Food variance and temporal discounting in socially foraging chicks

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Previous studies have shown that domestic chicks, *Gallus gallus domesticus*, trained in a competitive foraging condition would subsequently develop a high degree of impulsiveness in an intertemporal choice paradigm. Competition inevitably causes variance in the amount of food that the foragers gain. However, it is not known whether the food variance is causally linked with the impulsiveness. In experiment 1, we compared four groups of chicks trained in combinations of two social conditions (pseudocompetition or isolated) and two food conditions (variable or constant food). The food variance was introduced by varying the number of grains in each trial according to a binomial distribution. The subject chick was separated from the competitors by a transparent wall, and no actual interference occurred. Chicks were subsequently tested in binary choices between a small reward after a short delay (SS) and a large reward after a long delay (LL) in an isolated and constant food condition. If chicks had been trained under the pseudocompetition and variable food, they chose LL significantly less frequently than the other three groups. The effect disappeared when the LL delay was omitted, suggesting that chicks accurately memorized the food amount. The food variance is thus a necessary condition for the stronger temporal discounting. Otherwise, the observed effect could be ascribed to a paradoxical risk proneness associated with the variable option. In experiment 2, we compared four groups of chicks in which food amount varied either in SS or LL, or both. The subsequent binary choice tests revealed that the chicks chose SS irrespective of whether SS or LL had varied. These results cannot be explained in terms of a greater risk-prone choice of the variable option. Coincidence of perceived competition and food variance, at least in one option, is sufficient for chicks to develop choice impulsiveness.

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Animals (including humans) often choose an immediate reward over a larger alternative that is available after a delay. According to a widely accepted psychological framework of choice behaviour (Mazur, 2002), preference for an immediate option can be explained in terms of temporal discounting of subjective value (Ainslie, 1974, 1975). The degree of discounting is measured in an intertemporal choice paradigm, in which a small/immediate option and a large/delayed alternative are simultaneously presented for the subject to choose one. If the slope of the discounting function is sufficiently steep, the immediate reward will have a higher value than the larger discounted alternative, particularly in the short period before the immediate reward is gained. The subject will thus choose the small option. Because the smaller rewards reduce the overall payoff in the long run, choosing the immediate reward appears to contradict optimization theory (Herrnstein & Mazur, 1987; also see; Herrnstein, 1997).

In studies of foraging behaviour (Stephens & Krebs, 1986), however, animals are assumed to have a limited knowledge of food resources. Encounters with prey items will therefore follow a Poisson process. Under this constraint, theoretically, foragers construct an optimal diet menu uniquely based on the profitability of each prey item (Charnov, 1976). Here, profitability (e/h) is given as the ratio of the energetic gain (e) divided by the total handling time (h). Foragers are thus assumed to discount prey items according to a hyperbolic function of time. Empirical evidence is generally in favour of the hyperbolic discounting theory (Kalenscher et al., 2005; Kalenscher & Pennartz, 2008). However, behavioural data are not in favour of the zero-one rule, one of the major predictions of the diet menu model. Instead, the choice ratio follows the relative value of the profitability of the food reward in domestic chicks, *Gallus gallus domesticus* (Aoki, Csillag, & Matsushima, 2006; Izawa, Zachar, Yanagihara, & Matsushima,

2003; Matsushima, Kawamori, & Bem-Sojka, 2008), as would be expected from Herrnstein's matching rule (Herrnstein, 1997) in which response rate is given by the relative reinforcement rate. Also note that the self-control choice is reported to be highly context-dependent in domestic fowl (Abeyesinghe, Nicol, Hartnell, & Wathes, 2005).

In nature, animals do not always forage individually. They can gain food also by scrounging prey items from producers, i.e. other individuals that search and find food for themselves. Intensive theoretical and empirical studies of social foraging behaviour have enabled us to characterize this producer–scrounger game (Barnard & Sibly, 1981; Giraldeau & Lefebvre, 1986; Giraldeau, Soos, & Beauchamp, 1994; Mottley & Giraldeau, 2000; also see the monograph by; Giraldeau & Caraco, 2000). Briefly, producers and scroungers will inevitably reach a stable Nash equilibrium, at which point both player types will yield comparable suboptimal payoffs. However, switchable players would benefit by flexibly changing the producer/scrounger roles in a frequency-dependent manner.

The behaviour of chicks can also be described using the game-theoretical situation of social foraging behaviour (Fig. 1). If a chick has no competition for food, the same amount of food will be expected irrespective of the distance between the chick and the food (Fig. 1a). As the profitability of the distant food is lower, the chicks will choose the more proximate food (Matsushima et al., 2008). Actually, they show spatial discounting in a manner similar to the temporal discounting (Aoki, Suzuki, Izawa, Csillag, & Matsushima, 2006). On the other hand, when two chicks compete over a food item (Fig. 1b), the chick located closer to the food source (yellow) will gain more than the other chick (blue). If this sharing rule generally holds, a different payoff is expected in the producer–scrounger situation (Fig. 1c). Here, the producer chick (yellow) searches for and finds the food item, and the other chick (red) scrounges. As the producer is closer to the food, she will enjoy the finder's share (Giraldeau & Caraco, 2000; Giraldeau & Dubois, 2008) and gain more than the scrounger, as would be assumed in most cases of scramble kleptoparasitism. Furthermore, the producer's share will be higher in the proximate food option than in the remote alternative, if the ratio of the individual distance to food determines the finder's share. The impulsive producers may thus gain a fitness advantage in the competitive condition.

However, the share of the finding producer is known to depend on a variety of factors such as social status of the foragers and the richness of the food patch (Giraldeau & Caraco, 2000). Divisibility of food patches is known to be particularly important in social foraging of relatively nonaggressive birds such as finches (Giraldeau, Hogan, & Clinchy, 1990). If the food item is not shareable (such as a single grain), the probability of not gaining food will be high (Fig. 1d) as would be the case in aggressive kleptoparasitism. Conversely, if the food consists of shareable pieces (such as multiple grains) and thus is simultaneously exploited by competing foragers, the ratio of the variance to the expected gain (or the coefficient of variation) will be low (Fig. 1e). The consequence of social foraging therefore also depends on how the food can be shared.

The ability to adjust temporal discounting according to foraging conditions (such as density of the competitive foragers and variance in the food resource available) would therefore be highly adaptive. Such adjustments may rely on two factors: the presence of scroungers and the variance of food gain. As predicted, chicks trained in competitive conditions develop a high degree of choice impulsiveness; when trained in a pseudocompetitive situation in which scrounging is mimicked, chicks tend to choose a small and short-delay option (SS) more frequently than a large and long-delay alternative (LL) in a subsequent choice test (Amita, Kawamori, & Matsushima, 2010). However, whether the food variance associated with social foraging is necessary for the development of choice impulsiveness has not been examined. We addressed this issue in experiment 1 by comparing four groups of chicks trained in a 2×2 block design, i.e. social condition (pseudocompetition or isolated) and food condition (variable or constant amount).

Conditioned impulsiveness may arise from stronger temporal discounting for both SS and LL options. Alternatively, the apparent impulsiveness might be caused by the risk sensitivity of chicks. Animals generally avoid variable food, and thus are 'risk averse' (Kacelnik & Bateson, 1996). Chicks also show risk aversion when the amount of food varies, but they are paradoxically prone to risk when the delay to the food varies instead (Kawamori & Matsushima, 2010; for a theoretical account, see Kaceknik & El Mouden, 2013). Food variance may influence SS and LL choices in a different manner, leading to biased choices towards SS options. If that is the case, the effect of variable SS options should therefore be different from that of variable LL options. In experiment 2, we addressed this possibility by comparing four groups of chicks trained according to a 2×2 block designed with SS (variable or constant food) and LL (variable or constant food).

METHODS

Subjects

We purchased newly hatched male domestic chicks (White Leghorn strain) from local suppliers (Iwamura Poultry Ltd./Hokkaido Central Poultry Ltd., Yubari, Japan). The chicks were housed in groups of three in transparent plastic cages (15×28 cm and 12 cm high) illuminated by white LED lamps (12:12 h light:dark with the light period starting at 0900 hours) in a room at a controlled temperature (ca. 28 °C). As a daily diet, the chicks received a mixture of millet grains and mash food, and the amount of food was adjusted so that the chicks (1) actively consumed food during the behavioural experiments, and (2) steadily increased in body weight by 5–10% per day. If not stated otherwise, food was provided once a day after the behavioural experiments. To avoid competition for food, individual chicks were isolated during feeding.

Ethical Note

We did not perform any invasive treatments or stressful handling during the course of the experiments. If a chick produced distress calls while in the experimental apparatus, we immediately stopped the experiment and discarded it. We thus excluded nine of the 128 chicks used in this study. Of the remaining chicks, 12 were excluded because they stopped operant pecking and/or consuming food in the experimental apparatus. In addition, another set of 29 chicks did not reach the criteria during pretest retraining (see below). Behavioural data were obtained from the remaining 78 chicks, and the other ca. 50 chicks served as companions. The experiments were conducted according to the guidelines and approval of the Committee of Animal Experiments at Hokkaido University. The guidelines are based on the national regulations for animal welfare in Japan (Law of Humane Treatment and Management of Animals, after partial amendment No.68, 2005). After the experiments, the chicks were euthanized using carbon dioxide.