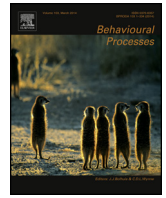




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journal homepage: www.elsevier.com/locate/behavproc



The roles of vocal and visual interactions in social learning zebra finches: A video playback experiment

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ARTICLE INFO

Article history:

Received 4 October 2016
Received in revised form
12 December 2016
Accepted 19 December 2016
Available online xxx

Keywords:

Copying
Foraging
Social interaction
Social learning
Video playback
Zebra finch

ABSTRACT

The transmission of information from an experienced demonstrator to a naïve observer often depends on characteristics of the demonstrator, such as familiarity, success or dominance status. Whether or not the demonstrator pays attention to and/or interacts with the observer may also affect social information acquisition or use by the observer. Here we used a video-demonstrator paradigm first to test whether video demonstrators have the same effect as using live demonstrators in zebra finches, and second, to test the importance of visual and vocal interactions between the demonstrator and observer on social information use by the observer. We found that female zebra finches copied novel food choices of male demonstrators they saw via live-streaming video while they did not consistently copy from the demonstrators when they were seen in playbacks of the same videos. Although naïve observers copied in the absence of vocalizations by the demonstrator, as they copied from playback of videos with the sound off, females did not copy where there was a mis-match between the visual information provided by the video and vocal information from a live male that was out of sight. Taken together these results suggest that video demonstration is a useful methodology for testing social information transfer, at least in a foraging context, but more importantly, that social information use varies according to the vocal interactions, or lack thereof, between the observer and the demonstrator.

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1. Introduction

Learning through interactions with, or observations of, other individuals occurs across a large range of animals and behaviours, including foraging, mate-choice, tool manufacture and use, nest-site location, and nest-material selection (i.e. social learning, e.g., Heyes, 1994, 2012; Auersperg et al., 2014; Guillette et al., 2016; Kendal et al., 2015; Loukola et al., 2012; Trompf and Brown, 2014; Vakirtzis, 2011). Many of these studies are conducted in the laboratory using a live observer–demonstrator paradigm, which allows control of *who* provides information to the observer. The trade-off to using this paradigm is that even after extensive training the performance of the demonstrator and thus the social information provided to the observer can vary substantially from trial-to-trial. The housing and training of the demonstrator individuals can also be time consuming. Video playback may provide a way to standardize the demonstration and to reduce the total number of animals

needed, as well as providing repeatability and stimulus control (D'Eath, 1998; Oliveira et al., 2000).

Video stimuli has been shown to elicit natural behaviour in some animals. Chimpanzees (*Pan troglodytes*) and budgerigars (*Melopsittacus undulatus*) yawn more in response to videos of conspecifics yawning than to control videos in which conspecifics were engaged in other behaviours (Campbell and de Waal, 2011; Gallup et al., 2015). Male zebra (*Taeniopygia guttata*) and Bengalese finches (*Lonchura striata*) sing directed song to video presentations of female conspecifics (Ikebuchi and Okanoya, 1999) and female zebra finches will perform courtship display to videos of male conspecifics (Swaddle et al., 2006). Gloomy octopus (*Octopus tetricus*) readily approached and touched the video screen when presented with a crab video, and reduced their activity, a natural response for this solitary species, in response to a video of a conspecific (Pronk et al., 2010). Videos of 'audience' hens (*Gallus domesticus*) potentiate alarm calls produced in the presence of a predator model (Evans and Marler, 1991) and male Jacky dragons (*Amphibolurus muricatus*) produce aggressive displays in response to videos of conspecific males (Ord et al., 2002). In some of these cases there is no qualitative difference in the response to live versus video stimuli (e.g. Evans and Marler, 1991; McQuoid and Galef, 1993; Ord et al., 2002; Rieucou and Giraldeau, 2009), however, in other cases an attenu-

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<http://dx.doi.org/10.1016/j.beproc.2016.12.009>

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ated (e.g. Ikebuchi and Okanoya, 1999) or enhanced response to video stimuli was reported (Swaddle et al., 2006). In the latter, an enhanced response of female courtship to videos compared to live males may be due to the non-interactive nature of video demonstration. The females who saw the non-interactive videos may have increased their courtship displays to elicit a response from the video male.

In addition to soliciting natural behaviour videos playback have also been used, albeit to a lesser extent, to examine social learning. In a sub-set of these studies the degree to which animals learn from live demonstrators relative to what they learn from demonstrators on video was compared: budgerigars copy the actions of a live or video demonstrators in a two-action test (Heyes and Saggerson, 2002; Mottley and Heyes, 2003) and Burmese red jungle fowl (*Gallus gallus spadecius*) copy foraging choices of live and video demonstrators (McQuoid and Galef, 1993, 1992). In the former test, the audio that accompanied the video demonstration was always played, while in the latter study one condition included both video and audio and a second condition included video only. The observers used social information only when both video and audio were available. In other tests of social learning of mate-choice in Japanese quail (*Coturnix japonica*) and tool manufacture and use in chimpanzees sound was not necessary for social learning to occur (Ophir and Galef, 2003; Price et al., 2009). Taken together these results suggest that social learning across species and/or context may require different types/quality of social information/interaction between the observer and the demonstrator.

The zebra finch is a gregarious species that takes well to laboratory conditions. Perhaps this is why the zebra finch has become a popular model species for studying song learning, neurobiology, mate choice, animal personality and cognition (Healy et al., 2010; Schuett and Dall, 2009; Zann, 1996). It is also a useful species to test hypotheses regarding the conditions under which animals should use social information. For example, developmentally stressed zebra finch chicks have weaker social associations with their parents compared to control chicks that were not stressed during development (Boogert et al., 2014) and early-life stress results in juveniles learning from unrelated adults (Farine et al., 2015). Female zebra finches, when faced with making a novel foraging decision, will copy the choice of live male demonstrators, whereas male zebra finches observing male demonstrators do not (Guillette and Healy, 2014). Males do, however, use social information in other situations: first-time nest-builders will copy the nest material choice of familiar, but not unfamiliar males (Guillette et al., 2016). Furthermore, zebra finches also pay attention to vocal information: not only are they vocal learners (Zann, 1996) with both males and females preferring their fathers songs over unfamiliar songs (Riebel et al., 2002), female zebra finches' preference for their pair-bonded mate declines when auditory cues from their mate are masked by white noise (Swaddle et al., 2006) and zebra finch pairs will vocal duet at the nest (Elie et al., 2010).

In the current set of experiments we had two objectives. The first was to determine whether video demonstrators have the same effect on the behaviour of observers as do live demonstrators. To do this we followed the methodology of a previous study in which we found that zebra finch females, when faced with making a novel foraging decision, copied the choice of live male demonstrators while males did not copy anyone (Guillette and Healy, 2014), but in which we replaced live demonstrators with demonstrators presented on video. We presented a live video of male demonstrators feeding from one, but not a second novel feeder, to females or males on a thin-film-transistor (TFT) screen. TFT screens have constant illumination and can accommodate the higher flicker-fusion frequency of birds (Galoch and Bischof, 2007; Ikebuchi and Okanoya, 1999). As the demonstrator was in the same room but was visually occluded from the observer, the observer and the demonstrator

could vocally interact, but the only visual information available to the observer was provided by the TFT screen. If video presentations are to be useful as a methodology for investigating social learning the live streaming video demonstration should produce the outcome described in Guillette and Healy (2014) in which female observers copied the foraging decisions of male demonstrators while male observers did not copy the foraging decisions of male demonstrators.

Second, we wanted to test the importance of social interactions in the transfer of information from a knowledgeable demonstrator to a naïve observer. To do this we ran three more manipulations in which we varied the type of social interaction that was available. Different observers were used in each experiment. In Experiment 2 the videos, with audio, of the male demonstrators recorded in Experiment 1 were played back to female observers. Thus, the observers could see and hear the demonstrators, but they lacked the vocal interaction in Experiment 1. In Experiment 3 we presented the demonstrator videos to female observers without the audio. In Experiment 4, we presented the same videos to female observers coupled with placing a decoy male in the room with which the females could vocally interact but could not see. This decoy male was not the male on the video. Therefore, in Experiment 4, the female observers could interact vocally with a male but he was not the demonstrator. In comparing the results of these four experiments we can determine both whether video playback is a valid experimental tool for assessing social learning about foraging and what social interactions are important for this learning.

2. Methods

2.1. Subjects

The subjects were either bred at the University of Andrews or purchased from a local breeder. All birds were housed in cages of same-sex individuals (8–10 individuals per cage, 100 × 50 × 50 cm or 15–30 individual per cage, 140 × 71 × 122 cm) and kept on a 14:10 light:dark cycle with temperature at ~20°C and humidity at ~50%. Birds were given free access to mixed seeds, water (vitamin-supplemented 3 days per week), cuttle bone, oystershell, and vitamin block and fresh spinach (3 × per week). Each cage had several perch sizes and types and floors were covered with pressed wood pellets. At the end of the experiment birds were returned to the group housing cages described above. Birds were visually assessed for health at least two times per day by the researcher (LMG) and one additional time per day by the animal care staff. All birds were between one and three years of age at time of testing. 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 a test room that contained a demonstrator cage and four observer cages. White opaque curtains between each cage allowed subjects to hear and vocally interact but not see each other for the duration of the experiments. Each observer cage (100 × 50 × 50 cm see Fig. 1) contained two water bowls, a cuttlefish bone and a vitamin block and six perches and two grey food dishes on the opposite side of the cage from where the experimental feeders were located. During the observation and subsequent test phase (described below) coloured feeders (one pink, one purple, wrapped in coloured opaque paper) were attached to each cage. A video screen (ViewsSonic Thin Film Transistor, model # VS15804) situated 15 cm from the long side of the observer cage was concealed by a white opaque curtain. The demonstrator cage was identical to that of the observers', with the exception of the

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