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Preference for spatial cues in a non-storing songbird species

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Abstract Male mammals typically outperform their conspecific females on spatial tasks. A sex difference in cues used to solve the task could underlie this performance difference as spatial ability is reliant on appropriate cue use. Although comparative studies of memory in food-storing and non-storing birds have examined species differences in cue preference, few studies have investigated differences in cue use within a species. In this study, we used a one-trial associative food-finding task to test for sex differences in cue use in the great tit, *Parus major*. Birds were trained to locate a food reward hidden in a well covered by a coloured cloth. To determine whether the colour of the cloth or the location of the well was learned during training, the birds were presented with three wells in the test phase: one in the original location, but covered by a cloth of a novel colour, a second in a new location covered with the original cloth and a third in a new location covered by a differently coloured cloth. Both sexes preferentially visited the well in the training location rather than either alternative. As great tits prefer colour cues over spatial cues in one-trial associative conditioning tasks, cue preference appears to be related to the task type rather than being species dependent.

Keywords Cue preference · Food-storing · Great tit · Sex differences · Spatial memory

Introduction

Food-storing birds appear to rely more heavily on spatial cues (e.g. the spatial arrangement of multiple landmarks) than colour and/or pattern cues (of individual landmarks)

to locate food whereas non-storing species, tested in the same experiments, prefer spatial and colour cues equally (e.g. Brodbeck 1994; Clayton and Krebs 1994; Brodbeck and Shettleworth 1995; Hampton and Shettleworth 1996). This has been interpreted as being correlated with the apparent increase in demand for spatial information processing required for successful cache retrieval, a demand not faced by the non-storing species. However, variation in cue preference has also been observed within non-storing species, both in mammals and birds. In both groups, males prefer to use spatial cues while females prefer to use colour/pattern cues (humans, *Homo sapiens*: Halpern 1991; rats, *Rattus norvegicus*: Williams and Meck 1991; domestic chicks, *Gallus domesticus*: Vallortigara 1996; shiny cowbirds, *Molothrus bonariensis*: Astié et al. 1998; fish, *Xenotoca eiseni*: Sovrano et al. 2003). The preference in male mammals for spatial cues correlates with their superior performance over conspecific females in spatial tasks and with variation in hippocampal volume (the brain area thought to be heavily involved in processing of spatial information); males have larger hippocampal volumes than do females (Jacobs et al. 1990; Raz et al. 1997; Kavaliers et al. 1998; Perrot-Sinal et al. 1998; Sandstrom et al. 1998).

The relationship between demand for spatial information processing, hippocampal volume and cue preference in birds is much less clear. For example, female shiny cowbirds, which have a larger relative hippocampal volume than do male conspecifics (Reboreda et al. 1996), were no better than males at locating food provided in a specific location, but did retrieve food faster than males when food was associated with colour/pattern cues (Astié et al. 1998). A similar result has been found in female domestic chicks (Vallortigara 1996; Tommasi and Vallortigara 2004). In this study, we chose to examine the cue preferences of female and male great tits, *Parus major*, a species which, when tested by Clayton and Krebs (1994), had no preference for spatial over colour/pattern cues. One possible explanation for their results was that the individuals tested were both males and females. If males and females differ in cue preference, the average preference for the species is likely to appear to be no different. The hypothesis, then, is that there

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is a sex difference in cue preference and, in this experiment, we tested the prediction that females prefer to use colour rather than spatial cues and the males prefer to use spatial cues.

Methods

Subjects

The subjects were six female and six male great tits (all wild-caught in deciduous woodland in Edinburgh, Midlothian). Sex was determined by the width of the breast stripe, and later confirmed by testosterone radioimmunoassay. Birds were housed individually in wire-mesh cages (77 cm long \times 44 cm wide \times 44 cm high) and were in full auditory and visual contact with one another. Birds were fed daily with ad libitum water and an insectivorous bird food mixture (Orlux, Sunring Cooke, Greasbrough, Rotherham, UK), supplemented by peanuts, sunflower seeds and wax moth larvae. They were maintained on a 13.5:10.5 h light/dark cycle (0630 hours lights on, 2000 hours lights off) and under a temperature range of 16–19°C. For both training and experiments, birds were deprived of food at 0800 hours each morning, tested from 1000 hours, and provided with fresh food when their session was complete. Birds tested later in the day were provided with nuts through the day.

Apparatus

The experimental tray consisted of a Perspex board, 29 cm \times 22 cm, containing 48 circular wells (1 cm diameter, 1 cm deep) arranged in an 8 \times 6 array. The wells were surrounded by a ring of Velcro for attaching square pieces of felt cloth (2.5 cm \times 2.5 cm).

Training

To start with, the experimental tray was placed into the centre of a bird's home cage with half the wells containing reward (a small piece of pine nut) to familiarise the birds with feeding from the tray. Gradually, flaps were introduced to cover the rewarded wells. Once birds were lifting the flaps to find the food the number of covered, rewarded wells was reduced to one.

Trials

For each trial, once the bird had displaced the cloth flap and removed the food, the tray was removed for 3 min. It was then returned to the bird's cage with the reward in the same location and covered by the same coloured cloth. This procedure was repeated until the bird had received ten presentations of the tray. On the 11th presentation of the tray, the test phase, a further two wells were covered. The pre-

viously rewarded well was covered with a novel-coloured cloth (correct location) while the coloured cloth from sample phase covered a different well (correct colour). Both of these wells contained reward. A third, different, novel-coloured cloth covered an empty well not used before (the distractor). The bird was allowed to lift one flap only. The covered wells were always positioned at the same distance from one another (there was always at least one well in between covered wells) in different quadrants to control for the effect of well proximity, and the location of the rewarded well was rotated after each trial. Each bird received ten trials with unique cloth colour and location of the rewarded well for each trial. Birds received one trial a day for 10 days.

Results

Test phase response distributions were analysed using the G -test (Sokal and Rohlf 1981). In the test phase, both sexes chose the stimulus in the correct location more often than either alternative. The overall distribution of choices differed significantly from random ($G_{(2)}=15.20$, $P<0.001$) and the distributions did not differ between the sexes ($G_{(2)}=1.94$, $P>0.1$). To test for cue preference, the distribution of rewarded responses was analysed (i.e. responses to the distractor were omitted). The overall distribution of correct choices, consistent with one of the sample attributes, differed significantly from uniform ($G_{(1)}=13.82$, $P<0.001$) and there was no difference in distribution between the sexes ($G_{(1)}=1.28$, $P>0.1$). Both males and females chose the well in the correct location significantly more often than they chose the well covered by the correctly coloured flap (Fig. 1).

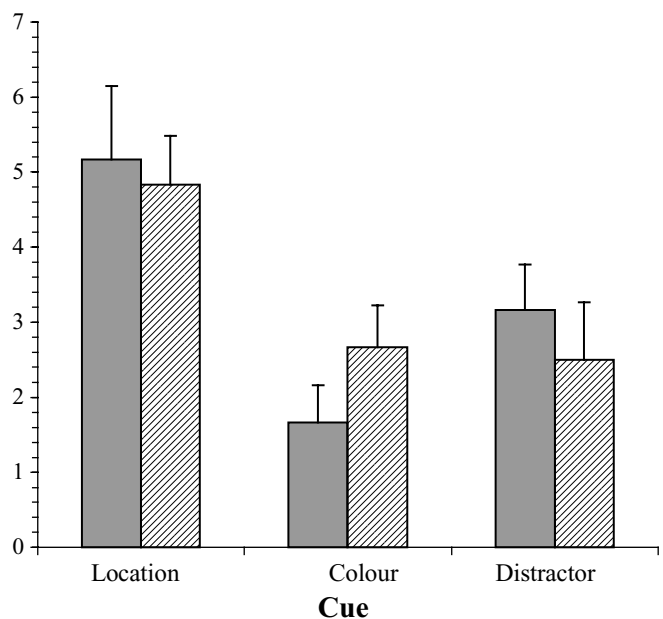


Fig. 1 Mean (\pm SE) number of times a cue was used by great tits, *Parus major*, of each sex across ten trials. Males ($n=6$; shaded bars) and females ($n=6$; white bars). The dashed line at 3.3 indicates random choice

Discussion

Male and female great tits did not differ in their use of cues in the food-finding task: both preferred the spatial to the visual cue. Our results contrast with the findings from rodents and birds where females either have no preference or prefer to use visual cues (e.g. Williams et al. 1990; Astié et al. 1998). They are also not consistent with Clayton and Krebs (1994) results where great tits did not prefer location cues. While that result may have been due to both males and females being tested (relevant data not provided), we suggest that there are at least two alternative explanations.

The first possibility comes from the finding that variation in testosterone (T) appears to underlie the sex difference in mammals: females with enhanced levels of T both prefer to use location cues and perform as well as males on spatial tasks (Roof and Havens 1992). Additionally, for at least the mammalian species tested, the sex difference in performance is seen only in the breeding season, when T levels are relatively high (Galea et al. 1994; Galea and McEwen 1999). As the birds in the current study had been kept under the same light cycle for several months it is possible that they were photorefractory. Continued exposure (7–10 weeks; Bentley et al. 1998; Meddle et al. 1999) to long days eventually leads to a centrally mediated desensitisation of the hypothalamo–pituitary–gonadal axis to the stimulating effects of long days and birds become photorefractory (Nicholls et al. 1988; Juss 1993). As our birds were maintained on a prolonged long daylength it is unlikely that the males' T levels were high. Although increasing daylength is usually correlated with increasing levels of T, prolonged exposure to long daylength results in T falling to basal levels (Nicholls et al. 1988; Juss 1993; Meddle et al. 1999). On this daylength, and if T does underlie a sex difference in cue preference in birds, we should have seen no cue preference at all because T levels should not have differed between the sexes. T levels alone, then, seem an unlikely explanation for both males and females preferring the spatial cue to the same degree.

However, we think there is an even more plausible explanation, which is that the female preference for spatial cues was a result of our testing procedure. Unlike the tests more typically used to compare cue use within or between species, we gave our birds multiple experiences of the rewarded location and its cloth flap before testing for cue preference. A switch from one cue type to another with increasing experience (i.e. perhaps females began by preferring to use the colour cues, but switched preference as training proceeded) has been little explored to our knowledge. It is, however, a familiar observation that once animals have learned the location of a food source, their return to that location is very accurate even when the visual cues immediately surrounding the reward are absent. For example, pet owners need not have produced the food bowl for the pet to wait in the place food is usually delivered. Consistent with this view is that pigeons' cue preferences can be experimentally manipulated by changing the salience or value of the cues (Kelly et al. 1998). However, it is possible that the preference in females for the spatial cue was sim-

ply an artefact of the testing procedure. It is not clear how similar our testing scenario might be to the natural foraging conditions for a great tit. It is possible that there may be sex differences in cue preference after a single experience. We do not claim that there is no sex difference in cue preference, rather that its demonstration may be dependent on the experimental design.

It seems that the preference we observed in our experiment for spatial cues following repeated visits to the rewarded location is a sensible strategy for both sexes, due to the likelihood that local visual cues are more vulnerable to change over time (Saucier et al. 2002). It is possible that cue preferences in other species also changes with increasing experience, but it has been typical to test for such preferences after only a single exposure. It also remains to be seen if the sex difference in spatial cognition, which diminishes with increased training, such that females eventually solve spatial tasks as well as do males, is due to females switching from visual to spatial cues.

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