The main reason for this might be that foraging effort motivates pigeons less than rodents, because of noticeable differences in their respective foraging strategies. We are well aware that we mostly are reporting negative data. However, we are convinced that systematic and hypothesis-driven attempts are the key to understanding the mechanisms of behavior and brain. Such attempts necessarily also produce negative findings that then still fill an important hole in our scientific exploration.

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