



Anticipatory and foraging behaviors in response to palatable food reward in chickens: Effects of dopamine D2 receptor blockade and domestication



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HIGHLIGHTS

- A role of dopaminergic regulation of reward processes in chickens is supported.
- Leghorns show more anticipatory behavior to signaled rewards than Red Junglefowl.
- Domestication may have changed the threshold for expressing appetitive behaviors.
- Domestication may have resulted in higher sensitivity for rewarding stimuli.

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ABSTRACT

Behaviors associated with anticipation and search for palatable food may provide information about dopaminergic reward processes and positive motivational affect in animals. The overall aim was to investigate the involvement of dopamine signaling in the regulation of cue-induced anticipation and search for palatable food reward in chicken, and whether domestication has affected expression of reward-related behaviors. The specific aims were to describe effects of mealworms (palatable food for hens) and haloperidol (a dopamine D2 antagonist) on foraging behaviors and cue-induced anticipatory behaviors in Red Junglefowl (RJF; the wild ancestor of modern laying hens) and a white layer hybrid (LSL). RJF ($n = 26$) and LSL ($n = 20$) were initially trained on a conditioning schedule to anticipate mealworms (unconditioned stimulus; US) 25 s after exposure to a red light (conditioned stimulus; CS). For the experiment, hens received haloperidol or saline injections 30 min before exposure to one CS + US combination. Behavior was registered 10 min before CS and 10 min after US (foraging behaviors), and during the CS–US interval (anticipatory behaviors). Higher frequencies of CS-induced anticipatory head movements, faster approach to rewards, and higher frequency of foraging behaviors were found in LSL compared to RJF. Haloperidol suppressed CS-induced head movements in both breeds, and the frequency of foraging behaviors after reward delivery. The results support a role of dopamine signaling in the regulation of reward processes in chickens, and suggest that domestication has changed the threshold for perceiving food incentives and/or for expressing reward-related behaviors that may be indicative of positive motivational affect in hens.

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1. Introduction

Acceptance that commonly farmed animal species are capable of experiencing positive and negative affective states, and that these

affective states can be studied indirectly through changes in behavior and physiology, has greatly advanced animal welfare science [1]. However, compared to the study of negative affective states such as fear (e.g. [2]), the positive emotional processes and the associated positive affective states have only recently received scientific attention (e.g. [3–7]). Emotions are likely to have evolved from basic mechanisms that gave animals the ability to avoid harm and seek valuable resources [8]. Thus, positive emotional states can be described as what fuels motivation, which again drives goal-directed behavior, i.e. the seeking of

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valuable resources in “opportunity situations” [4]. It has therefore been proposed that behaviors elicited by the anticipation, search and ingestion of palatable food rewards (i.e. appetitive and consummatory behaviors) can yield indirect information about positive affect in animals [6,9,10].

Changes in behavior and physiology expressed in response to a conditioned stimulus (CS) signaling the arrival of palatable rewards (unconditioned stimulus; US) are suggested to be indicative of a “wanting” type of affect in animals linked to dopaminergic brain reward processes [6,9]. In a series of experiments in laying hens, we found that a CS signaling mealworms induce a high frequency of head movements while standing alert with head and neck stretched [11–13]. The frequency of CS-induced head movements is higher, the more palatable the signaled food reward is: hens display more frequent head movements when expecting worms (which are ranked over other types of palatable food rewards [14]) than when expecting whole wheat [13]. We have therefore suggested that CS-induced head movements represent a “wanting” type of positive motivational affective state or arousal that is indicative of the chickens appraisal of the expected reward.

In mammals, the mesolimbic dopaminergic system and opioid brain reward circuits involving the ventral tegmental area (VTA) and the nucleus accumbens (Nac) are recognized for their central role in motivated behaviors and reward processes (e.g. [9,10,15,16]). Thus, studies of behaviors associated with anticipation, search for and ingestion of palatable food may provide indirect information about brain reward processes and positive motivational affect in animals. Although the avian brain anatomy differs from that of mammals, avian brain reward system homologues of VTA and Nac have been described [17] and neuronal activities in basal ganglia [18] and the ventral striatum [19] have been identified. Previously, we found that a dopamine D2 receptor antagonist (i.e. haloperidol) decreases the frequency of CS-induced head movements during anticipation of mealworms [12]. Thus, it can be suggested that the frequency of head movements in chickens in response to a CS signaling a palatable US may be due to activity in brain reward areas that are homologous to similar areas in mammals. Furthermore, dopaminergic pathways have been recognized as a key component in mediating motivational aspects of foraging behaviors in vertebrates [9,20,21], and it could be proposed that foraging behavior in response to palatable food may reflect a dopamine controlled “wanting” type of positive affect. However, dopamine control of foraging behaviors in chickens in response to palatable food rewards has not yet been investigated.

Red Junglefowl (RJF) is considered to represent the wild ancestor of the laying hen. Comparative studies using RJF and modern breeds of laying hens revealed that the domestication process has resulted in a changed frequency of several behaviors, and it was suggested that these differences may be due to a changed threshold for eliciting such behaviors [22,23]. For instance, it was found that RJF performed more exploratory behavior in the search for food compared to laying hens genetically selected for production characteristics [24–27]. On the other hand, it was found that a modern layer breed ingested food at a higher frequency than RJF (i.e. consumed more food per time unit; [24]), although the total foraging activities did not differ. These studies investigated feeding and explorative behaviors in response to standard diets, and it is not known whether domestication has affected frequencies of foraging behaviors such as litter pecking or scratching in response to more palatable food sources. Furthermore, CS-induced anticipatory behaviors in response to signaled palatable rewards have not yet been described in RJF. Little is also known about how domestication has affected the dopamine system in chickens, and it is not known whether there are differences in behavioral effects of dopamine blockade on reward-related behaviors between RJF and modern breeds. As dopaminergic activity is probably correlated with the strength of “wanting” as stated above, finding out whether domestication has changed the influence of dopaminergic systems on CS-induced anticipatory

behaviors and foraging behaviors could be a way to start understanding the effect of domestication on the emotional life of farm animals including chickens.

In order to gain more knowledge about reward processes and positive motivational affective states in chickens, the overall aim of this study was to investigate the involvement of dopamine signaling in the regulation of CS-induced anticipation and foraging behaviors in response to palatable rewards, and whether expressions of reward behaviors are affected by domestication. More specifically, the aims were: 1) To describe how the level of foraging behaviors in RJF and a selected strain of White Leghorn laying hens (LSL) are affected by administration of a palatable food reward, 2) to test whether frequencies of CS-induced anticipatory behavior differ between RJF and LSL, and 3) to test whether haloperidol influences frequency of CS-induced anticipatory or foraging behaviors in both breeds, and whether there are differences between breeds in the effect of haloperidol.

2. Material and methods

2.1. Animals and husbandry

Two breeds were included in the experiment: Red Junglefowl (RJF, $n = 26$), and Lohmann White Selected Leghorn laying hens (LSL, $n = 20$). Fertilized eggs from RJF birds originating from the research facilities at Linköping University in Sweden [24] and from LSL birds from a commercial breeder (Steinsland, Bryne, Norway), were hatched in the same incubator at the Norwegian School of Veterinary Science. At one day of age, chicks were vaccinated against Marek's disease. The birds were reared together in one large floor pen (approximately 3 m × 1.5 m) covered with litter. Perches were placed 40 cm above the ground. Our previous studies on reward anticipation were conducted in female chickens [11–13] and it is not known if reward anticipation differs between sexes and/or is affected by a mixed-sex group. It was therefore decided to exclude males from the study as soon as it was possible to visually observe sex differences based on comb characteristics. At 14 weeks of age, the first replicate of hens was moved in same-breed pairs (LSL + LSL or RJF + RJF) into six adjacent experimental pens in a separate room. Each experimental pen was 227 cm high, and the floor (151 × 95 cm) was covered with wood-shavings. Hens had access to perches. All walls of each pen were solid below 143 cm. Hens were allowed to acclimatize to the experimental pens for one week before the experimental procedures started. A standard layer diet (Kromat, Felleskjøpet, Norway) and water were supplied ad libitum throughout the study. After completing the first replicate of the experiment, a new replicate of chicken was housed pairwise in the pens, and a total of four replicates were used for the study. (Replicate 1: 3 pairs of LSL and 3 pairs of RJF; replicate 2: 3 pairs of LSL and 3 pairs of RJF; replicate 3: 3 pairs of LSL and 3 pairs of RJF; and replicate 4: 2 pairs of LSL and four pairs of RJF.) One pair of LSL from replicate 3 was excluded from the study due to severe pecking. As the chickens had been hatched together, each replicate was approximately three weeks older than the previous. Furthermore, 12 hens were moved from the rearing pen to the experimental pens for each replicate. Therefore, the remaining hens in the rearing pen were kept at a lower density for each replicate; i.e. hens from the first replicate had been kept at the highest density, and hens from the fourth replicate had been kept at the lowest density and for nine weeks longer than the first replicate.

2.2. Habituation and training procedures

A reward delivery apparatus attached to the pen door at approximately 1 m height was used for mealworm delivery and cue-reward training [for details, see 11,13]. Live mealworms (approximately 30 worms) were placed in the small cylinder shaped chambers (approximately 2 cm width × 2 cm height) in the reward feeder wheel. When the apparatus was activated a portion of worms was automatically

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