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Spatial relational learning in rufous hummingbirds (*Selasphorus rufus*)

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Abstract There is increasing evidence that animals can learn abstract spatial relationships, and successfully transfer this knowledge to novel situations. In this study, rufous hummingbirds (*Selasphorus rufus*) were trained to feed from either the lower or the higher of two flowers. When presented with a test pair of flowers, one of which was at a novel height, they chose the flower in the appropriate spatial position rather than the flower at the correct height. This response may also have been influenced by a preference for taller flowers as acquisition of the task during experimental training occurred more readily when the reward flower was the taller of the pair. Thus, it appears that although learning abstract relationships may be a general phenomenon across contexts, and perhaps across species, the ease with which they are learned and the context in which they are subsequently used may not be the same.

Introduction

Animals can learn spatial relationships between objects in their environment in order to return to rewarding locations such as home or good foraging sites. For example, Clark's nutcrackers *Nucifraga columbiana* learn to find rewards located halfway between two landmarks as shown when tested with landmarks at distances that differ from the training distances (Jones et al. 2002; Kamil and Jones 1997). A more common finding is that animals can learn to search in the middle of an arena for food (e.g. Gray et al. 2004; Tommasi and Vallortigara 2000; Tommasi et al. 1997).

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Whether or not animals learn a relationship between stimuli can be tested using a transposition paradigm in which subjects are trained to discriminate between two stimuli differing in a single physical dimension (e.g. size, shape, brightness or colour, rhesus monkeys: Harmon et al. 1982; cichlid fish: Mark and Maxwell 1969; Californian sea lion: Schusterman and Krieger 1986; pigeons: Wills and Mackintosh 1999; children: Zeiler and Salten 1967). In the test situation the animal is presented with the previously reinforced stimulus and a novel stimulus varying in the same dimension as, but outside the range of, the training stimuli (e.g. small and medium (rewarded) objects presented during training, followed by medium and large objects in the test). If the animal has learned the physical relationship between the stimuli it should choose the novel stimulus in the test (i.e. the large object): this is transposition. If choice is determined by memory for the rewarded stimulus specifically, however, the original stimulus (i.e. the medium sized object) will be chosen.

As some foraging animals, such as nectarivores, make hundreds of foraging choices each day, they may use learned spatial relationships when making choices at a new location, as appears to be the case for those Hymenoptera that always move up inflorescences (Waddington and Heinrich 1979). Although transposition has rarely been tested in the spatial domain, bumble bees *Bombus impatiens* learn relative flower heights (Wiegmann et al. 2000). Bees were trained with two flowers at different heights, the lower flower sucrose-filled and the higher flower containing water and then tested with two water-filled flowers, one at the rewarded training height and a yet lower flower. Bees that had visited both flowers during training chose the lower flower significantly more often in the test. Foraging bumble bees, thus, seem to learn relational properties of flowers when foraging.

Like bumble bees, rufous hummingbirds (*Selasphorus rufus*) appear to encode flower locations relative to those of the other flowers in the array as long as flowers are no further apart horizontally than 40 cm (Healy and Hurly 1998). Hummingbirds were also faster to learn which flowers were rewarded if they occupied the same array positions,

thus appearing to use the spatial configuration between rewarded flowers (Hurly and Healy 2002). This learning of positions occurred even when the flowers in the second array were of different colour patterns to those in the training array. Little, however, is known of the way in which animals encode, or use, z-dimensional information, although it is plausible that it is of especial relevance to flying animals such as bumble bees and hummingbirds. Additionally, other than the work on Clark's nutcrackers, little has been done to examine the use of discrete landmarks, rather than extended surfaces, in encoding spatial relationships.

In this study, we wanted to determine whether the positional encoding of flowers that occurs in the horizontal plane also occurs in the vertical (z-dimension), or, whether hummingbirds encode the actual heights of those flowers. To do this, we used a design similar to that of Wiegmann et al. (2000) to determine whether such positional encoding would lead hummingbirds to transpose the spatial relationship between two flowers to a novel test situation.

Methods

Study site and subjects

The subjects were 16 male rufous hummingbirds defending feeding territories in a valley in the Eastern range of the Rocky Mountains (49°29'N; 114°25'W), Alberta, Canada. Before the experiment, birds were accustomed to feeding from artificial feeders (containing 14% sucrose solution), placed on trees (more than 150–200 m apart) along the valley, around which they established territories. Each male was individually identifiable by a small mark of non-toxic ink applied to their breast feathers. All training and experimental trials were conducted in open meadows within each male's feeding territory. Observations were made between 0800 and 2000 h (Mountain Standard Time).

Initial training

Birds were initially trained to feed from an artificial flower (a white cardboard disc, diameter 6 cm, set on a small cork), mounted on a wooden stake (height 60 cm), placed in the ground. Birds rapidly learned to feed from a small well containing a 20% sucrose reward (a blue syringe tip, capable of holding 120 µl solution) mounted vertically in the middle of the flower. The stakes were moved 50–100 cm between successive visits. Once the bird had approached and fed from this flower on a number of occasions (around 10 visits), the experiment began. This initial training usually took 1–2 h. When a bird was not being trained or tested, its feeder was returned.

Experimental training

Two different trial types were used in the experiment: short/medium (S–M) and medium/tall (M–T). All 16 birds

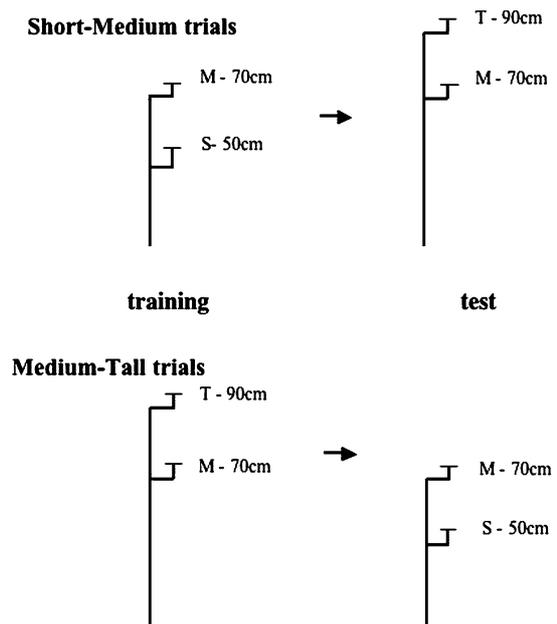


Fig. 1 A schematic diagram of the arrangement of flowers in the two types of trial (S–M and M–T). S = short, M = medium, T = tall

experienced both trial types. The training phase of both involved the presentation of two identical flowers mounted on a stake, with one flower 20 cm directly above the other. A short length (5 cm) of clear plastic tubing was used to attach the flowers to the central column of the stake. The centre of a flower was about 5 cm from the stake itself (see Fig. 1). The flowers were the same size and shape as those used in the initial training. The colour patterns on the flowers were trial-unique and composed of only two colours (yellow, green, orange, blue, white, pink, red and purple). Because of limited flower patterns some patterns were used for more than one subject, but care was taken to balance multiple uses across trial types.

In both S–M and M–T trial types one flower (the M-flower) contained a sucrose reward (120 µl, 30% sucrose) while the other (either the S- or the T-flower) contained the same quantity of water, which the birds prefer to avoid. In the S–M trials, the sucrose-containing M-flower was mounted at 70 cm while the water-containing S-flower was mounted at 50 cm. In the M–T trials, the water-containing T-flower was mounted on the stake at 90 cm with the sucrose-containing M-flower at 70 cm (Fig. 1).

At the start of a day's experimentation the bird's feeder was taken down and a stake with two flowers presented. After each foraging bout the stake was moved about 25 cm and the emptied sucrose well was refilled. We considered that a bird had completed a foraging bout at the stake when it flew away, having probed at either or both of the flowers (a visit). The criterion level for task acquisition was three consecutive bouts in each of which the first visit was to the sucrose-containing M-flower at 70 cm. An additional requirement was that the bird must have visited the water-filled flower at least once during the training. The time and sequence of visits to flowers in each foraging bout were recorded.

Test phase

In the test phase of a trial, a bird was presented with a stake with two empty flowers and we recorded which of these flowers was visited first by the bird. Following S–M training (flowers at 50 and 70 cm), birds were presented with flowers at heights of 90 and 70 cm. Following M–T training (flowers at 70 and 90 cm), birds were presented with flowers at 70 and 50 cm (see Fig. 1). Once the training and test phase for the first trial type was complete, the bird began training for the second trial type.

Sixteen birds each completed two trials (one of each type, separate training and test phase for each), with the order of presentation of S–M and M–T trials drawn from a random schedule.

Results

Our subjects were tested under two conditions: trained with S–M and tested with M–T vs. trained with M–T and tested with S–M. If they remember the rewarded flower in terms of its absolute height then we would expect them to choose the M flower under both test conditions because it is at the same absolute height as the rewarded flower during training. If, however, subjects remember the rewarded flower in terms of its relative height in comparison with the non-rewarded flower, then we would expect them to transpose the relative relationship to the test conditions. Specifically, transposition should cause birds under the S–M training condition to choose the tallest flower during the test, whereas under the M–T training conditions they should choose the shortest flower during the test.

To assess the competing absolute vs. relative hypotheses the data are best visualized in terms of the two choices made by each subject (Table 1). Subjects who remembered the rewarded flowers in terms of their absolute heights should appear in the lower left cell of Table 1. No subjects exhibited in this pattern. Subjects who remembered the rewarded flowers in terms of relative heights should appear in the upper right cell of Table 1. Indeed, seven subjects exhibited this pattern. That is, they chose the tallest test flower after S–M training and the shortest test flower after M–T training. A McNemar test for significance of changes (Sokal and Rohlf 1995) indicates that the birds made significantly different choices following the two training conditions ($p < 0.003$). For this data set with a relatively small sample size, Sokal and Rohlf (1995) recommend a binomial version of the test and this produces a similar result ($p < 0.02$). Thus, the data indicate that recall of the rewarded flower seems to be based upon transposition of relative height. There is absolutely no evidence for remembrance of absolute height in this experiment.

In addition to the seven subjects that transposed height in both tests, the remaining subjects transposed during only one set of tests (Table 1). For example, six subjects selected the tallest flower following both sets of training. However, it is difficult to determine whether these subjects

Table 1 Choices to the shortest or tallest flower in the M–T choice test as a function of the choice made in the S–M test

| Choice in S–M test (M–T training) | Choice in M–T test (S–M training) | | Total |
|--------------------------------------|-----------------------------------|---------|-------|
| | Shortest | Tallest | |
| Shortest | 3 | 7 | 10 |
| Tallest | 0 | 6 | 6 |
| Total | 3 | 13 | 16 |

exhibited transposition under S–M training but not under M–T training, or whether they merely preferred visiting the tallest flowers. We examined this possibility in two ways. Firstly, we looked at the choice made by each bird on its very first visit to a pair of flowers during Experimental training and whether they were more likely to visit the taller than the shorter flower. They were not: of these six birds, three visited the taller flower and three of the birds visited the shorter flower (these data are in accordance with those from all the birds, as eight birds visited the taller flower and eight the shorter flower on their very first visit). There was no evidence, then, for an initial height preference. However, we also looked at the ease with which the birds learned which was the rewarded flower in each of the trial types. The birds required significantly more training trials to reach criterion in the M–T trials than they did in the S–M trials (two-tailed paired t -test: $t = 3.10$, $p = 0.007$, d.f. = 15; Fig. 2). Thus, when birds quickly learned the reward flower, they showed the strongest evidence for transposition (13 of 16 in Table 1). When birds were slower in learning the reward flower, they showed weaker evidence of transposition (10 of 16 in Table 1). It would appear, then, that a height preference may have developed during training, and that preference may have interfered with both task acquisition and transposition.

The period between a bird's last visit of the training phase and his return to the flowers in the test (the "return interval") was variable and determined solely by the birds. There was no difference between the trial types in the return interval (two-tailed, paired t -test: $t = 0.76$, $p = 0.458$, d.f. = 15; range 8–35 min). As the time taken to return did

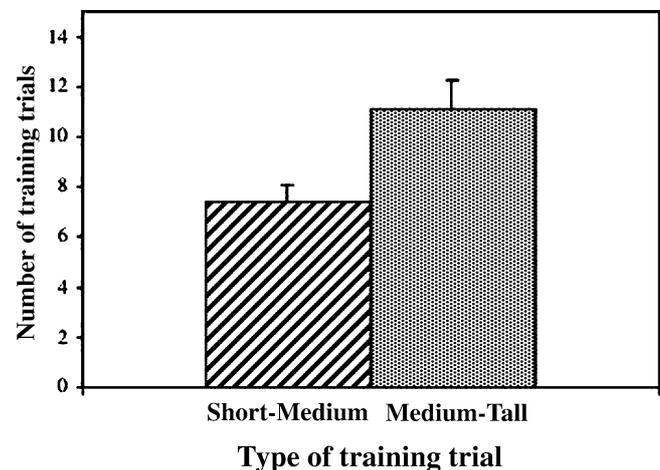


Fig. 2 Mean number of training trials (\pm S.E.) before reaching criterion in both trial types (S–M and M–T)

not differ for the two trial types, it does not appear that this would explain the apparent differences between them in task acquisition or tendency towards transposition.

Discussion

The hummingbirds in this study were trained to feed from a flower at 70 cm that was coupled with an alternative unrewarded flower at either 50 cm (S–M trials) or 90 cm (M–T trials). The birds appeared to have learned the spatial relationship between the flowers visited in training in that they transposed that relationship in the test phase, rather than visiting the test flower at the same absolute height as the rewarded training flower. Specifically, all birds appeared to transpose during at least one of the two tests, seven birds transposed during both tests, and none of the birds showed preference for absolute height in both tests. However, although all the evidence is in favour of transposition, we cannot rule out some influence of a developed preference for tall flowers.

One possible explanation for these results is that six of the birds simply preferred to visit taller flowers under any circumstances. This would be consistent with reports that rufous hummingbirds prefer to feed from feeders at the tallest positions (Blem et al. 1997, also see Henderson et al. 2001). Blem et al. (1997) interpreted this preference as a predation avoidance strategy even though predation is a rare event for rufous hummingbirds. Alternatively, it is possible that taller flowers are preferred because they are more conspicuous to the birds as they fly in from nearby treetop perches. We do not have the data to distinguish between these two possibilities but our data show that the birds did not have a conspicuous height preference at the beginning of the experiment. Such a preference may have developed as training progressed as it required more trials to reach the set criterion when the rewarded flower was the lower of the two than when it was the higher of the two (birds were required to visit the rewarded flower first on three consecutive training trials).

A height preference alone, however, cannot explain our hummingbird data. Most importantly, seven birds transposed in both directions. An additional three birds transposed downward following M–T training. If a height preference was highly important in this experiment, then we would not expect that 10 of 16 birds would select the shortest flower following M–T training.

In previous transposition experiments it has often been the case that the harder it is for the animal to learn the relationship between the training stimuli, the more likely they are to be able to transpose it to a test situation (Hebert and Krantz 1965; Thompson 1955; Wiegmann et al. 2000). The hummingbirds in this experiment exhibited the opposite pattern: subjects reached criterion more easily during S–M training and they seemed to transpose more readily. Again, we cannot completely exclude some influence of a developed preference for taller flowers, but there is certainly no evidence for an association between difficulty in learning the task and ease of transposition.

In comparison with Wiegmann et al.'s bumble bees (compare 23/32 hummingbird spatial transpositions with 13/16 bumble bee spatial transpositions), the relational ability of these hummingbirds appears poor. Like our hummingbirds, however, the bumble bees seem to have had a height preference that took some training to overcome: the bumble bees that eventually transposed the learned spatial relationship (8/24 did not reach the test) made as many as 22 visits to the taller flower in training before reaching the set criterion of five consecutive visits to the shorter flower, whereas the greatest number of errors made during training by any of our birds was eight. Perhaps if we had set a higher criterion than three consecutive visits, we would have seen stronger transposition in both our trial types. On the other hand, our birds were faced with flowers that differed only in their height unlike the bees, which had to fly 8 cm horizontally between flowers. Perhaps this difference made the initial training easier for our birds by making the height aspect of the spatial relationship more obvious and if difficulty of training is positively correlated with likelihood of transposition, then we may have, counterintuitively, decreased the probability that the birds would learn the spatial relationship between the flowers. It does seem from both studies, that a height preference may be a general phenomenon and future experiments should be designed to take this into account.

What does seem unlikely from these data is that the birds learned the exact height of the rewarded flower, as they did not choose the flower at 70 cm in the tests better than at chance in either of the trial types and not one of the birds chose the 70 cm flower in both trial types. This outcome, then, is consistent with data from experiments in which birds tested on horizontal arrays of flowers learned which were the rewarded flowers relative to each other, as long as they were separated by 40 cm or less (Healy and Hurly 1998). As rufous hummingbirds can remember flower heights when the flowers are 70 cm apart (Henderson et al. 2001) but not when the flowers are 20 cm apart, this suggests that they may encode information in the *z*-dimension (height) in a way that is quantitatively similar to the way they encode information in the horizontal plane (*x*–*y* dimensions).

A final unlikely explanation is that the data were due to an experimental artefact. Reese (1968) suggested that duplicate stimuli should be used in transposition tests to guard against the possibility that subjects might respond to features intrinsic to the objects used previously. In this experiment, the same flowers were used for training and testing within a trial. We think it unlikely that the birds learned subtle visual details of each flower for two reasons. Firstly, although new flowers were not used in the test phase there was no systematic bias as to which position the two flowers used in the training phase were placed in the test phase. Secondly, rufous hummingbirds have been shown in several experiments to ignore visual cues provided by the flowers when repeatedly revisiting a rewarded location (Healy and Hurly 1995). In this experiment, strong evidence for transposition cannot be explained by the birds using small visual differences between the flowers used.

There is considerable evidence that animals use relational rules when making choices between stimuli both in the primary sensory modalities as well as in the horizontal plane in a spatial context (e.g. Anderson et al. 2004; MacDonald et al. 2004). There is, however, rather little evidence showing that animals can transpose z -dimensional relationships from one situation to another. Both animals used thus far (bumble bees and hummingbirds) fly and therefore use z -dimensional information constantly. It might be interesting for future experiments to examine use of such information in terrestrial and arboreal animals to determine whether familiarity with particular kinds of information is related to the flexibility or ease with which it can be used. Such an ecological rationale has been used in the context of behaviours such as food storing and spatial memory but also in explanations for the use of spatial information in a more abstract context, e.g. the ability of Clark's nutcrackers, a food-storing species, to find hidden food halfway between two landmarks (see also Jones and Kamil 2001; Kamil and Jones 1997, 2000). The ability of our hummingbirds to transpose a spatial relationship would be consistent with such an ecological explanation, as would the difference between the ease with which they learned and used the rule that the taller flower was rewarded versus the rule that the shorter flower was rewarded. On the other hand, as there is increasing evidence that a range of species are able to learn abstract spatial relationships, such abilities may be much more general (Jones et al. 2002; Sovrano et al. 2002), or even correlated with developmental stage (see, for example, MacDonald et al. 2004). We require more comparative data to determine which of these possibilities is the better explanation.

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