



Cue-based and algorithmic learning in common carp: A possible link to stress coping style



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ABSTRACT

Common carp that had been screened for stress coping style using a standard behavioural test (response to a novel environment) were given a learning task in which food was concealed in one of two compartments, its location randomised between trials and its presence in a given compartment signalled by either a red or a yellow light. All the fish learned to find food quickly, but did so in different ways. Fifty five percent learned to use the light cue to locate food; the remainder achieved the same result by developing a fixed movement routine. To explore this variation, we related learning strategy to stress coping style. Time to find food fell identically with successive trials in carp classified as reactive or proactive, but reactive fish tended to follow the light cue and proactive fish to adopt a fixed routine. Among fish that learned to follow the light, reactive individuals took fewer trials to reach the learning criterion than did proactive fish. These results add to the growing body of information on within-species variation in learning strategies and suggest a possible influence of stress coping style on the use of associative learning as opposed to algorithmic searching during foraging.

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1. Introduction

There is increasing interest in the fact that cognitive traits may vary within species, as well as between them (e.g. Thornton and Lukas, 2012). For example, different patterns of learning among individuals of the same species have been documented in mammals (e.g. Guenther et al., 2013), birds (e.g. Guillette et al., 2011; Brust et al., 2013), reptiles (e.g. Carazo et al., 2014) and fish (e.g. Sneddon, 2003; Overli et al., 2007). There is also increasing interest in understanding the causes and consequences of such variation and it has been suggested that one influential factor may be what is sometimes referred to as stress coping style or animal personality (e.g. Carrere and Locuto, 2011; Sih and Del Giudice, 2012).

The extensive literature on stress coping styles in animals shows that in many species of vertebrate, including mammals (Koolhaas et al., 2010), birds (Van Oers and Naguib, 2013) and fish (Moretz et al., 2007), and some invertebrates (Mather and Logue, 2013), individuals differ consistently in how they respond, behaviourally

and physiologically, to a variety of challenges. In other words, they show different stress coping styles, with individuals lying at different points along a proactive–reactive axis (Carere and Maestripieri, 2013). At one extreme, proactive individuals react positively to challenge, tend to take risks, show relatively high levels of aggression and readily form behavioural routines. Physiologically, challenges induce predominantly adrenaline-based responses. At the other extreme, reactive individuals avoid risk and conflict, respond to challenge by freezing or hiding, are behaviourally flexible and show a predominantly cortisol-based physiological stress response (review: Caramaschi et al., 2013).

In a discussion of potential links between stress coping style, learning and cognition, Sih and Del Giudice (2012) point out that an animal's behavioural type may determine the probability that it encounters a learning situation (e.g. bold, proactive animals may simply find themselves exposed to a learning task quicker than do reactive, shy ones), how it processes information once in the learning situation (e.g. proactive animals are often relatively insensitive to new information) and whether and how it uses this information to produce learned behavioural changes. Sih and Del Giudice (2012) predict a number of differences in cognitive processes between proactive and reactive animals, based on a trade-off

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between speed and accuracy during information gathering and learning.

A number of studies have demonstrated links between personality/stress coping style and various aspects of learning. Going back to some of the examples given at the start of this paper, in caviés (*Cavia aperea*), boldness, activity and aggressiveness are all positively related to how quickly individuals learn to use a visual cue to find food; aggressiveness is negatively related to speed of reversal learning in this context (Guenther et al., 2013). In black capped chickadees (*Poecile atricapillus*), fast exploring birds take longer to achieve reversal learning in an acoustic discrimination task than do slower exploring individuals (Guillette et al., 2011). In zebra finches (*Taeniopygia guttata*), there are no effects of personality on initial performance of a spatial learning task in which coloured cues signalled the presence of food, but more active, fearful birds are faster to learn to associate a new cue with food (Brust et al., 2013). Rainbow trout (*Oncorhynchus mykiss*) assessed bold on the basis of time spent in an open area are faster to learn to approach a light to gain food than are fish assessed as shy (Sneddon, 2003), whereas proactive (bold, aggressive) rainbow trout are slower to lose a conditioned response once it is no longer reinforced (Overli et al., 2007). Not all studies find a simple relationship between personality and learning. For example, in water skinks (*Eulamprus quoyii*), there is a non-linear relationship, with both bold and shy individuals learning quickly to use a particular shelter to avoid attack, but intermediate animals performing poorly (Carazo et al., 2013). In great tits differences in the speed with which birds learn to pull a lever to gain food are unrelated to a measure of boldness (Cole et al., 2011). Clearly, there is need for research on more species before a clear picture of the complex relationship between personality/stress coping style and cognition emerges.

In the studies quoted above, cognitive variation took the form of differences in the speed with which individuals perform a particular feat of learning, but it is also possible that the processes themselves may differ. At the species level, Page et al. (2012) suggest that animals following a slow life-history trajectory should learn associations between sensory cues and hidden food, while those on a fast trajectory are expected to rely on fixed decision rules (algorithmic searching). This suggestion was supported by a comparison of two species of similar size but with different life history traits, bats (*Myotis nattereri*) and shrews (*Sorex araneus*), which have slow and fast life histories respectively. When searching for food in a four-arm maze; the majority of shrews follow fixed rules, while most of bats use cue-directed searching. In the within-species context of stress coping style, proactive individuals often have a high metabolic rate and fast growth, while reactive animals show the opposite traits (e.g. Biro and Stamps, 2008; Careau et al., 2009; Réale et al., 2010). Following the logic of Page et al. (2012), proactive animals might therefore be expected to use simple stereotyped behaviour patterns to find hidden food, while reactive animals might be expected to use learned associations between environmental cues and food.

With this background, the first aim of the present study was to investigate the strategies used by common carp (*Cyprinus carpio*) when offered the opportunity to learn an association between a visual landmark and food. A second aim was to determine whether any observed differences in learning could be explained by differences in stress coping style. To reduce the chances that any differences may be an indirect result of variation in risk taking (Sih and Del Giudice, 2012) as opposed to learning processes per se, subjects were fully familiarised with the experimental set-up before learning trials started (as in Page et al., 2012). Common carp were used because stress coping strategies are known to be linked to differences in metabolic rate in this species (Huntingford et al., 2010) and so possibly to life history patterns (Biro and Stamps, 2008; Careau et al., 2009).

2. Methods

2.1. Screening for stress coping style

Eighty common carp (mean length 8.4 cm; mean weight 10.1 g) were individually marked with alcian blue dye, under anaesthesia and using a Panjet inoculator (Hart and Pitcher, 1959. UK Home Office licence 60/3679). They were then housed in large groups and fed daily to satiation with frozen chironomid larvae. At least a week after marking, stress coping style was assessed in groups (carp are highly stressed by isolation) as described by Jenjan et al. (2013). Fish were deprived of food overnight (at least 12 h, sufficient time to ensure empty stomachs at the holding temperature, 22 °C), placed in groups of 8 in a darkened settling chamber (30 × 38 cm × 31.5 cm) and left for 20 min before the door was opened giving access to a well-lit novel area (70 × 38 cm × 31.5 cm) containing visible food. The time taken by each fish to leave the settling chamber was recorded (up to a cut-off of 20 min). This was repeated three times for each fish, with at least 24 h between trials. Fish were assigned to groups randomly in successive trials, to reduce possible effects of social interactions within the holding tanks. Emergence time was repeatable across tests (ANOVA: $F_{2,63} = 3.68, P = 0.001$) and a clear distinction could be made between fish that emerged in less than 10 min in all three tests, designated proactive, and those that consistently failed to emerge, designated reactive. The remaining fish, with intermediate emergence times, were omitted from further study. Previous studies have shown that differences in emergence time of the magnitude seen here are predictive of other aspects of stress coping style, including success in gaining access to restricted food and metabolic rate (Huntingford et al., 2010). Fast-emerging, proactive and slow-emerging, reactive fish did not differ in weight (mean ± SE = 9.62 ± 0.68 g proactive and 10.51 ± 0.57 g reactive; $df = 38; T = 1.00; P = 0.33$), length (mean ± SE = 8.30 ± 0.19 cm proactive and 8.56 ± 0.18 cm reactive; $df = 38; T = 1.04, P = 0.31$) or condition factor (weight/length³; mean ± SE = 3.40 ± 0.17 proactive and 3.64 ± 0.13 reactive; $df = 38; T = 1.10, P = 0.28$).

2.2. Training carp to associate a light signal with food

Forty fish were trained in 1 m glass tank comprising an enclosed settling chamber (30 × 38 cm × 31.5 cm) at one end, linked by a plastic tunnel with a removable cover to a larger section (70 × 38 cm × 31.5 cm, Fig. 1). At the opposite end the tank was divided by opaque dividers into 2 hidden feeding compartments. A small light was placed above the entrance to each compartment to signal the presence or absence of food. Based on the known spectral sensitivity of carp (Tomita et al., 1967), red and yellow light sources were used.

To avoid isolation-induced disturbance, carp were trained in fixed pairs of the same stress coping style. The aim was to use the

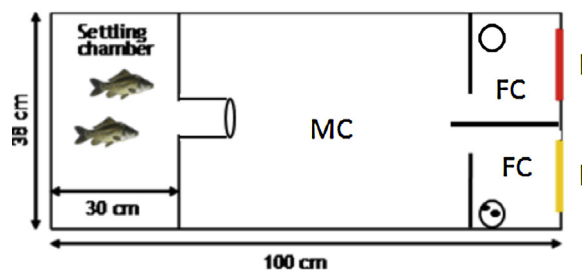


Fig 1. Schematic diagram of the learning tank. Lights (L) above each feeding chamber (FC) were visible to the fish from the point at which they entered the main chamber (MC).

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