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Wild, free-living hummingbirds can learn what happened, where and in which context

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Studies in the laboratory have shown that animals can combine multiple kinds of information to form integrated memories for rules and events. Less is known about how animals make use of these integrated memories in the wild. Here we tested whether wild, free-living, rufous hummingbirds, *Selasphorus rufus*, could learn to identify rewarded flowers in a naturalistic foraging situation, by remembering, over multiple exposures, what flower was rewarded, where and in which context. Birds were presented with boards on which four artificial flowers were mounted, one containing a food reward, the others containing water. Which flower (its colour and location) contained a reward was indicated in one condition by the presence of visually distinctive background boards and in a second condition by the sequential order in which the boards were presented. In both conditions, birds combined these pieces of information and learned to use the context to determine which of the four flowers was rewarded. Although they were not required to do so here, it is possible that these birds might be able to combine pieces of information to form integrated memories for single events.

It is well established that animals are capable of forming memories involving the integration of different types of information (Pearce, 1994; Pickens & Holland, 2004). Much of this research has addressed the neural underpinnings of these memories (see Rudy, 2009 for a review), typically, in the laboratory, training and testing animals with procedures including operant conditioning (Iordanova, Burnett, Aggleton, Good, & Honey, 2009; Iordanova, Good, & Honey, 2008; Penick & Solomon, 1991), object recognition paradigms (Mumby, Gaskin, Glenn, Schramek, & Lehmann, 2002; Norman & Eacott, 2005) and computer-based memory tasks (Browning, Easton, Buckley, & Gaffan, 2005; Eacott & Gaffan, 2005). Less is known, however, about how animals might make use of integrated memories in their daily lives (Clayton, Griffiths, Emery, & Dickinson, 2001; Clayton, Yu, & Dickinson, 2001). In this study, we investigated whether wild, free-living rufous hummingbirds, *Selasphorus rufus*, could form integrated memories for what was rewarded, where and in which context, in a naturalistic foraging situation.

Hummingbird foraging is a plausible model for examining whether animals can combine different kinds of information into memories. Not only can these birds learn to avoid visiting recently emptied flowers (Healy & Hurly, 1995) and to return to flowers that contain a consistent reward (Gass & Sutherland, 1985; Healy & Hurly, 2003; Hurly, 1996), they can also remember both where and when flowers refill (Henderson, Hurly, Bateson, & Healy, 2006; Marshall, Hurly, & Healy, 2012) and associate this with variations in nectar quality (González-Gómez, Bozinovic, & Vásquez, 2011). Whether rufous hummingbirds, or any other animal foraging in the wild, can combine three pieces of information, including contextual cues, into memories is not yet known.

The combination of elements into a memory is one of the prerequisites for episodic-like memory (Tulving, 1972), which involves the integration of what, where and when information (Clayton, Griffiths, et al., 2001) or what, where and which occasion information (Eacott & Easton, 2010; 2012) about a single event. If, in the current experiment, the birds could form a combined memory for these three features of episodic-like memories over repeated exposures, it would suggest that, in principle, they may also be able to form combined memories for single events. Potentially, this could provide a real-world paradigm for addressing the value of episodic-like memories.

To assess whether hummingbirds can form combined memories, we based our experimental design on a scene-learning paradigm in which rhesus macaques, *Macaca mulatta*, learnt the

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location and visual features of rewarded and unrewarded symbols in a visual scene (Gaffan, 1994). In the first condition of our experiment hummingbirds were allowed to forage from sets of artificial flowers on two visually distinctive experimental boards, which were presented repeatedly, one at a time. Both boards comprised matching sets of four flowers, with two colours of flower placed in two locations on the board. A different flower, in a different location, was rewarded on each board. As the four flowers were the same on both of the boards, a bird could not identify which flower contained the reward by remembering only a flower's colour (what) or its location (where). The reward could be found, however, if the bird formed an integrated memory of the flower's colour, location and the context in which it was presented.

In a second condition, we investigated whether hummingbirds could also form a combined memory involving a temporal context. As hummingbirds use timing cues in their daily lives (Henderson et al., 2006; Marshall, Hurly, Sturgeon, Shuker, & Healy, 2013) we hypothesized that they could integrate temporal sequential cues with other kinds of information. To test this we repeatedly presented birds with a single white board with four flowers, but we alternated the colour and position of the rewarded flower each time we presented the board. The birds had to attend to this alternating sequence in order to identify the rewarded flower. We compared the learning speed and errors the birds made in each of the two conditions to determine whether hummingbirds can form combined memories involving both visual and sequential contexts.

Figure 1. One of the experimental subjects feeding from a board in the Visual Condition. Boards measured 30 × 35 cm. Photograph: T.A. Hurly.

METHODS

Subjects

The subjects in this experiment were eight wild, free-living, adult male rufous hummingbirds that had established their territories around commercial hummingbird feeders, containing 14% sucrose solution, set out in the spring. The experiment was conducted in a valley in the eastern Rocky Mountains, Alberta, Canada (49° 21′ N, 114° 25′ W). Rufous hummingbirds migrate to this valley to breed and males establish and defend feeding territories. The territory holder typically feeds from the commercial feeder every 10–15 min, chasing away intruding conspecifics. To enable individual identification, birds with established territories were caught, by putting a mesh cage around a feeder, and the white plumage on their chests was colour marked with nontoxic ink.

The data were collected between 0800 and 2000 hours Mountain Standard Time, from May to July 2011. All of the work was carried out under permits from Environment Canada and Alberta Fish and Wildlife, with the ethical approval of the University of St Andrews and the University of Lethbridge, and was conducted in adherence with the ASAB Guidelines for the Treatment of Animals in Behavioural Research.

Experimental Apparatus

Prior to the experiment we trained birds to feed from the experimental apparatus, which was placed conspicuously within a bird's territory. The apparatus consisted of a 30 × 35 cm piece of foam board, mounted onto a 1 m high stake, on which four artificial flowers were positioned. Two small holes were made at both the top and the bottom of each board (10 cm apart, and 3 cm from the edge of the board) into which artificial flowers were inserted (Fig. 1). The artificial flowers were formed from syringe caps inserted into the centre of coloured cardboard discs (6 cm diameter). The syringe cap created a well in the centre of the flower from which the bird could feed. The capacity of an artificial flower (600 μl) was substantially more than a hummingbird could drink in a single visit. On each board only one of these four flowers contained desirable 25% sucrose solution and the remaining three flowers contained water, which the birds find distasteful.

Experimental Procedure

All birds took part in two conditions, a Visual-cue condition and a Sequential-cue condition, with the order counterbalanced across birds. Both conditions followed the same format, in which one rewarded flower on a board could be identified by attending simultaneously to the flower's colour (what), the flower's location (where) and the specific board presentation (which context). The same flowers were presented every time; however, a different flower was rewarded in each of the two contexts. We used two different colours of flower (e.g. green and pink) and presented one flower of each colour in each of two locations on the board (i.e. top or bottom, Fig. 2). Which position (left or right) that each flower colour occupied at the top and at the bottom was randomized by coin toss before each trial. Thus the experience for a typical bird would be that in the first context a pink flower at the top of the board was rewarded and in the second context a green flower at the bottom of the board was rewarded (Fig. 2). The boards were presented repeatedly until birds demonstrated that they had learnt the identity of both rewarded flowers, defined by reaching our criterion number of correct responses: choosing the rewarded flower six times in a row (three times on each board). If the criterion was not reached, an upper limit was set at 100 board presentations (50 presentations of each board), at which point the condition was terminated.

Visual Condition

In the Visual Condition, the which-context cue was a visually distinctive background scene, painted on to the experimental boards (Fig. 2). The order of the board presentations in the Visual Condition was pseudorandomized. In every four presentations, each board was seen twice but boards could be presented in any order within these sets (for example, 1-2-1-2 then 2-2-1-1). This ensured that the two boards were seen equally often throughout the experiment, but that the rewarded flower was not coupled with