



Effects of signalled reward type, food status and a μ -opioid receptor antagonist on cue-induced anticipatory behaviour in laying hens (*Gallus domesticus*)



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ABSTRACT

Studies using classical conditioning have shown that hens display high frequencies of dopamine-controlled cue-induced anticipatory behaviours in the cue-reward interval when signalling mealworm rewards. However, it is not known whether anticipatory behaviours are reward specific, and whether the opioid system is involved in their control. The purpose of the present study was to investigate (1) effect of incentive value of rewards, and (2) the involvement of μ -opioid receptor activation, on the expression of cue-induced anticipatory behaviours in laying hens. Incentive value was manipulated by reward type (mealworm and whole wheat) and by physiological state (sated and fasted hens). Hens ($n = 14$) were trained to associate a cue (green or red light) with a reward (whole wheat or mealworms). Blue light served as an unrewarded control stimulus. Cue-induced anticipatory head movements (latency to first head movement after cue presentation, and frequency of head movements in the cue-reward interval), steps (frequency), and pecking at reward (latency), were registered in sated and fasted hens during a 25 s cue-reward interval. An involvement of the opioid system in mediating cue-induced anticipatory behaviours was tested by intraperitoneal injection of the μ -opioid receptor antagonist naloxone at 5.0 mg kg^{-1} . Saline served as control. Injections were administered 30 min before the light cues. Individual hens were tested on all treatment combinations: sated/saline, fasted/saline, sated/naloxone, and fasted/naloxone. Incentive value of signalled reward was differentially reflected by the frequency of cue-induced head movements ($P < 0.0001$). Hens displayed more head movements in response to signalled mealworms (33.1 ± 0.9) than signalled whole wheat (28.5 ± 1.1) and unrewarded cue (17.2 ± 1.0). The frequency of steps was higher in response to the cue signalling mealworms (12.2 ± 1.0) and whole wheat (9.9 ± 0.7) than to the unrewarded cue (6.3 ± 0.7 , $P < 0.0001$ and $P = 0.0003$, respectively), but there was no difference between the rewarded cues. Latency to initiate the first head movement was longer in response to the unrewarded cue than to cues signalling whole wheat and mealworms ($P = 0.051$ (tendency) and $P = 0.0017$). Hunger amplified the frequency of head movements ($P < 0.002$) and tended to affect frequency of steps ($P < 0.072$). No effects of treatment with naloxone were found as tested here. In conclusion, cue-induced anticipatory head movements reflect incentive value of food rewards in laying hens. The role of opioid regulation of reward processes in hens needs to be further investigated.

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1. Introduction

An animal's behaviour in unconditioned choice and conditioned instrumental operant tests can be used to assess what animals prefer and the strength of their motivation for incentives (Dawkins, 1990; Kirkden and Pajor, 2006). Studies show that domestic laying hens prefer mealworms over whole wheat in an unconditioned choice test, and work more for mealworms compared to other food types in a conditioned operant test, indicating that they rank the incentive value of mealworms higher than that of whole wheat (Bruce et al., 2003). Furthermore, studies of animal behaviours induced by a conditioned stimulus (CS) predicting a reward have been suggested as a tool to understand what and how much an animal wants a reward (Spruijt et al., 2001). Using classical conditioning, ad libitum fed hens trained to associate a light cue (CS) with a mealworm reward (unconditioned stimulus; US) display a sequence of anticipatory behaviours including a high frequency of head movements in the CS–US interval, i.e. before the actual arrival of the signalled reward (Moe et al., 2009, 2011). In contrast, hens trained on a random CS–US schedule displayed negligible response to the same type of CS (Moe et al., 2009). These previous findings indicate that the high frequency of conditioned cue-induced behaviours in hens reflect motivation for mealworms which is independent of metabolic state (Mendoza et al., 2005; Merkesteyn et al., 2013). However, whether cue-induced behaviours are food reward specific as found in mice (Hsu et al., 2010) and could indicate how strongly the hens want differentially ranked rewards, or if they represent a more general behavioural response to any reward hens like more than the ad libitum available standard diet has not been tested in laying hens. In other words: do hens indicate by the frequency of their cue-induced behaviours how much they want differentially liked signalled rewards?

Previous studies have provided evidence regarding the neurobiological basis for liking and wanting food rewards in mammals, and the link between activity in brain reward circuits and its behavioural correlates. Briefly, conditioned cue-induced wanting is mediated by dopamine which leads to and facilitates a consummatory phase, i.e. liking mediated by opioid brain reward circuits involving the ventral tegmental area (VTA) and the nucleus accumbens (Nac), and these systems interact (e.g. Berridge, 1996; Spanagel and Weiss, 1999; Spruijt et al., 2001; Peciña, 2008; Berridge, 2009; Kest et al., 2012). In line with this, blocking dopamine and opioid receptors with antagonists decrease the frequency of cue-induced anticipatory behaviours in rodents (Dum and Herz, 1984; Blackburn et al., 1987, 1989). Previously, we found that cue-induced anticipatory behaviour (i.e. frequency of head movements in the CS–US interval) was attenuated by the dopamine D2 antagonist haloperidol (Moe et al., 2011) which suggests the involvement of the dopamine system in cue-induced wanting also in laying hens. Despite the anatomical differences between avian and mammalian brains, chick brains contain μ -opioid receptor subtypes (Csillag et al., 1990) which may be involved in food consumption (McCormack and Denbow, 1987, 1989), avian brain reward system homologues i.e. VTA and Nac (Bálint and Csillag, 2007), and

there is evidence for a mediating role of μ -opioid receptors in dopaminergic pathways in chickens (Baldauf et al., 2005). However, the role of μ -opioid receptors in mediating behaviours in response to a cue signalling attractive food rewards has not yet been demonstrated or tested in laying hens.

We hypothesize that the frequency of anticipatory behaviours, in particular cue-induced head movements previously identified as a behaviour underlying dopamine control, reflects the incentive value of differentially ranked signalled food rewards. The incentive value of food rewards can be altered either by using rewards differing in incentive value as ranked in choice and operant tests as described above (Bruce et al., 2003), and by increasing their incentive value by caloric deprivation (Berridge, 1991). We predicted that the incentive value of differentially ranked food rewards (mealworms compared to whole wheat) would modulate the frequency of behaviours in response to the reward cue. We expected that exposure to a cue signalling the more attractive reward (i.e. mealworms) would result in the higher frequency of cue-induced anticipatory behaviours, and that hunger would amplify the frequency of cue-induced behaviours. Furthermore, we hypothesized that μ -opioid receptors are involved in mediating cue-induced anticipatory behaviours in hens. We predicted that blocking μ -opioid receptor transmission with the μ -opioid receptor antagonist naloxone would attenuate the frequency of anticipatory behaviours in the cue-reward interval.

The aims of this study were to investigate control of cue-induced anticipatory behaviour in laying hens, by (1) investigating effects of incentive value of rewards on the frequency of conditioned anticipatory behaviours, and (2) investigating the potential involvement of μ -opioid receptor transmission on the frequency of cue-induced anticipatory behaviours by systemic injections of the μ -opioid receptor antagonist naloxone before exposure to the conditioned stimulus.

2. Methods

2.1. Animals and housing

Brown Leghorn laying hens ($N = 18$) were purchased at 17 weeks of age from a commercial breeder (Oraug, Askim, Norway) and kept in experimental floor pens at the Laboratory Animal Unit at the Norwegian School of Veterinary Science (Oslo, Norway). Details regarding housing conditions are described in detail elsewhere (Moe et al., 2009). Briefly, hens were housed singly in six adjacent experimental floor pens separated by solid wooden walls (Fig. 1). Each pen was 227 cm high, and the floor (151 cm \times 95 cm) was covered with a thick layer of wood-shavings. A perch for rest and sleep was placed 38 cm above floor-level along the back wall. To allow time for acclimatization to the experimental pens, hens were left undisturbed for 3 weeks after arrival except for daily feeding and husbandry routines. The experiment was run in three blocks consisting of six hens each, starting approximately when hens were 20 weeks of age. A standard layer diet (Kromat, Felleskjøpet, Norway) and water were supplied ad libitum throughout

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