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Title:

Neuro-economics in chicks: foraging choices based on amount, delay and cost

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Abstract

Studies on the foraging choices are reviewed, with an emphasis on the neural representations of elementary factors of food (*i.e.*, amount, delay and consumption time) in the avian brain. Domestic chicks serve as an ideal animal model in this respect, as they quickly associate cue colors with subsequently supplied food rewards, and their choices are quantitatively linked with the rewards. When a pair of such color cues was simultaneously presented, the trained chicks reliably made choices according to the profitability of food associated with each color. Two forebrain regions are involved in distinct aspects of choices; *i.e.*, nucleus accumbens – medial striatum (Ac-MSt) and arcopallium intermedium (AI), an association area in the lateral forebrain. Localized lesions of Ac-MSt enhanced delay aversion, and the ablated chicks made impulsive choices of immediate reward more frequently than sham controls. On the other hand, lesions of AI enhanced consumption-time aversion, and the ablated chicks shifted their choices toward easily consumable reward with their impulsiveness unchanged; delay and consumption time are thus doubly dissociated. Furthermore, chicks showed distinct patterns of risk-sensitive choices depending on the factor that varied at trials. Risk aversion occurred when food amount varied, whereas consistent risk sensitivity was not found when the delay varied; amount and delay were not interchangeable. Choices are thus deviated from those predicted as optima. Instead, factors such as amount, delay and consumption time could be separately represented and processed to yield economically sub-optimal choices.

Contents

1. Introduction

2. Are animals optimal foragers?

2.1. Optimal foraging theory

2.2. Matching law

3. Chick economics and neural substrates

3.1. Profitability

3.2. Arcopallium and ventral striatum constitute executive control pathway

3.3. Delay, nucleus accumbens and impulsiveness

3.4. Amount and delay in risky choices

3.5. Consumption time, arcopallium and cost aversion

Figure legends

References

1. Introduction

Do animals have mind? Do non-primate vertebrate animals in particular have similar mental processes to humans? Recent progresses in comparative (and evolutionary) cognitive neuroscience have shown a spectrum of non-primate cases, that suggest the commonality between birds and us [30]. Particular attention has been paid to higher cognition such as memory, categorization, communication, anticipation and prospects. A brief list of such outstanding case studies includes; object constancy in newly hatched domestic chicks [37], episodic-like memory in food-storing scrub jays [11], categorical discrimination of paintings by Picasso and Monet in pigeons [49] (also see [50] for Van Gogh and Chagall), possible insight of other individuals cognition [16],

and verbal labeling and communication in grey parrots [33]. System neurophysiological studies on “prefrontal cortex” of pigeon cerebrum for working memory and executive control of behaviors [14,15,27] are also highly suggestive of the commonality.

We can simply assume that birds are similar to us, as common selection pressures shaped both birds and humans in the course of evolution. The similarity is therefore superficial, representing an analogy through evolutionary convergence. Alternatively, we may assume that physiological constraints are highly conserved, and the brain-mind linkages cannot be easily dissociated. The similarity thus represents a genuine homology, and the common mental processes are rooted deeply in the common basic architecture of brains of amniotic vertebrates. In order to address this issue in a biologically realistic manner, we have accomplished a series of neuro-behavioral studies using domestic chicks as subjects. We will critically review our recent findings in the context of behavioral ecology and neuroscience. Examination of foraging choice behaviors, particularly their impulsiveness in binary choices, revealed that chicks are not maximizing their gain. Instead, aspects of chick choices seem to be sub-optimally organized with different important factors of food represented in a parallel fashion, so that their decisions are controlled adaptively in response to environmental demands. We will encourage readers to refer to monographs by Vauclair [48], Rogers [40] and Hauser [20] for comprehensive discussions on the issues of ‘animal minds.’ The recent review article on ‘animal rationality’ by Kacelnik [26] is of a particular importance for those who wish to have a clear idea about the relationships among different meanings of rational decisions.

2. Are animals optimal foragers?

Are animal behaviors optimally designed so that consequent gain is maximized? It has been assumed that phenotypic traits that enable animals to reproduce best, and therefore the underlying sets of genes, are likely to be transmitted to subsequent generations in evolutionary time scale [1]. If this is the case, foraging choices would have been selected and conserved for maximization of long-term gain rate, as formulated by Charnov [10] in his pioneering theory of optimal foraging; also see Stephens and Krebs [47] for comprehensive reviews of normative theories. The challenge for behavioral neuroscience thus will be to reveal the neuro-cognitive bases of the optimal behaviors. If optimality necessitates a uniquely determined cognitive process, we would expect to see a convergent evolution among animals with distinct phylogenetic backgrounds. Common selection pressure favoring the gain maximization would lead mammals and birds to develop common cognitive processes of evaluation and execution. If otherwise and distinct cognitive machineries could achieve comparable success, we could find a divergent spectrum of cognitive processes in different phylogenies, and cognition in birds might be totally different from mammals.

2.1. Optimal foraging theory

Let us briefly introduce one of the conventional theories formulated by Charnov [10], or the diet menu model. The model assumes that the forager maximizes the long-term averaged gain rate, or energetic gain per total time invested for foraging behavior (*i.e.*, searching and consuming food items). Further assumptions are: 1) the forager is omniscient and has complete information about the food types available, although 2) food is randomly distributed and the forager does not know which food the

forager will encounter at a given moment. It is assumed that a food item has an energetic gain e , and forager must spend time h for handling and consuming the food; e and h are constants unique for each food type for the forager. The ratio e/h is referred to as profitability. It is noted that the profitability is a function of the food quality and the forager's skill to attack and consume the food. Upon encountering such a food item, the forager faces a conflicting choice between attacking the food to gain e , or otherwise, passing it over to spend the time h for searching for better alternatives.

The optimality theory yields a simple prediction. If profitability of a food item is large enough, the forager must always attack it. If otherwise and the profitability is smaller than the long-term averaged gain rate expected in the foraging field, the forager must pass the food over (Fig.1). Another important prediction is that the forager always attacks a given food item or always passes it over, following 'zero-one' rule [47]. The point is that the forager does not necessarily plan ahead in order to maximize its long-term gain. Instead, the forager must precisely evaluate the profitability of each food item; short-sighted behaviors can give rise to optimization. In other words, a rational decision maker maximizes the long-term gain through the limited prospect of immediate benefits.

Figure 1 around here

2.2. Matching law

In sharp contrast to the optimal theory, empirical data obtained in psychology laboratories have put on a totally different theory, the matching law of Herrnstein [21, 31]. When confronted with a simultaneous choice of two options, the subjects (pigeons and humans) often matched their choices to the relative rate of reinforcement, rather than the 'zero-one' rule. It has been argued that the same rule of melioration, or

rule-to-make-better, stands in a wide range of animals including human. In choices between two options with reinforcement rates R_1 and R_2 , meliorating decision makers will allocate the frequency of choices C_1 and C_2 according to the relative values of the rates, so that the choice ratio of the first option will be given by;

$$C_1 : C_2 = R_1 : R_2 \quad (1)$$

in which the choice matches the reinforcement [21].

The choices assumed here differ from those in the optimal foraging theory in several points. First, the optimal theory assumes rational decisions to be made *a priori*, in a sense that each option is given a uniquely determined value before the final decision is made. In the melioration choices, on the other hand, rational decisions might be made *a posteriori*. The subject is given multiple series of trials, and interacts with the uncertain world with a series of choices. A decision at a trial is valued based on the consequence of each trial, so that the subject changes the choice in the subsequent trials. Second, the optimal theory assumes asymmetrical choices where the subject must choose between two alternative actions, namely to attack or to pass over. The melioration choices, on the other hand, assume choices between simultaneously presented pair of targets. Among several simultaneously presented (but mutually exclusive) options, the subject must choose one. It is also to be pointed out in the choice theory that the choice of a small-immediate reward is called as “impulsive choice,” whereas the choice of a large-delayed reward as “self control” [31]. In view of the foraging theory, these two alternatives may have a comparable value, since the profitability of the large reward is reduced by the long delay that it accompanies. In some ecological contexts, the self control choice may even be worth in terms of the consequent fitness gain. With these two frameworks in mind, let us examine how

chicks make choices.

3. Chick economics and neural substrates

Three-days to two-week old chicks of domestic chicken (*Gallus gallus*) can be trained to selectively peck at a colored bead when reinforced by food reward delivered after a short delay. Chicks at this age peck at conspicuous small objects such as beads in their habitat, as if chicks are actively examining whether the objects are edible. Subsequently, chicks precisely memorize the visual features (colors and textures), which are quickly associated with several factors of food reward. These factors include; amount of food reward (number of pellets), delay (time to be spent until the food is reached) and consumption time (the time spent after the food is reached and until it is consumed). Major advantage gained by using chicks as subjects is that these factors are quantitatively controlled and measured at the precision of pellet number and second [30].

3.1. Profitability

Chicks are highly impulsive in choices between two colored beads, or associated pair of food rewards. In training trials, pecking at a green bead was followed by a reward of 1 pellet delivered immediately (Fig.2); pecking at a red bead was followed by a reward of 6 pellets delivered after a delay (*D*), ranging between 0 to 3 sec as experimental variable [24]. A blue bead was not rewarded, irrespective of whether the chick actually pecked at the bead or not. Chicks were reliably trained to discriminate between rewarding beads (green / red) and non-rewarding bead (blue) within a few days. Trained chicks were subsequently tested in binary choices between green (small-immediate food) and red (large-delayed food).

Figures 2 and 3 around here

We measured the ratio of trials in which the red bead (i.e., the large food) was chosen (Fig.3). The choice ratio proportionately differed in 4 groups of chicks depending on the delay D ; largest at $D = 0$ sec and smallest at $D = 3$ sec. Clearly, the choice policy of chicks was not the ‘zero-one’ rule predicted from the optimal theory, so that the long-term averaged gain rate was not maximized. Violation of optimality was further evident when the long inter-trial interval (30-60 sec in this case) was taken into account. Most likely, chicks matched the choice ratios with immediate *profitability* for each option, which is given by;

$$profitability = \frac{energetic\ gain}{delay + consumption\ time} \quad (2)$$

In our experimental situation, the *profitability* is explicitly given in a simple form. Assume the unitary energetic gain obtained from a pellet of food (grains of millet or sesame) to be 1, and the number of pellets to be represented by n . The average number of pecks required for consuming a pellet is given by κ , which proved to range from 1 to ~10 depending on the condition of food. For example, sesame seeds scattered on a sponge plate makes $\kappa \approx 1.2$, so that the chick consumes 5 pellets after ~6 pecks in average. If scattered on a flat plastic plate, the same food turns out to be more costly with $\kappa \approx 2$. When κ exceeds ~10, most chicks stop feeding and go away from the food. D is the delay to the food as above. The energetic cost spent for pecking action is negligible and disregarded. On the other hand, the time spent for a peck ($\tau = 0.3$ to 0.5 sec) was not negligible, particularly when n was large. The *profitability* of the n -pellet food reward is given by;

$$profitability(n) = \frac{n}{D + \tau\kappa n} \quad (3)$$

We assume that the matching law (1) stands for the *profitability* as reinforcement rate R , so that the choice ratio (fraction of trials in which 6-pellet food is chosen) is given by;

$$\text{choice ratio}; \frac{C_6}{C_6 + C_1} = \frac{\text{profitability}(6)}{\text{profitability}(6) + \text{profitability}(1)} \quad (1')$$

Through substitution of the function (3) in the formula (1'), we have the following quantitative predictions.

(prediction 1: effects of delays)

If the delay differs between the two options (D_n for n -pellet food), then the choice ratio will be given by;

$$\begin{aligned} \text{choice ratio} &= \frac{n(D_1 + \tau\kappa)}{nD_1 + D_n + 2n\tau\kappa} \\ &= \frac{6(D_1 + \tau\kappa)}{6D_1 + D_6 + 12\tau\kappa} \quad (\text{for } n = 6) \end{aligned} \quad (4)$$

indicating that the ratio is a monotonically decreasing function of D_6 , asymptotically approaching to 0 for $D_6 \gg 6D_1$ (Fig.3A). In other words, chicks would rather choose the small food if a long delay accompanied the large food.

(prediction 2: effects of consumption time)

If the delays are identical between the two options ($D_6 = D_1 = D$), then the choice ratio will be given by;

$$\text{choice ratio} = 0.5 + \frac{(n-1)a}{2[(n+1)a + \kappa]} \quad (a = D/n\tau) \quad (5)$$

indicating that the ratio is a monotonically decreasing function of κ , asymptotically approaching to 0.5 for $\kappa \rightarrow \infty$ (Fig.3B) for any n . In other words, chicks would not care the amount when the accompanying consumption cost was considerably large. Both of these predictions generally hold true for a range of large food reward, not specifically for the 6-pellet food.

These predictions proved to approximately match the chick choices (Fig.3A-D). Furthermore, a series of lesion experiments revealed dissociations of delay and consumption cost in respective representations in the pallio-striatal pathway.

3.2. Arcopallium and ventral striatum constitute executive control pathway

The nucleus accumbens and medial striatum (Ac-MSt) constitute the medial part of the ventral striatum, and were collectively referred to as lobus parolfactorius before the nomenclature reform [39]. Characteristic biochemical changes suggested that this area serves as neural substrate for long-term memory storage in the passive avoidance learning paradigm [43-45]; also see [17, 18] for recent advances in neuropharmacological studies of the avoidance memory formation. Detailed tract-tracing studies combined with neurochemical and ultrastructural characterizations suggest that the ventral striatum plays a pivotal role in controlling memory-based decision paradigms [12]. Actually, in appetitive color discrimination tasks, a population of neurons responded to visual cues associated with rewards, irrespective of whether operant peck was required or not [25, 52]; so far, however, reliable data are not available as to whether the same ensemble of neurons are responsible for both appetitive and aversive memories. Similar reward-related anticipatory activities have been found in a variety of regions including arcopallium [4] and nidopallium caudolaterale [27, 42]. Most probably, the ventral striatum is involved in the pallio-striatal (or “cortico”-striatal) pathway responsible for evaluation and executive control of foraging behavior.

Bilateral lesions to extensive areas of the ventral striatum caused an anterograde amnesia in reinforcement learning, so that the ablated chicks failed to associate cue colors with reward, whereas filial imprinting remained intact [23]. The lesion also

delayed the extinction of operant responses [22], suggesting a common process shared by association and extinction. Further localized lesions confined in the most medial part of the ventral striatum, however, failed to cause memory deficiencies. Instead, localized lesions changed executive control, in which chick makes use of the memorized associations among sensory cues, motor action and consecutive rewards.

3.3. Delay, nucleus accumbens and impulsiveness

Chicks with localized lesions to Ac-MSt revealed highly enhanced impulsiveness in their choice selectively between a small-immediate reward and a large-delayed alternative [24]. The effect was evident particularly when the delay associated with the large reward (6-pellet food) was set at 1~2 seconds. On the other hand, the lesion had no effects in choices between a large and a small food reward both delivered immediately. Impulsiveness was enhanced also in other tasks, in which the reward was delayed by placing the larger food at a distance (80 - 140 cm) in a Y-maze [3]; the temporal proximity is therefore interchangeable with the spatial proximity.

Post-hoc analysis of effective lesion areas in reference to recent studies on the basal ganglia [5, 6, 12, 32, 38] shows that the areas included all of nucleus accumbens (Ac; both core and shell subdivisions are involved), dorsal part of bed nucleus of stria terminalis (BSTL) and medial part of medial striatum (MSt); other regions in the basal ganglia (intermediate to lateral part of MSt, lateral striatum, globus pallidus and ventral pallidum) were not involved. These areas fairly matched to the distribution of neurons that responded to rewarding cues [25]. It is reasonable to assume that the chick Ac covers a somehow larger area than that delineated in the chick brain atlas [29]. The area named as accumbens nucleus (Acb) in the most recent atlas [35] corresponds to the “rostral LPO,” which is a functionally distinct region since its lesion had no effects on

impulsiveness [24]. In mammals, comparable effects were found also after lesions localized to the nucleus accumbens core [8]; it is thus reasonable to suggest that the Ac defined by Bálint and Csillag [6] corresponds better to the mammalian counterpart, rather than the Acb outlined in the atlas by Puellas et al. [35].

What does the enhanced impulsiveness mean? In our study, impulsive choice is operationally defined as a tendency to choose small reward when the larger alternative was delayed. For simplicity, let us disregard the consumption time and assume that subjective value (V) of food is represented as amount (A) per delay time (D). We thus have;

$$V = A / D \quad (6)$$

for each option 1 and 2. When a subject makes an impulsive choice, the following inequality stands;

$$A_1 / D_1 < A_2 / D_2 \quad (7)$$

in which the option 1 (and 2) represent the large-delayed (and small-immediate) reward, respectively. It is equivalent to

$$A_1 / A_2 < D_1 / D_2 \quad (7')$$

meaning that the ratio of delay is dominant over the ratio of amount. In other words, the degree of impulsiveness is equivalent to the situation that a priority is given to the delay rather than to the other decision factor such as the amount of food. It is possible to assume that the network in Ac-MSt actively controls the degree of priority to the factor of delay.

3.4. Amount and delay in risky choices

Dissociation between proximity and amount is also evident in risky choices, in which the probability to gain a large food reward is lower than that for a small food

alternative [28]. In a T-maze, a behavioral titration paradigm was applied to binary choices of two opposing feeders, one of which supplied 0 or 10 pellets at equal probability randomly in successive trials. Another feeder consistently supplied a certain amount, and the amount was experimentally adjusted so that the chicks equally chose these two feeders. Equilibrium was reached when ~3 pellets were supplied to the consistent feeder, an amount significantly smaller than the expected food amount available from the variable feeder; the chicks were risk averse for the food amount. When the risky feeder had variable delays rather than amounts, chicks behaved quite differently even though the expected profitability and its deviations were identical. One feeder supplied a 5-pellet food after a constant delay (ranging in 0-8 sec) when the chick arrived, whereas the alternative feeder supplied the same 5-pellet food immediately or after 8-sec delay, at equal probability randomly in successive trials. In this condition, consistent risk-sensitivity vanished and the chicks showed a strong tendency to stick to the early choices that each chick made. Clearly, the amount and the delay are not interchangeable in chick choices.

A similar separation has also been documented in details using starlings as subjects [7, 34, 36], although the brain mechanisms have not yet been studied. In rats, on the other hand, lesions to the nucleus accumbens have been reported to enhance risk aversion for the food amount [9]; therefore, the risk sensitivity might be functionally linked to the impulsiveness [8].

3.5. Consumption time, arcopallium and cost aversion

A longer consumption time deteriorates the food profitability just as a longer delay does, since the handling time is given by a linear sum of the two (see the formula (2)). However, in terms of the brain regions involved, these two factors of time were doubly

dissociated in lesion experiments. Excitotoxic lesions were bilaterally made to arcopallium intermedium (abbreviated as AI according to the reformed nomenclature [39]). Lesion to AI selectively reduced the frequency of choices of 6-pellet food, a large food reward that is demanding due to a considerable consumption time [4]; control chicks with sham lesions and lesions localized to bilateral Ac-MSt did not show such changes. The alternative 1-pellet food was chosen more frequently in these AI-lesion chicks, although the choice ratio (*i.e.*, 6-pellet vs. 1-pellet) was not reversed below 0.5 in contrast to the impulsive choices caused by the Ac-MSt lesions. The lesioned chicks behaved as if the 6-pellet food were served in a highly laborious condition, requiring a significantly large number of pecks to consume the food. However, the actual number of pecks per pellets (*i.e.*, experimentally measured κ) remained unchanged, indicating that the consumption cost investment did not increase. The lesions caused no effects in those choices based solely on the amount of food [4], as in the case of Ac-MSt lesions [3,24]. Furthermore, in a Y-maze task for choices between a small-immediate and a large-distant alternative [4], the lesion had no effects on the impulsiveness. A similar separation of responsible brain pathways for decision costs has been reported in the frontal cortex of primates, namely, anterior cingulate cortex lesions for physical efforts and the orbitofrontal cortex lesions for waiting time for reward, respectively [46]. The functional distinctions among decision variables in pallial / cortical networks might have some relevance to respective foraging ecology in birds and mammals.

The effective area in AI was previously referred to as archistriatum intermedium pars ventralis in the atlas by Kuenzel and Masson [29]. In the Puelles' recent atlas [35], the area is named as amygdale and its core nuclei (abbreviated as ACo1 to ACo4).

Neurophysiological characterization of single unit activities in this area [2] does not fit in well with the connotations ascribable to the term amygdala, since this area included also those neurons coding for the working memory for auditory cues for turning responses, a feature that is not found in the mammalian amygdala [41]. Furthermore, tract tracing studies [13, 51, 53] revealed that AI has massive descending projections to the midbrain tegmentum and optic tectum, quite different from the mammalian amygdala. When viewed solely from a functional standpoint, AI might be a part of nidopallium – ventral pallium complex involved in the mnemonic and executive control [14, 15, 19, 27]. It is required to develop a common set of tasks and experimental procedures, so the data obtained in different brain areas can be systematically compared.

Chick choices in the present experimental conditions do not maximize the gain. Do chicks (and birds in general) have particularly reasons to deviate from gain maximization? Or otherwise, the deviations represent pathological byproducts of chick behaviors in artificial situation, and consideration of optimality has a limited accountability in the present context? Further studies are required in order to unravel the underlying proximate brain mechanisms of the impulsiveness, and to specify the ecological / evolutionary backgrounds that cause the deviations.

Figure legends

Fig. 1. Choice choices and diet-menu model of optimal foraging theory. When a forager encounters a food item, it is not always an optimal behavior to attack (peck) it to gain the energetic benefit (e). Instead, the forager may pass it over and spend the handling time (h) for searching for a better alternative food. To do the task, the forager must precisely anticipate the profitability (e/h), so that the appropriateness of the choice is determined in reference to the available food type available.

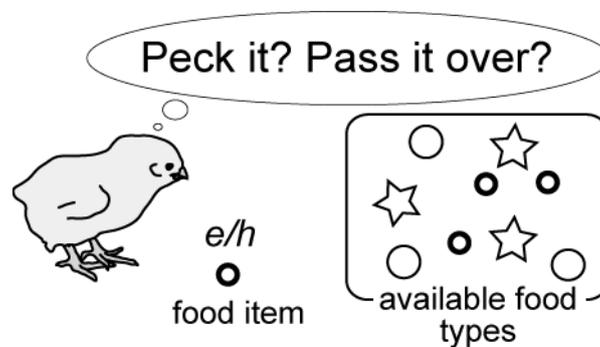


Fig. 2. Measuring impulsiveness. Chicks were trained to peck a green bead to gain 1-pellet food immediately, and a red bead to gain 6-pellet food after a delay (e.g., = 3 sec). At test, a green and a red bead were simultaneously presented. We measured the ratio of trials in which the red bead was chosen.

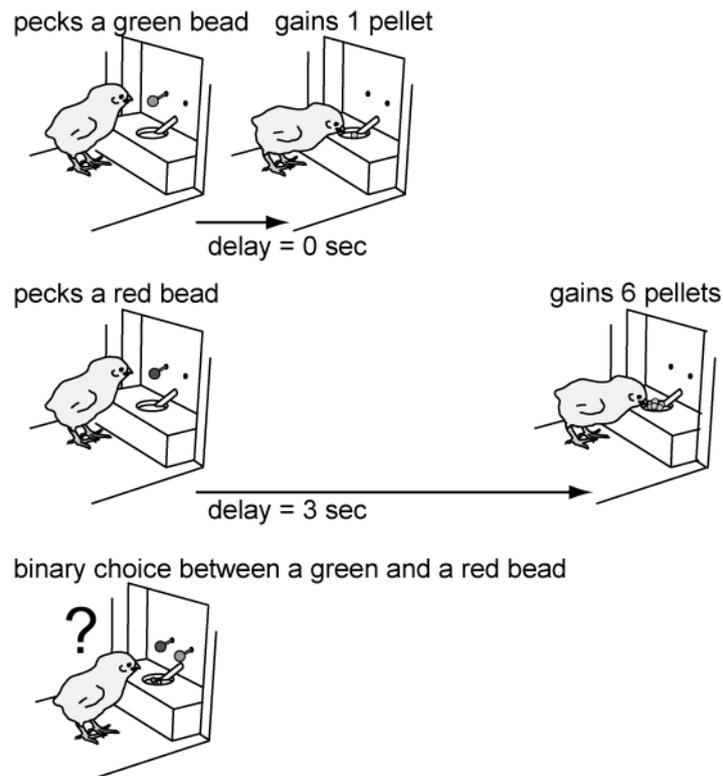
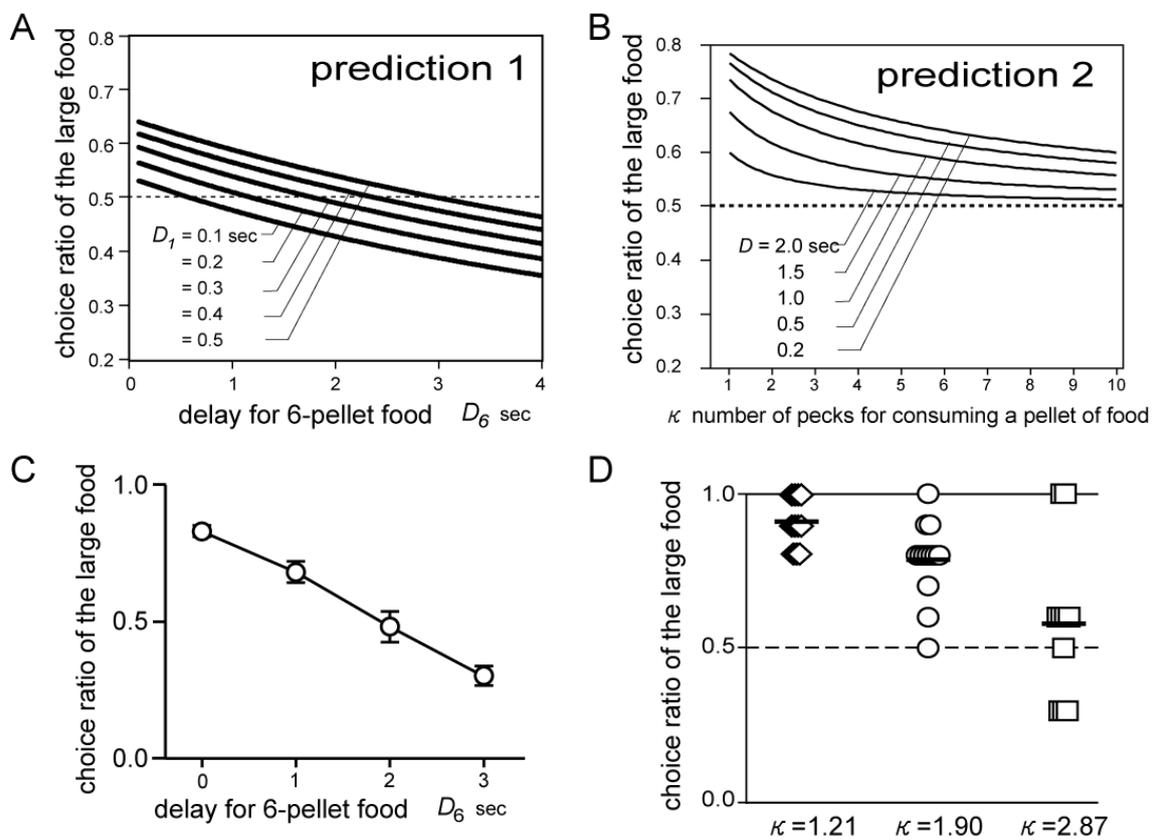


Fig.3. Choices based on profitability. The choice ratio of large reward (6-pellet food) was plotted against the delay allocated to the large food (A and C), or against the number of pecks for consuming a pellet of food (κ) (B and D). A: predicted relationships at various values of D_1 ranging from 0.1 to 0.5 sec. C: experimental data. B: predicted relationships at various value of D ranging from 0.2 to 2.0 sec. D: experimental data obtained at $\kappa=1.21, 1.90$ and 2.87 , respectively.



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