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Short communication

Exploration and learning of demand-feeding in Atlantic cod (*Gadus morhua*)

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ABSTRACT

A bite-and-pull demand-feeding system was introduced to groups of cultured cod (*Gadus morhua*). For half of the groups trigger actuations were rewarded with food, while actuations were unrewarded in the other groups. Initially, cod responded with frequent triggering, irrespective of whether triggering was rewarded with food or not. The high initial curiosity-driven triggering rate declined rapidly, and was almost perfectly described by an exponential decay model with a decay rate of 7% min^{-1}. After 3 h, the triggering frequency of the rewarded fish diverged from that of unrewarded fish, and it remained higher throughout the 9 days of the experiment. The initial curiosity-driven triggering allowed the cod to establish the relationship between action and reward in a short time. It is inferred that the time trajectory of action frequency of rewarded fish is the result of several factors and that operant learning can only be verified by comparing action frequencies of rewarded and unrewarded fish, and not by the temporal development in action frequency of rewarded fish alone.

1. Introduction

Operant learning is when an association is formed between a behavioural action (response) and its outcome (reinforcement). The probability that a spontaneous action will be repeated increases if it is rewarded and decreases if it is unrewarded. Fishes' ability of operant learning allows the use of demand-feeding (or self-feeding), where fish learn to operate a feeding device that delivers food upon a demand, e.g. pulling a string or pushing a rod. Many fish search actively for food and investigate, with their mouth or in other ways, what is food and what is not, and this behaviour is the basis for demand-feeding. When a certain action of the search behaviour results in triggering of the feeding device, this particular action is rewarded by the delivery of food. When the action has been rewarded for a sufficient number of times the fish learns the relationship, increasing the frequency of the rewarded behaviour. Demand-feeding is used in commercial production of farm fish (Jobling et al., 2001), and as a research tool to investigate for example food preferences (Geurden et al., 2005), feeding activity (Azzaydi et al., 1998), and group dynamics (Millot and Begout, 2009), and numerous studies on demand-feeding have been published. The time taken to learn is often addressed in these demand-feeding studies. However, there is no established method to estimate the time to learning, and estimates reported are often based on when the triggering rate has reached a stable level (e.g., Adron et al., 1973; Rubio et al., 2004) or a percentage of a final rate (Mizusawa et al., 2007; Noble et al., 2005). Such estimates do not make a clear distinction between triggering actuations due to search behaviour or curiosity and actuations due to the fish having learned that triggering is rewarded, i.e., operant learning. Also, the triggering rate may be modulated by time varying motivation, e.g., stomach fullness or circadian feeding rhythms (Adron et al., 1973; Chen et al., 2007; Millot and Begout, 2009), and fish may continue to actuate triggers that are never rewarded, though at a low rate (Adron et al., 1973).

A method for distinguishing between triggering as search behaviour (i.e., before learning), and triggering as a demand for food (with operant learning) is to compare the rate of triggering of fish rewarded for actuations with that of unrewarded fish. In the present study, we identify the time taken to establish a difference in triggering rate between rewarded and unrewarded Atlantic cod (*Gadus morhua*). To the best of our knowledge, this is the first published study of operant learning and demand-feeding in cod.

2. Materials and methods

2.1. Experimental setup

The experimental tanks were squared, 1.5 × 1.5 m, and filled with 35 cm of sea water (8 °C, 35 PSU) and a water flow of 50 l min^{-1}, maintaining the O_2 saturation above 80%. The light regime was L:D 24:0, i.e. continuous light. Feeders (ArvoTec TD2000, ArvoTec, Huutokoski, Finland) hung above each tank, and were connected to a bite-and-pull demand-feeding system (InnovaFeed, InnovAqua SLL, Sevilla, Spain), in which pulling a thin wire switches on a relay, sending a trigger registration to a computer system and starting the feeder. The system was programmed to turn on the feeders for 1 s when the wire was pulled for 0.25 s or more. A 2 cm plastic "bait" was attached at the end of

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the triggering strings, immediately below the surface. In order to keep the wire straight enough to ensure constant water contact, we attached a stainless nut (M6, width 10 mm) to the bait.

2.2. Experimental fish and procedure

The experimental cod were reared in a pond the first three months after hatching, then in a sea cage for three months, and thereafter in indoor tanks. They were around 10 months of age at the time of the experiment. Eight groups of 25 cod (mean weight 150 g) were transferred to the tanks and allowed to recover for one day before the experiment started. So that fish would not become familiar with the triggering strings in advance of the experiment, the strings were kept outside the tank during this initial recovery period. The experiment started with the triggering strings being carefully put into the tanks and lasted for a total of 9 days. For 4 groups, the feeders connected to the demand-feeder device were empty and, thus, triggering was not followed by food (unrewarded procedure). These groups were fed from pre-programmed feeders with a total of 0.8% of their biomass per day over three meals of 34 s duration with 3-hour intervals (food type: Skretting Amber Neptun, 3 mm, Skretting). For the remaining 4 groups, the demand-feeders were filled with the same type of dry food, with triggering being followed by an average of 0.8 g food (rewarded procedure), corresponding to ~0.02% of the tank biomass. Thus, each reward corresponded to ~1/40 of the offered daily ration of the unrewarded fish.

There was one incidence in each of two tanks in the unrewarded procedure where the triggering string was unavailable for the fish. In the first incidence, the string fell off the relay (minutes 87–183), and in the other, a fish jumped out of the tank with the string in its mouth (minutes 396–713). These data points were excluded from analysis.

2.3. Data analysis

All triggering activity was continuously recorded on the computer system, available as number of trigger actuations per minute. In the unrewarded and rewarded procedures, 87.4 ± 5.7% and 77.5 ± 4.6%, respectively, of all 1-min intervals with triggering contained only 1 trigger actuation. We observed that in the rewarded procedure fish often pulled the trigger while chasing and eating food that had just been delivered by a previous trigger actuation, possibly because they confused the trigger bait with food pellets, or due to an increased arousal during feeding. To avoid overestimation of the willingness to pull the trigger in the rewarded groups due to this potential artefact, the triggering values of each 1-min interval was converted to either zero or one values, and each 1-min interval containing at least one trigger actuation was defined as a triggering bout. Thus, for the rewarded groups, more than one food batch were released during triggering bouts consisting of more than one actuation, i.e. the number of food batches delivered was somewhat higher than the number of triggering bouts.

Our conceptual model for analyzing the data was that the triggering rate of unrewarded fish attenuates exponentially as a function of time t (Fig. 1A.) Initially, the fish would be attracted to the novel object with a relatively high triggering probability, with this novel object appreciation (curiosity) attenuating exponentially towards an "acquainted" frequency, i.e. the triggering frequency at $t\,\infty$. Data of the unrewarded fish were fitted to the Non-linear Least Square model:

$$\text{Triggering rate} = a + b^{*}\exp((t-1)^{*}c)$$

using the "nls" method in R software system Version 2.9.0 (Copyright 2009, The R Foundation for Statistical Computing, Vienna, Austria). Here, $a + b$ equals the initial triggering frequency, b is the acquainted frequency, and c is the exponential curiosity attenuation rate. Rewarded fish (Fig. 1B) should initially display the same triggering rate as the unrewarded fish, but when they have learned to associate triggering with reward, their attraction to the trigger should increase with the triggering rate diverging from the trajectory of the unrewarded fish (Fig. 1C).

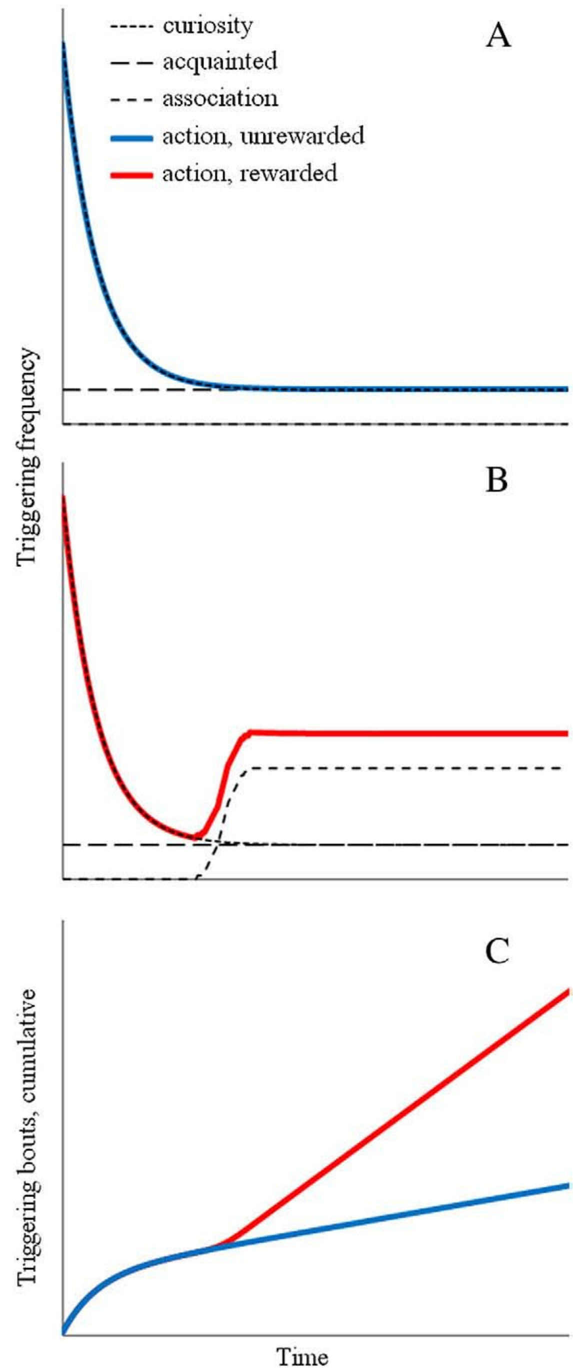

Fig. 1. Outline of our conceptual model for triggering propensity as a function of motivation that can be due to curiosity towards novel objects or due to an established cognitive association between action and reward. A) Fish that are offered a novel bait that does not provide any reward. B) Fish that are offered a novel bait that does provide a reward. C) Cumulative triggering bouts for rewarded (red line) and unrewarded (blue line) fish. Time to learning can be identified from when the curves diverge. The sustained increase in cumulative bouts for unrewarded fish reflects that the acquainted triggering rate is >0.

3. Results and discussion

The triggering rate for the entire experiment was higher in the rewarded than in the unrewarded procedure (Welch Two Sample