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Research report

# Competitor suppresses neuronal representation of food reward in the nucleus accumbens/medial striatum of domestic chicks

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## HIGHLIGHTS

- Pseudo-competition shortens peck latency even without a conflict in food.
- Pseudo-competition suppresses cue-period activity associated with food.
- Pseudo-competition does not change delay- and reward-period activity.
- The selective suppression may enhance choice impulsiveness.

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## ABSTRACT

To investigate the role of social contexts in controlling the neuronal representation of food reward, we recorded single neuron activity in the medial striatum/nucleus accumbens of domestic chicks and examined whether activities differed between two blocks with different contexts. Chicks were trained in an operant task to associate light-emitting diode color cues with three trial types that differed in the type of food reward: no reward (***S***–), a small reward/short-delay option (***SS***), and a large reward/long-delay alternative (***LL***). Amount and duration of reward were set such that both of ***SS*** and ***LL*** were chosen roughly equally. Neurons showing distinct cue-period activity in rewarding trials (***SS*** and ***LL***) were identified during an ***isolation*** block, and activity patterns were compared with those recorded from the same neuron during a subsequent ***pseudo-competition*** block in which another chick was allowed to forage in the same area, but was separated by a transparent window. In some neurons, cue-period activity was lower in the ***pseudo-competition*** block, and the difference was not ascribed to the number of repeated trials. Comparison at neuronal population level revealed statistically significant suppression in the ***pseudo-competition*** block in both ***SS*** and ***LL*** trials, suggesting that perceived competition generally suppressed the representation of cue-associated food reward. The delay- and reward-period activities, however, did not significantly different between blocks. These results demonstrate that visual perception of a competitive forager *per se* weakens the neuronal representation of predicted food reward. Possible functional links to impulse control are discussed.

## 1. Introduction

Choice impulsiveness has been a topic of intensive experimental research in a wide range of behavioral sciences, including psychology [1,2], psychopharmacology [3–6], behavioral ecology [7–10] and neuroscience [11–16]. To understand choice impulsiveness in a comprehensive manner, specifying the brain areas and networks that are specifically responsible for the choice of delayed reward is critical [17–19]. While the basal ganglia could play a pivotal role, their contribution to choice impulsiveness under natural conditions is not yet fully understood, primarily because an appropriate animal model has been lacking.

In a series of lesion experiments using domestic chicks, we have shown that localized lesions of the medial striatum (MSt) and nucleus accumbens (NAc) in the ventromedial basal ganglia enhance choice impulsiveness in 1-week-old domestic chicks [20] without affecting choices based solely on the amount of reward

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or the work-cost associated with the options [21]. Further, electrophysiological experiments in freely behaving chicks revealed that MSt/NAc neurons encoded the amount or proximity of reward during the initial cue period in which the color cue signaled the associated food reward [22]. MSt/NAc neurons with cue-period activity were also activated during delay and reward periods in which food reward was predicted and delivered [23]. However, a functional role for these multiple codes related to food reward remains elusive, except for an indirect suggestion that they might be involved in the computation of prediction error, as in cases of extinction [24]. Furthermore, a causal link between impaired coding of amount and proximity of reward in the MSt/NAc [22] and impulsive choice behavior in chicks remains unsubstantiated. Furthermore, neurons in isocortical areas (*e.g.*, arcopallium in domestic chicks [25] and nidopallium caudolaterale in pigeons [26,27]) also code aspects of anticipated food reward. Some of these isocortical neurons have been shown to represent integrated value in terms of temporally discounted food amount [26], thus could play an important role in the control of choice impulsiveness. To examine these issues, we turned to the ecological theory of kleptoparasitism [28] for natural and physiological conditions in which choice impulsiveness could be modulated using behaviorally tractable manipulations that were neither invasive nor pharmacological in nature.

Kleptoparasitism describes the stealing/exploitation of resources that have already been obtained by other conspecifics. Scramble kleptoparasitism is a special form of kleptoparasitism in which each food item is sharable among competitive foragers. Under these circumstances, animals differentiate their tactics into producers and scroungers according to the frequency dependence of fitness. For a producer, choosing a proximate food option is more profitable when being followed by a scrounging individual. This theoretical prediction has proven valid in domestic chicks. When compared with those trained in ***isolation***, chicks trained in competition gradually develop enhanced impulsiveness when forced to choose between a small amount of food following a short delay and a large amount of food following a long delay [29].

Although this finding initially seemed to match well with the collection-risk hypothesis [30–32], actual threat to food gain *via* competition proved unnecessary for development of choice impulsiveness. Even when chicks were physically separated from competitors and food scrounging did not occur, simply seeing a competitor that coincidently foraged nearby (presence of a potential competitor, or *pseudo-competition*) caused an identical impulsive shift [29,33]. It is to be stressed that subject chicks did not instantaneously change the choice impulsiveness in the context of ***pseudo-competition***, though operant peck latency was shortened as an acute effect [33]. Chicks had to be trained in the competitive social context consecutively for 1–3 days until they showed significantly higher impulsiveness in inter-temporal choice test performed in isolation. The social context thus does not directly modulate choices, but gradually contributes to the impulsiveness through processes and mechanisms that are not yet fully specified.

Here, as a step toward understanding the role of social context on the neuronal representations of food reward, we tested whether ***pseudo-competition*** could modulate cue-period activity in MSt/NAc neurons.

## 2. Materials and methods

### 2.1. Animals

Male chicks (*Gallus domesticus*, white leghorn) were used as recording animals (subjects) as well as companions. New hatchlings (post-hatch day 1) were purchased from a local supplier and housed in transparent cages (15 cm × 28 cm × 12 cm) in groups of two, and were placed in a thermo-controlled pen kept at ∼26–30 °C under a 12-h light:12-h dark cycle starting at 08:00. On days 2–4, chicks were fed with 1, 2, and 3 g of food per day (mixture of millet and mash food), respectively. Experiments began on day 5, and from then on chicks received 0.5–1 g of food during experiments and 4 g in the evening. Each day, chicks were moved to a training/experimental box (see Section 2.2), and returned to the home cage afterward. Water was freely available in the home cage. After completion of experiments, brains were dissected out after an overdose of anesthesia. In cases in which neuronal recordings were not made, chicks were euthanized by carbon dioxide. Experiments were conducted under the guidelines and approval of the committee of animal experiments at Hokkaido University. These guidelines are based on the national regulation for animal welfare in Japan (law for the Humane Treatment and Management of Animals, after a partial amendment No. 68, 2005).

### 2.2. Apparatus and training/test procedures

A thermo-controlled box (21 cm × 19 cm × 25 cm, maintained at 26–30 °C and illuminated by DC-powered light bulbs) was used for training and recording (see Fig. 1). The box was partitioned into two chambers (10 cm and 11 cm wide) by a Plexiglass wall and an electric liquid crystal shutter, so that subject chicks were physically separated from companions. In ***isolation*** (abbreviated as ***isol***), the shutter was turned on and the companion was not visible, while in ***pseudo-competition*** (abbreviated as ***comp***), the shutter was off allowing the subject and companion to see each other. Note that food was delivered separately, and as in our previous studies, food acquisition was not disturbed or altered in any way [26,30]. On all trials in which the subject chick gained food, the companion simultaneously received 2 grains of millet.

The front panel of the subject's chamber was equipped with a pair of multi-color light-emitting diodes (LEDs) (3 cm apart and 5.5 cm above floor) and a corresponding pair of holes for response bars (1.5 cm below the LEDs). Pecks were recorded by microphones placed below the bars, and the sounds were stored together with neuronal signals. Three reward conditions were associated with three different LED color cues. No reward (***S***−) was indicated by red, small reward/small delay (***SS***, 1 grain, 0 s) by green, and large reward/large delay (***LL***, 6 grains, 1.5 s) by blue. A short tube at the center supplied millet food to the feeder. The companion's chamber was equipped with a feeder, but not with LEDs or response bars.

Trials started with color-cue onset (time 0) followed by protrusion of the response bars after 0.5 s. After another 1 s, the cue was turned off and the response bars were withdrawn. Thus, the cue lasted 1.5 s, and the bars were protruded for 1 s. Food was supplied if the subject chick pecked at a response bar before it was retracted. The next trial began after a variable inter-trial interval ranging from 15 to 20 s that was not adjusted depending on the preceding trial type (see Fig. 1 and the time chart in Fig. 3A). Note that a brief mechanical lag ($\Delta = 0.2$–$0.3$ s) inevitably occurred before the food was supplied. Based on our previous studies [29,33], the delay for ***LL*** (or ***SS***) was fixed at $1.5 + \Delta$ s (or $\Delta$ s) in all chicks studied, so that chicks could have chosen ***LL*** and ***SS*** options equally if tested in binary choices. It is to be noticed that we did not routinely examine chicks in binary choice tests and did not adjust the ***LL*** delay accordingly. Therefore, the subjective values of the ***SS*** and the ***LL*** options were not necessarily equal, rendering direct comparison of neuronal activities to be inappropriate between ***SS*** and ***LL***.

Training began on post-hatch days 5–7 after the subject had been habituated to the apparatus. Chicks were trained in two blocks (an ***isol*** block followed by a ***comp*** block) per day. Each block consisted of 80 pseudo-randomly arranged trials (20 ***LL***, 20 ***SS***, and 40 ***S***−). The sides of the LED and response-bar protrusion were