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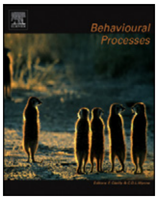

The role of context, colour and location cues in socially learned novel food source preferences in starlings, *Sternus vulgaris*

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ABSTRACT

Although the opportunity for errors in social learning is widely recognised, as yet little research has been directed towards understanding specific inaccuracies, biases and limitations in social learning and the mechanisms that give rise to them. In two experiments I ask how starlings, *Sternus vulgaris*, identify exemplars of novel feeders previously learned about socially. I find that starlings have a stronger response to feeders in the same context as that in which social learning took place, compared to identical and nonidentical feeders in a different context. Within a context that matches where social learning took place, starlings prefer feeders that show the same location and colour as the feeder demonstrated by the demonstrator starling, and show no preference when colour and location cues are dissociated. This suggests that starlings are relatively accurate social learners, since they show strong responses to novel foraging options only if they match the context, colour and location of options learned about socially, and they do so after very few trials. Furthermore, the responses of the subjects were compatible with conditioned learning-like mechanisms, which provide a useful basis for the further investigation of the origins and implications of errors in social learning.

1. Introduction

The acquisition and spread of novel behaviours, or innovations, is an important aspect of cultural or proto-cultural change (Reader, 2003; Bonnie et al., 2007). While the opportunity for error in the social acquisition of innovations is widely recognised (e.g. Laland and Williams, 1998; Laland, 2004), less attention has been given to characterizing and seeking to understand the origins of variance, errors or biases associated with social learning of innovations. Examining this issue may shed light on the mechanisms of social learning as well as its limitations and potential evolutionary trajectories. Here I consider a specific example. When foraging in a novel environment, animals may be faced with the problem of identifying exemplars of novel food sources that they have previously learned about socially. A given type of food source will be associated with a variety of features, such as size, colour, shape, and location. Some of these features may correlate well with exemplars of a given food source, and others less well. As the cost of sampling an unknown food source is potentially high, foragers in novel environments should be more likely to respond to learned features that are good predictors of food sources, given the environment and evolutionary history of the species. In two experiments, I investigate the roles of colour, location and contextual cues in recognising exemplars of novel food sources that have been learned about socially. I worked with starlings, *Sternus vulgaris*, an omnivorous social bird species known for its abilities to exploit anthropogenic landscapes and to learn socially (Clergeau and Quenot, 2007; Templeton and Giraldeau, 1995; Campbell et al., 1999).

2. Experiment 1

Saliency of stimuli to a searching forager's decisions is a function of the species' ecology and evolutionary history. Location of a novel food source may be an adaptive feature to favour if local abundances of food and local landmarks change at a slower rate than the rate of foraging bouts. During asocial learning, food-hoarding birds choose to respond to location rather than colour cues associated with reward, if location and colour are dissociated at test (Brodbeck and Shettleworth, 1995; see also Shettleworth, 1990; McGregor and Healy, 1999). By contrast, non-food-hoarding birds show no preference for cue type when choosing between dissociated colour and location cues, choosing colour and location cues equally (Brodbeck and Shettleworth, 1995; see also McGregor and Healy, 1999). The functional adaptive explanation is that food-hoarding birds, unlike non-food-hoarding birds, benefit from and experience positive selection as a result of remembering the locations of dozens or hundreds of seeds that they have hoarded. For

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food-hoarding birds, location is the most adaptively salient cue for reward recovery.

Few experiments on social learning of preferences for novel food sources have looked at biases towards spatial versus colour cues (see Heyes and Saggerson, 2002). Studying social learning about mates, White and Galef (1999) found that female quails preferred males whom they found in the previous location of a male whom they had seen mating, over the mated male himself in another location. In that case, location trumped other cues. In the following experiment, I asked whether a bias towards location cues over other cues guided foraging starlings' recognition of a food source they had learned about socially, similarly to White and Galef's study (1999). The null hypothesis is that following social learning foragers are indifferent between location and colour cues when those are dissociated, as is generally the case for non-food-hoarding birds learning asocially. More specifically, by "indifference" between cues I do not mean that the original learned preference is eliminated or altered due to the experience of seeing them dissociated (this would be a separate hypothesis which I do not address here), but that the food source of preference is not recognised primarily on the basis of any one of the cues, hence individuals respond to both cues without showing a preference for either of them.

To test the hypothesis, I used a within subject design to compare responses when choosing between two novel feeders, one of which had been demonstrated by a demonstrator. In one condition, the feeders appeared in the same positions at demonstration and test, while in the comparison condition, the feeders' positions were switched, so that colour and location cues were dissociated. A subject preferring colour cues should choose the feeder in the non-demonstrated location, and a subject preferring location cues should choose the feeder in the demonstrated location.

2.1. Materials and methods

2.1.1. Subjects and demonstrators

Subjects were nineteen adult wild-caught starlings held under English Nature license. Three did not respond in any experimental trials and were excluded from the data set. Subjects had been caught in either December 2004 or December 2005. During the experiment, subjects were housed individually in cages 60 cm $(h) \times 45$ cm $(w) \times 120$ cm (l) or 53 cm × 45 cm × 120 cm with two perches to fly between. For welfare purposes, cages which did not provide a view of other starlings contained a small mirror mounted at floor level, which starlings frequently stood in front of. The cages were also enriched with baths twice a week. Lights were on for 14 h, off for 10 h. Starlings were provided with *ad libitum* access to turkey crumbs, Orlux®, and water. Before trials subjects were deprived for approximately four waking hours.

Five demonstrator starlings were used during the experiment. Each demonstrator had been trained to demonstrate one of the four counterbalanced colour–location combinations (see below). On one trial, one of four regular demonstrators did not demonstrate as required, and was replaced by a replacement demonstrator trained to approach the same colour and location combination. Demonstrators were housed in the same way as subjects.

2.1.1.1. Training. Subjects received no pre-training but had previously experienced related procedures in different testing arenas with different feeders. Prior experience in these pilot tests could be interpreted as affecting the results of this study in some way. However, based on personal observation of high levels of neophobia in starlings in captivity I expected the subjects to react towards the test situation in this experiment as though it were novel. Indeed, the long average response times (see Section 2.2) suggested that, as expected, subjects continued to experience neophobia and were not habituated to or familiar with the testing situation.

Demonstrators were trained to approach the feeders until they reached the criterion of approaching the feeder immediately and eating at least one mealworm. Training consisted of allowing the demonstrators to watch another trainee demonstrator forage in the testing arena, followed by a session of up to 10 min in the testing arena. The order of demonstrators' training sessions was alternated. No deliberate shaping by the experimenter was involved.

2.1.1.2. Apparatus. Trials took place in an arena consisting of a "puppet theatre" set up in a small room. The feeders were positioned in the arena approximately 48 cm from the puppet theatre. In the experimental sessions, feeders consisted of a plastic orange bowl and a plastic pink bowl, each taped to a purple plastic plate. In the control condition, both bowls were yellow and the dishes green. Starlings are tetrachromatic, making them better able to distinguish colour differences than humans (Hart, 1998; Smith et al., 2002). The bait consisted of five mealworms placed inside the bowl and visible from the starlings' eye level. The visibility of the mealworms during test means that the problem for the subjects was not to locate food, but to choose which bowl to visit first (or only).

Starlings accessed the testing arena through the window of the puppet theatre via the holding cages. The holding cages were mounted on wheels and could be rolled back and forth to position either the demonstrator's cage or the subject's cage in front of the puppet theatre window, giving a view of the arena. The front and top of the holding cages was barred while the sides and back were opaque. The holding cages were also lit by a 50 W halogen lamp each. The starlings flew towards the light without training, and this spontaneous phototaxis was used to make them go into the arena or back into the holding cages at the beginnings and ends of trials. See Fig. 1.

2.1.1.3. Procedure. Spontaneous phototaxis was used to move the starlings from one area to another during the trials. Prior to the trial, the subject was released from its living cage and allowed to fly towards the lighted holding cages in the testing room. If subjects did not fly into the holding cages, they were caught and moved by hand. Subjects were then enclosed in the holding cages and allowed to habituate in the dark for 1 min. The feeders were positioned and baited out of view of the subject. In step (1) the arena was lit and the demonstrator's holding cage door was opened to induce it to enter the arena. In step (2), the demonstration phase, the subject's holding cage was positioned in front of the puppet theatre window so that the subject could observe the demonstrator eating mealworms from one of two feeders. This step was not timed, however demonstrations never lasted more than 2 min, and were generally much shorter. In step (3) the arena light was turned off and the demonstrator's holding cage light was turned on, inducing it to return to its holding cage. Both feeders were then re-baited out of view of the subject. In step (4) the arena was lit and the subject's holding cage door was opened, to induce the subject to go into the arena. In step (5), the test phase, the subject was given up to 20 min to approach one of the feeders, with the demonstrator occluded. Approach was defined as the foot or beak crossing the edge of the feeder. Trials were stopped following the first response, so the average trial length is similar to the average time to respond as described in Section 2.2. The subject was allowed to eat the mealworms in the bowl that it approached, but the trial was ended when it moved away from the bowl regardless of the number of mealworms eaten, to prevent an approach to the other bowl which might have affected subsequent preferences. In step (6) the arena light was turned off and the holding cage light was turned on, and the subject entered the holding cage. The subject was then caught and brought back to its living cage.