



Research report

Dissociation of the neural substrates of foraging effort and its social facilitation in the domestic chick

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HIGHLIGHTS

- Electrolytic lesion of the medial striatum suppressed foraging effort.
- Electrolytic lesion of the lateral tegmentum suppressed social facilitation.
- Dopamine depletion in the medial striatum had no effect on foraging behavior.

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ABSTRACT

The frequency or intensity of behavior is often facilitated by the presence of others. This social facilitation has been reported in a variety of animals, including birds and humans. Based on Zajonc's "drive theory," we hypothesized that facilitation and drive have shared neural mechanisms, and that dopaminergic projections from the midbrain to striatum are involved. As the ascending dopaminergic projections include the mesolimbic and nigrostriatal pathways, we targeted our lesions at the medial striatum (MSt) and substantia nigra (SN). We found that a bilateral electrolytic lesion of the MSt suppressed baseline foraging effort, but social facilitation was intact. Conversely, an electrolytic lesion targeted at the unilateral SN (on the right side) partially suppressed social facilitation, while baseline foraging effort remained unaffected. However, selective depletion of catecholaminergic (tyrosine hydroxylase immunoreactive) terminals by micro-infusion of 6-hydroxydopamine (6-OHDA) to bilateral MSt had no significant effects on foraging behavior, whereas it impaired formation of the association memory reinforced by water reward. Neurochemical assay by high-performance liquid chromatography also revealed a significant decrease in the dopamine and noradrenaline contents in MSt after 6-OHDA micro-infusion compared with intact control chicks. Thus, we conclude that the neural substrate of social facilitation can be dissociated from that responsible for reward-based foraging effort, and that ascending dopaminergic pathways do not appear to contribute to social facilitation. Based on our detailed analysis of the lesion areas, we discuss fiber tracts or neural components of the midbrain tegmental area that may be responsible for social facilitation.

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1. Introduction

Social facilitation, a phenomenon originally described as an enhanced frequency or intensity of behavior in the presence of

others [1,2], has been found in animals ranging from insects [3,4] to humans [5,6]. A variety of behaviors appear to be facilitated, *i.e.*, motor activities, such as running [3], nest-building [4] and cycling [5], as well as cognitive tasks in humans (*e.g.*, word association, [6]). Of these activities, foraging behaviors are socially facilitated in many vertebrates (*e.g.*, fish [7], amphibians [8], birds [9,10], rats [11,12] and humans [12–14]), implying common psychological and neural processes.

As a generalizable account of social facilitation, Zajonc [15] proposed the "drive theory". Specifically, he hypothesized that the presence of other individuals increases the general arousal or "drive" level, so that a dominant behavior (or well-learned

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behavior) is consequently facilitated. Here, Zajonc uses the term “drive” to denote a non-selective enhancer of behavior, just as Hull [16] argued in his classic study. In the 1960s, the “drive” concept was challenged, and the field shifted its focus toward “incentive motivation” [17,18]. However, “incentive motivation” is not mentioned in most recent studies of social facilitation. Note that the term “social facilitation” does not necessarily implicate any unitary mechanisms. Clayton [19] argued that the term should be used descriptively, and that the causal mechanisms could vary among different species and contexts.

Subsequently, based on human cognitive studies, Baron [20] developed “distraction-conflict theory” of social facilitation. He argued that the presence of others acts as a distractor, and attentional conflict occurs between an activity at hand and any other individuals present. He further noted the possibility that the conflict restricts the attentional focus of the subject, so that performance is facilitated. In concert with Baron’s theory, Huguet et al. [21] reported that performance on the Stroop task was socially facilitated. A meta-analysis of studies on human social facilitation [22] partially supported the Zajonc theory, although the analysis was generally in favor of the distraction-conflict theory. Baron [20] also argued that the distraction-conflict theory offered a parsimonious explanation for social facilitation in non-human animals. To the best of our knowledge, however, no empirical studies have tested the applicability of Baron’s theory to animal behavior.

Despite progress in the behavioral or cognitive studies, the neural basis of social facilitation has rarely been addressed. In a study using starlings, Cheng et al. [23] showed that the social facilitation of foraging behavior was reduced after lesions to the taeniae amygdala (TnA), an avian homologue of the mammalian amygdaloid complex. In the study, however, the authors analyzed behavioral synchronization rather than increases in the foraging effort, and so the observed lesion effects might be associated with other socio-sexual behaviors, such as courtship [24] and copulation [25]. So far, the number of neurobiological study using animals is quite limited, likely because an appropriate animal model has not been established.

The social facilitation of foraging behavior in the domestic chick [9,10] provides a unique opportunity to study the neural bases of this behavior because it is reproducible, thus allowing quantitative analyses [26]. Furthermore, the neural bases of foraging behavior have been well documented in a series of lesion [27–31] and electrophysiological experiments ([32–34]; also see Matsushima et al. [35,36] for reviews).

Based on Zajonc’s “drive” theory, we hypothesized that social facilitation and drive/incentive motivation have shared mechanisms. We were particularly interested in the role of dopaminergic projections from the midbrain to the striatum, as these could contribute to “drive” or incentive motivation [37–39]. In rats, both extensive dopamine depletion in the striatum [40] and systemic antagonism of dopamine transmission [41] are known to attenuate spontaneous foraging and bar pressing responses, respectively. In the avian brain, dopaminergic projections have been intensively studied [42–45], revealing two major ascending pathways that are conserved between birds and mammals [46].

The mesolimbic pathways from the ventral tegmental area (VTA) to the ventral striatum/nucleus accumbens play a critical role in controlling drive/incentive motivation [37,47]; but see Ref. [48]. The nigrostriatal projection is another major dopaminergic pathway that extends from the midbrain substantia nigra (SN) to the dorsal striatum, in which neurons represents expectation and delivery of food rewards [49–52]. Distinct functional roles have been suggested between these two pathways in mammals [53,54]. While the mesolimbic pathway is considered to be involved in the evaluation of and association between cues and outcomes [55,56],

the nigrostriatal pathway is considered to be critical for motor and action control [57,58].

There are two possible neural mechanisms underlying social facilitation. In one, social facilitation occurs through enhanced activity of the mesolimbic pathway, and the magnitude of a perceived food reward is augmented. In the other, social facilitation occurs through enhanced activity of the nigrostriatal pathway, and action-reward association is socially augmented. In this study, we wanted to examine whether these dopaminergic projections are required for social facilitation. Accordingly, we performed a series of lesion experiments in the medial striatum (MSt) and the SN using non-selective electrolytic lesions and dopamine-selective depletion by a localized infusion of 6-hydroxy dopamine (6-OHDA). Lesions placed in the MSt (or SN) were expected to impair the mesolimbic (or nigrostriatal) pathway, respectively; also see our Supplementary material.

2. Materials and methods

2.1. Subjects

We obtained male domestic chicks (*Gallus domesticus*, White Leghorn strains) that were new hatchlings, i.e., post-hatch day 1 (presumed hatching day), from a local supplier (Iwamura Poultry Ltd./Hokkaido Central Poultry, Yubari, Japan). The chicks were paired and housed in transparent plastic cages (15 cm × 28 cm × 12 cm) under illumination from white LED lamps (12L: 12D; light period starting at 08:00) and thermo-controlled at about 28 °C. We provided the chicks with two types of food: grains of millet and mash food. The total amount of food given per day was maintained such that (1) the body weight of the chicks gradually increased and (2) the chicks actively consumed food during the experiments. From post-hatch day 1, the chicks received 2 g (post-hatch days 1–3) and 2.5 g (from day 4 onwards) of mash food. From post-hatch day 2, we also provided 2 g (days 2 and 3) and 2.5 g (from day 4 onwards) of grains of millet (per chick per day). Until day 2, all chicks were fed communally with their cage-mates. From day 3 onward, the chicks were fed solitarily in a cage that was visually separated by a black plastic wall, so that the chicks could not see their cage-mates eating food. With the exception of feeding time, the chicks were communally housed. Water was available *ad libitum*.

Experiments were conducted under the guidelines and approval of the Committee on Animal Experiments of Hokkaido University. The guidelines are based on the national regulations for animal welfare in Japan (Law for Humane Treatment and Management of Animals; after a partial amendment No. 68, 2005). After the experiments, the brains were dissected under deep anesthesia. In cases in which surgical operations were not conducted, the chicks were euthanized by carbon dioxide.

2.2. Apparatus

We used an I-shaped maze equipped with two parallel lanes (Fig. 1A–c, B–c; 12 cm × 88 cm × 40 cm high) that were separated by transparent Plexiglas. Terminal walls were painted red (left) or blue (right), and were equipped with a pair of terminal feeders that supplied food simultaneously in both lanes. The feeders supplied each lane with a single grain of millet. If not stated otherwise, the intervals between the food supply randomly varied from 10 to 20 s (mean = 15 s), and this schedule was referred to as VI15. Two sponge-covered food trays (3 cm × 4 cm × 2 cm deep) were placed adjacent to each other in the ends of the lanes. To prevent the chicks from associating the mechanical sounds generated by the feeders with the food reward, dummy motors

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