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Mechanisms of copying behaviour in zebra finches

Lauren M. Guillette*, Susan D. Healy

School of Biology, University of St Andrews, St Andrews, UK

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ABSTRACT

When an individual is faced with choosing between unfamiliar food options, it may benefit initially by choosing the option chosen by other animals so avoiding potentially poisonous food. It is not clear which cues the naïve forager learns from the demonstrator for choosing between food options. To determine firstly which birds (zebra finches, *Taeniopygia guttata*) would copy a demonstrator's choice, in Experiment 1 we presented each observer with a demonstrator feeding from one of two differently coloured feeders and then tested the observer's feeder colour preference. Of the same-sex/mixed-sex demonstrator-observer pairs tested only females copied male demonstrators. In Experiment 2, birds did not prefer either feeder colour in the absence of demonstrators confirming the social learning effect observed in Experiment 1. In Experiment 3, copying females fed significantly more at the feeder of the demonstrated colour, rather than at the location of the demonstrated feeder. These data point not just to the identity of the individual to be copied but also to the kind of information learned.

1. Introduction

One of the potential advantages of group living is acquiring information from group mates. The information acquired may concern where and what objects with which to interact or how to behave in a way that results in a desirable outcome, for instance, obtaining food (Zentall, 2006). Social learning about foraging has been shown in a wide range of species (Danchin et al., 2004) and when an individual is faced with choosing between two unfamiliar food options, it may benefit initially by choosing the option chosen by other animals. Indeed, naïve rats prefer the flavour that matches that of food consumed by an experienced individual (Galef et al., 1998, 1984). In this way social learning enables the observer to consume a known, safe food while avoiding a potentially poisonous, unknown food. Moreover, one reason birds forage in flocks is because by doing so they find food more readily. For example, Burmese fowl (*Gallus gallus*) use both location and stimulus cues learned from an experienced demonstrator when foraging 48 h after observing the experienced bird (McQuoid and Galef, 1992).

Copying of food choices has also been demonstrated in zebra finches, *Taeniopygia guttata*, a species that forages in flocks on grass seed in Australia (Benskin et al., 2002; Katz and Lachlan, 2003; Experiment 2, Riebel et al., 2012). There is evidence that the extent of food copying varies among individuals (Rosa et al., 2012) and depends on experimental conditions (Guillette et al., 2014). A possible interpretation for the variation in whether birds copy might be that birds do not encode and/or use all of the cues available to them at the time of observation/test. This could be because some cues, such as colour (of the feeder) or spatial location (of the feeder), are more salient, reliable or easier to learn. Some animals, then, may learn socially about the location of food (local enhancement; Galef and Giraldeau, 2001) but not the colour (stimulus enhancement; Spence, 1937) of food, which may explain why zebra finches used their own information to choose between unfamiliar coloured feeders rather than copy experienced conspecifics (Hoppitt and Laland, 2008). Furthermore, for some animals it may be that both of these cues are important: both budgerigars (*Melospsittacus undulates*; Heyes and Saggerson, 2002) and starlings (*Sternus vulgaris*; Root-Bernstein, 2010), for example, copied a demonstrator's behaviour when the colour and location of food choices were held constant but failed to copy when colour and location were dissociated. In the zebra finch it is unclear which cues birds learn about while observing conspecifics: stimulus enhancement has been sufficient for social learning in some studies (Benskin et al., 2002; Katz and Lachlan, 2003) but not in others (Guillette et al., 2014). It is also not clear whether local enhancement plays any role in social learning in this species.

Our aim here was to determine what information copying zebra finches might acquire from their demonstrators. To do this, we used

* Corresponding author at: School of Biology, University of St. Andrews, Harold Mitchell Building, St Andrews KY16 9TH, UK. Tel.: +44 01334 46 3346.
E-mail address: lmg4@st-andrews.ac.uk (L.M. Guillette).

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an experimental design in which the observer had the opportunity to watch a demonstrator forage at only one of two differently coloured feeders (Guillette et al., 2014). In Experiment 1 we tested both same-sex and mixed-sex pairs to determine if birds would copy the food choice of a demonstrator when the location, in addition to the colour of feeders was held constant across the demonstration and testing phases. If they do this, they should preferentially eat from the hopper of the same colour as that from which they observed the demonstrator to feed. In Experiment 2 we tested whether the apparent copying behaviour reflected initial colour preferences. If the birds have pre-existing preferences they should prefer one colour feeder over the other. We would not expect, however, that they would all show the same preference. Finally, in Experiment 3 we dissociated colour and location cues in the test phase to examine which cue was guiding copying behaviour.

2. Methods

2.1. Subjects

The subjects were 65 zebra finches (*Taeniopygia guttata*; 30 males, 35 females) bred at the University of St Andrews. All birds were housed in cages of same-sex individuals (8–10 individuals per cage, 100 cm × 50 cm × 50 cm) and kept on a 14:10 light:dark cycle with temperature at ~20 °C and humidity at ~50%. Lights were fluorescent overhead bulbs. Birds were given free access to mixed seed, vitamin-supplemented water, cuttle bone, oystershell, and vitamin block. Each cage had several different perch sizes and types and the floor was covered with pressed wood pellets. At the end of the experiment all birds were returned to the group housing conditions described above. Birds were visually assessed for health at least two times a day by the researcher (LMG) and one additional time per day by the animal care staff. All birds were between 2 and 6 months of age at time of testing. All of the work described here was conducted with the approval of the University of St Andrews Animal Welfare and Ethics Committee.

2.2. Apparatus

The experiments were carried out in three test rooms. Each test room contained a demonstrator cage, an observer cage, and stock cages of same-sex zebra finches located 55 cm across the room from the experimental cages so that test birds were not visually isolated from conspecifics. All trials for Experiment 2 took place in one room. All trials for Experiment 3 took place in another room. Trials for Experiment 1 took place in the rooms where Experiments 2 and 3 took place, plus an additional room. The trials of the four experimental groups in Experiment 1 were randomized across all three rooms.

The cages (100 cm × 50 cm × 50 cm) for the demonstrator and for the observer bird were identical (see Fig. 1) and faced each other along the 100 cm side of the cage. A distance of 10 cm separated the demonstrator cage from the observer cage. A white opaque barrier between the cages prevented visual, but not vocal, interaction between the experimental birds. Each cage contained two water bowls, a cuttlefish bone and a vitamin block and six perches. The observer cage contained two grey food dishes on the side of the cage facing away from the demonstrator cage. During the observation and subsequently in the test phase (described below) coloured feeders (one pink, one purple, wrapped in coloured opaque paper) were attached to each cage. Each cage contained two bird box cameras (SpyCameraCCTV, Bristol, UK) connected to a laptop computer.

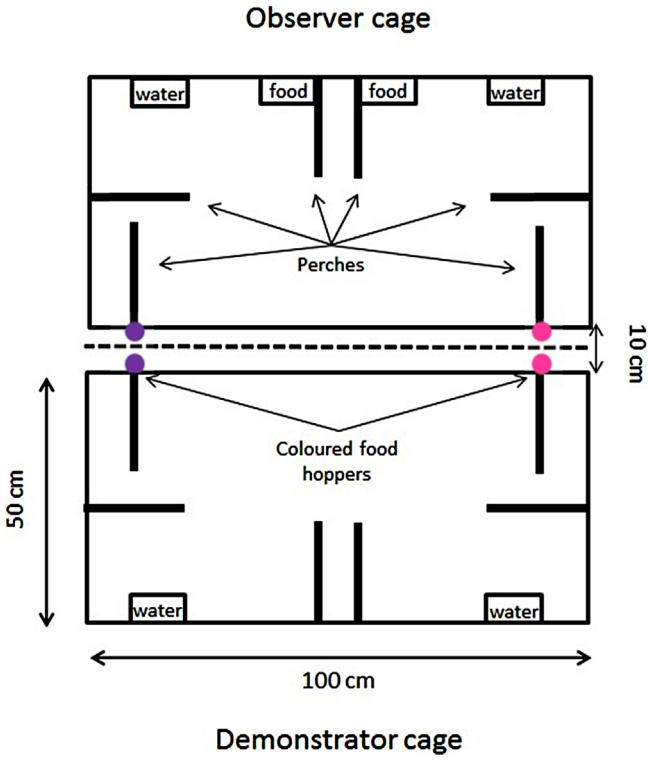

Fig. 1. Scale drawing top down view of the demonstrator and observer cages for Experiments 1 and 2. The dashed line between the cages represents the opaque barrier that was in place at all times except during the observation phase. We removed the food bowls on the front of the observer cage 2 h prior to the start of the observation phase. The location and colour of the feeders in the demonstrator and observer cage mirrored each other. In Experiment 3 the observer had 2 feeders (one of each colour) at each location.

2.3. Experiment 1

2.3.1. Subjects

The subjects for Experiment 1 were 46 adult zebra finches (24 male, 22 female) that were bred at the University of St Andrews. Birds were randomly assigned to the following four experimental groups: (1) female demonstrator with male observer ($n = 8$); (2) male demonstrator with female observer ($n = 7$); (3) female demonstrator with female observer ($n = 7$); and (4) male demonstrator with male observer ($n = 7$). Siblings were never paired. A different bird was used as a demonstrator in each trial. Once a bird had participated in a trial as an observer; it could then became a demonstrator bird in a subsequent trial.

2.3.2. Procedure

Each trial lasted approximately 24 h. Between 14:30 and 15:30 h on Day 1 one bird was placed in the demonstrator cage and another in the observer cage. At this time, the opaque barrier was in place so the demonstrator and observer birds were not in visual contact with one another but both could see male and female birds in the stock cages on either side of the experimental room. The only food available to the demonstrator bird was in one of two experimental feeders (pink or purple). Thus the demonstrator bird learned which feeder to 'demonstrate' during the observation phase (described below) the next day. On Day 2, food was removed from the both cages 2 h post light onset. The empty feeder (the non-demonstrated colour) remained in the demonstrator cage but was sham removed. The cage floors were replaced with clean floors so that the only food available to the birds was provided via the feeders. Across trials the location of the feeders remained fixed, but the colour at each location was randomized.