CrossMark

ORIGINAL PAPER

Multiple cue use and integration in pigeons (*Columba livia*)

Eric L. G. Legge[1] · Christopher R. Madan[1,2] · Marcia L. Spetch[1] ·
Elliot A. Ludvig[3]

Abstract Encoding multiple cues can improve the accuracy and reliability of navigation and goal localization. Problems may arise, however, if one cue is displaced and provides information which conflicts with other cues. Here we investigated how pigeons cope with cue conflict by training them to locate a goal relative to two landmarks and then varying the amount of conflict between the landmarks. When the amount of conflict was small, pigeons tended to integrate both cues in their search patterns. When the amount of conflict was large, however, pigeons used information from both cues independently. This context-dependent strategy for resolving spatial cue conflict agrees with Bayes optimal calculations for using information from multiple sources.

Keywords Cue integration · Spatial navigation · Bayesian · Pigeons · Hierarchical · Win-shift · Spatial cognition · Cue-conflict · Computational modeling

Introduction

Animals use many cues for navigation and goal localization. These cues can include auditory (e.g., Grohn et al. 2005; Rossier et al. 2000), olfactory (e.g., Steck et al. 2009; Wallace et al. 2002), and visual cues (e.g., Cheng et al. 2009; Spetch and Kelly 2006), as well as proprioceptive cues such as optic flow and stride length (e.g., Cheng 2005; Kearns et al. 2002). When trying to locate a specific location such as a hidden food cache, animals typically encode multiple cues that provide redundant information (e.g., Balda and Turek 1984; Brodbeck 1994; Goto et al. 2004; Lea and Wills 2008; Spetch and Edwards 1988). This redundancy is likely adaptive, as using multiple cues for goal localization increases search accuracy (Cartwright and Collett 1983; Kamil and Cheng 2001; Kamil et al. 2001) and allows a goal to be located even if one cue is missing (Spetch and Edwards 1988).

Though normally adaptive, encoding multiple redundant cues can be problematic if a cue becomes displaced, e.g., by the wind. In these situations, the displaced cue will provide information that conflicts with the information provided by other nearby cues (known as cue conflict). This conflict can lead animals to search in an incorrect location or become lost, thus wasting time, energy, and possibly increasing the risk of predation. Recent studies indicate that animals across a wide range of taxonomic classes (e.g., insects, Legge et al. 2014; mammals, Chalfoun and Martin 2010; birds, Legge et al. 2009) have developed complex methods for dealing with such spatial cue conflict.

One method for coping with cue conflict used by animals is a *hierarchical* strategy whereby animals only use the cue at the top of a hierarchy for localizing a goal (also known as a winner-take-all or take-the-best strategy; Lea et al. 2009; Gigerenzer and Brighton 2009; Legge et al. 2009; Spetch and Edwards 1988). Though this strategy may be useful in some situations due to its simplicity, relying on a single cue may be problematic because animals could discard relevant information from other nearby

✉ Marcia L. Spetch
mspetch@ualberta.ca

[1] Department of Psychology, University of Alberta, Edmonton, AB, Canada

[2] Department of Psychology, Boston College, Chestnut Hill, MA, USA

[3] Department of Psychology, University of Warwick, Coventry, UK

sources. Additionally, a strictly hierarchical strategy would cause an animal to search in an incorrect location if the cue at the top of the hierarchy was displaced.

Another strategy sometimes used by animals when searching for a goal is an *independent-source* strategy (Gaffan and Davies 1981; Hodges 1985; Hosoi et al. 1995). This strategy resembles a simple win-stay/lose-shift strategy, whereby animals alternate between the potential goal locations indicated by each cue, treating each cue as an independent source of information about the goal location. Thus, as with a strict hierarchical strategy, animals using this independent-source strategy would predominately search relative to a preferred cue. Unlike pure hierarchical strategies, however, if the most preferred cue did not lead to the goal, the animal would shift to using another encoded cue to search. Though an independent-source strategy could be more successful than a pure hierarchical strategy, it may also be costly in that animals may spend more time searching for a goal across a much wider area.

A third strategy for coping with cue conflict is to integrate the information provided by multiple cues to select a single location to search. This *integration* strategy allows animals to minimize discrepant information provided by a displaced cue so that the animal will search close enough to the goal for success. In a number of other sensorimotor domains, such integration occurs in a Bayesian manner, with information from different cues optimally integrated based on their reliabilities (e.g., Alais and Burr 2004; Ernst and Banks 2002; Körding and Wolpert 2004). Following from these observations, it has recently been suggested that animals may also combine information for spatial navigation through Bayesian integration (Cheng et al. 2007; Friedman et al. 2012; Legge 2013).

A further possibility is that animals will change their method of coping with cue conflict depending on the magnitude of that conflict (Kording et al. 2007; Pfuhl et al. 2011). If animals are optimally using spatial cue information, then as cue conflict increases, animals should switch from an integrative strategy which predicts a single goal location, to an independent-source strategy where cues predict multiple goal locations, once that cue conflict is sufficiently large (Pfuhl et al. 2011). In human multisensory perception, people do indeed shift from integrating cues to treating them independently as their degree of conflict changes (Kording et al. 2007). This experiment tests the prediction that pigeons (*Columba livia*) should adjust their search strategy according to the amount of cue conflict they face in a spatial search task. Specifically, pigeons were trained to find a hidden goal relative to two landmarks; these landmarks were then shifted to place them in varying degrees of conflict. In these shift tests, the goal was removed and pigeons' search attempts were recorded.

To better identify the search strategy employed by the pigeons, computational models corresponding to each of the three strategies outlined above (hierarchical, independent-source, and integrative) were fit to the pigeons' search behavior on each shift test. Each model was designed to quantify a specific hypothesis regarding how animals would cope with cue conflict, and each predicted different goal location(s). Specifically, the hierarchical model predicted pigeons would search relative to only the preferred cue, the independent-source model predicted pigeons would search relative to each cue individually within a trial in a win-stay/lose-shift fashion, and the integration model predicted animals would search at an intermediate location between the goal locations predicted by both cues.

Methods

Subjects

Subjects were eight adult pigeons (*Columba livia*) with varied previous experience in operant box and open-field tasks, but with no prior experience with landmarks similar to those used in this experiment. Subjects were maintained between 85 and 90 % of their free-feeding weights by pigeon pellets obtained during experimental sessions and supplemental feedings in their home cages. All subjects were housed in large individual cages under a 12:12 h light–dark cycle (light onset at 06:00). Grit and water were available ad libitum in their home cages.

Stimuli and apparatus

The experiment took place in a 2.05 m (width) × 3.20 m (depth) × 2.89 m (height) testing room (see Fig. 1). The room contained a large square plywood floor (2 m²) with a raised edge that was filled with aspen chips (see Fig. 1b). This floor also contained a hidden grid under the aspenchips for easy positioning of the landmarks. Two visually distinct landmarks were used to allow pigeons to pinpoint food located in a hidden goal container (0.03-m diameter bottle cap). One landmark (the *blue cue*) was a very large rectangle (0.92 m wide, 0.04 m deep, 1.56 m high) and consisted of dark blue fabric stapled tightly to a wooden frame. The second landmark (the *red cue*) was a small red cylinder (0.06 m diameter, 0.26 m high). A vertical white stripe, 0.05 m (width) × 0.26 m (height), was painted on the red cue as a directional feature.

Pigeons started each trial in an opaque enclosed start box (0.49 m wide, 0.39 m deep, 0.40 m high) that was built into the door to the testing room and contained a vertical sliding panel, which the experimenter opened to allow the pigeon into the room. After pigeons entered the
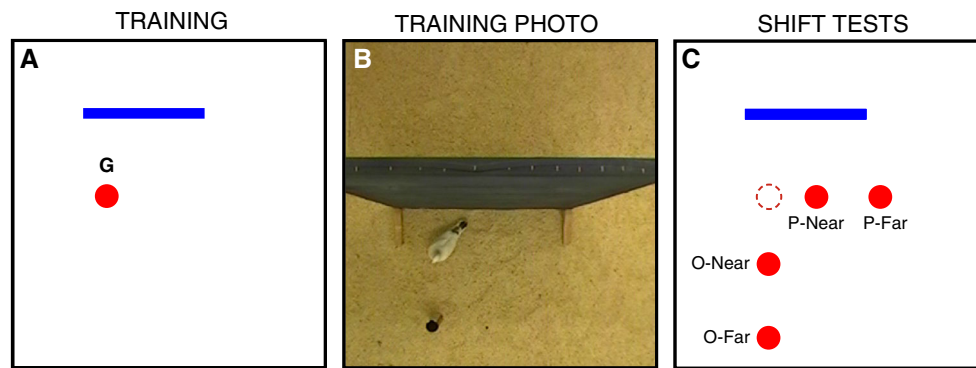
Fig. 1 Illustrations and photographs depicting landmark locations on training and testing trials. **a** A *diagram* depicting the position of the blue and red cues relative to each other in training. Note that while the distances by which the red and blue cues are separated are to scale relative to the size of the search space (figure panel), the width of the blue cue, and the diameter of the red cue have been expanded for illustrative purposes. In training, the red cue was located 21 cm left of the blue cue, along the parallel axis, and 49 cm closer to the entrance to the room, along the orthogonal axis of the blue cue. The goal (diameter of 3 cm) was located 22 cm away from the red cue along the orthogonal axis, positioned between the blue and red cues as indicated by the letter "*G*" in the figure. **b** An overhead image of a pigeon relative to both cues during training. **c** A *scale diagram* depicting the position of the both cues relative to each other on shift tests. The *dashed, unfilled circle* depicts the location of the red cue during training. For each test, the red cue was shifted by the following distance and direction relative to the blue cue from its training position: Orthogonal-Near: 47 cm away along the orthogonal axis; Orthogonal-Far: 98 cm away along the orthogonal axis, Parallel-Near: 35 cm away along the parallel axis; Parallel-Far: 83 cm away along the parallel axis. On all training and testing trials, the position of the two cues was varied within the room to prevent pigeons from using room features to help localize the goal as described in the main text (color figure online)

testing room, the sliding panel was closed until the trial ended. The start box contained a food well that was baited while the pigeon was in the testing room. When the trial ended, the door to the start box opened and the pigeon entered to eat from the food well. All test trials were video recorded and digitized before being scored.

Procedure

Training

The position of the landmark array and its corresponding goal location was translated in both directions within the aspen-chip-covered search space across trials, always keeping the orientation within the room constant. This prevented subjects from using stable environmental cues (e.g., room geometry, distance from walls, etc.) to localize the goal container. During training, subjects received 10 trials per day.

Subjects were initially trained to find a fully visible goal in relation to the two landmarks. After subjects reliably ate the food from the goal container, the container was gradually buried under the aspen-chip bedding across training trials until it was completely covered. Subjects learned to find the covered goal by sweeping the bedding with their beaks. On all training trials where the goal was completely covered by bedding, subjects were given a maximum of 2 min to find the goal. If subjects did not locate the goal within 2 min, the room lights were turned off and the start box door was opened to allow subjects to return (the start box was baited with a small amount of food and dimly illuminated to entice pigeons to return). Subjects were required to find the goal on at least 80 % of trials across three consecutive days to progress to the next phase.

The next phase of training adapted the birds to receiving partial reinforcement. Food was available in the goal on 8/10 trials per day for 2 days and then on 6/10 trials per day for the remainder of this phase. During unreinforced trials, the goal container was removed and subjects were given a maximum of 2 min or until 30 search attempts were observed. When either of these limits was reached, the room lights were turned off and the start box door was opened to allow pigeons to return to the baited start box. Trial order was pseudo-randomized each day with the restriction that the first trial was always reinforced and subjects could not receive more than two consecutive unreinforced trials. To progress to testing, subjects had to complete at least 5 days of this training and had to successfully locate the hidden goal on at least 5 out of 6 reinforced trials for three consecutive days.

Testing

There were two testing phases: (a) single-cue and (b) shift. In both phases, the position of the landmark array within the search space varied as in training. Additionally, as in the final phase of training, subjects received 10 trials per day, four of which were unreinforced, and the position of unreinforced trials in the trial sequence was pseudo-randomized as described above. Of these four unreinforced

trials, two were control trials, with the same landmark arrangement as in training. The remaining two unreinforced trials each day were unique to each stage of testing (single-cue or shift testing). Subjects had a maximum of 2 min to find the goal (reinforced trials) or to search for the goal (unreinforced trials) before they could return to the start box. After 2 min elapsed, the room lights were turned off, and the start box door was opened to allow pigeons to return to the baited start box.

Single-cue Two unique test trials were presented each day, in which only one landmark cue was present. Specifically, one trial provided only the blue cue, and one trial provided only the red cue. These tests allowed an independent measure of the subjects' search accuracy and variance relative to each cue in isolation. Subjects were tested until they completed at least 10 single-cue trials for each landmark and 20 control trials before proceeding to the shift tests.

Shift Shift tests placed the two cues in conflict by moving one of the cues relative to the other cue. Relative to the blue cue, the smaller red cue was moved either parallel to the blue cue or orthogonal to it (see Fig. 1c). These relative movements were either small (near tests) or large (far tests), producing four types of shift test trials: *Orthogonal-Near*, *Orthogonal-Far*, *Parallel-Near*, and *Parallel-Far*. Figure 1c illustrates the amount and direction of shift for each test trial. The type of shift test given to a subject each day was pseudo-randomized. Test type assignment was constrained so that only one trial of a specific shift test could be given to subjects each day. Subjects were given at least 10 trials of each type of shift test and 40 control trials before completing the experiment.

Scoring

Data were scored by five research assistants who were unaware of the study's hypotheses. Prior to independently scoring data, each assistant received a minimum of 5 training sessions with an experienced rater. During these sessions, the trainee was instructed on how to score video data and she/he observed the trainer score several videos. The trainee was then monitored while scoring a new set of previously scored video files, and the scores obtained by the trainee were compared to those obtained previously to ensure scoring reliability. In all cases, scored data by the trainee closely matched the previous scores in number and location of recorded pecks, and therefore the trainee was then permitted to score new video files. Furthermore, to prevent any potential effects of across-rater variance from differentially influencing experimental conditions, research assistants were assigned to score trials across all shift tests

for a given bird. When scoring video data, a transparency was overlaid on the computer monitor and the position of the cues and of each search location (beak sweep) were marked while playing the video in slow motion. During this process, each peck was numbered sequentially. After scoring, the data from each transparency was digitized using in-house software such that clicking on each cue and search location provided it with x- and y-coordinates that were later used in the computational modeling.

To further assure inter-rater reliability, we had a final independent rater, also naive to the hypotheses of the experiments, re-score 20 % of the shift trials from the original video recordings (two trials per bird per type of shift test). We estimated that the pigeons measured at least 5–6 cm from the back of their heads to tip of their beaks and that side-to-side sweeping behavior covered approximately 10–12 cm. Based on this, we used both a strict threshold of 5 cm as well as a more lenient threshold of 10 cm for determining whether the re-scored locations matched the originally scored locations. For comparison, the smallest landmark shift was 35 cm and the largest was 98 cm. We found that 82 % of the re-scored responses were within 5 cm of the originally scored locations, and 96 % were within the 10-cm threshold.

Data analysis

To account for spatial distortions in the video recordings, all landmark positions were extracted from the recordings. In shift testing, data were truncated by removing pecks that fell outside 1.5 standard deviations (SD) from the mean peck location on the non-shifted axis for each test (e.g., for an orthogonal-shift test, pecks that fell outside of 1.5 SD on the parallel axis were removed). This data truncation was implemented separately for each subject and each shift test. Across all shift tests and birds, data truncation removed 10.6 % of pecks from subsequent analyses.

Computational models

Three models were fit to the data, representing the three key hypotheses about how pigeons would combine the conflicting cue information (see Fig. 2).

1. *Hierarchical*. The first model predicted that subjects would cope with cue conflict by using a hierarchical search strategy. This *Hierarchical* model (M_H) assumes that, when cues provide conflicting information, subjects only rely on a single, preferred cue to locate the goal. First, two sub-models were fit to the data, based on each possible hierarchical strategy, one representing preference for the large, blue cue (M_B), and the other representing preference for
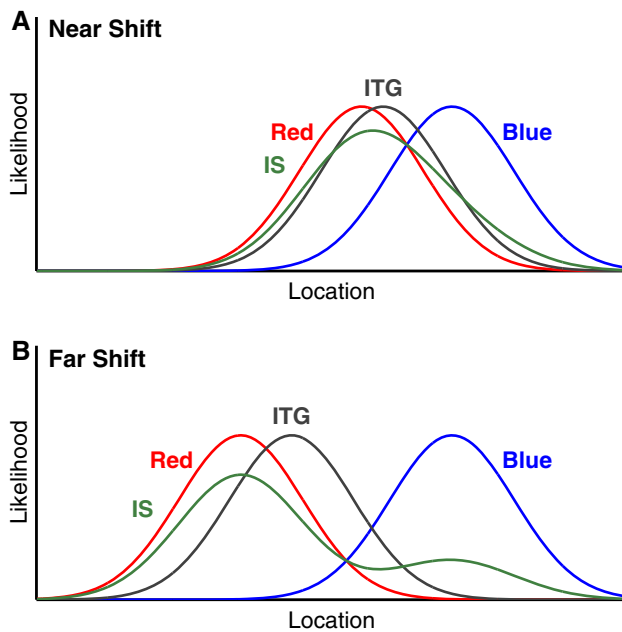
Fig. 2 Probability density function (PDF) plots for each model. *Red* and *Blue* denote the two *Hierarchical* models, based on the red or blue cue, respectively; IS denotes the *Independent-Source* model; ITG denotes the *Integration* model. Of the two *Hierarchical* models, the best-fitting model for each bird and test was used as M_H. **a** Orthogonal-Near (O-Near) tests. **b** Orthogonal-Far (O-Far) tests. PDFs shown here are based on data from bird 887 (color figure online)

the small, red cue (M_R). Of these two models, the better-fitting model for each bird and test was used as the *Hierarchical* model. Note that this model has an additional degree of freedom relative to other models, and this was taken into account in the model comparison below.

2. *Independent-Source*. The second model predicts that animals will respond to each cue individually within a trial, adopting a win-stay/lose-shift strategy. Specifically, this *Independent-Source* model (M_{IS}) predicts that subjects will search for the goal at the locations predicted by each cue individually, i.e., the same goal locations predicted by M_B and M_R above. Additionally, the *Independent-Source* model hypothesizes that the animal weights each cue according to the cue's reliability, which is measured as the inverse of the spatial variance of responding to that cue when presented alone (i.e., the variance of search locations observed when each cue is presented alone serves as an inverse indicator of the cue's functional reliability). The animal then allocates search attempts relative to each cue's predicted goal location according to this weighting. That is, if the blue cue had a weight of 0.30, and the red cue a weight of 0.70, M_{IS} predicts that the animal would allocate 30 % of its searches based exclusively on

the large, blue cue, and the remaining 70 % of its searches to the location based on the small, red cue (e.g., see Fig. 2). Thus, this model uses Bayesian inference to determine each cue's weight (Cheng et al. 2007; Friedman et al. 2012).

3. *Integration*. The third model tested whether animals would integrate information from both cues to predict a single, intermediate goal location. Specifically, the *Integration* model (M_{ITG}) assumes that animals will selectively weight each cue according to its subjective reliability to predict the goal location (Fig. 2). Unlike the *Independent* model, however, the *Integration* model predicts that animals will use the weights to determine a single predicted goal location (Cheng et al. 2007; Friedman et al. 2012).

Model comparison

For each model, the model likelihoods on the shift trials were calculated using the estimated goal locations and pooled variance from the single-cue trials. The models were then compared using the Bayesian Information Criterion (Schwarz 1978). Details of these calculations appear below.

Predicted goal locations   Each model predicted a different goal location for each shift test and each subject (see Figs. 4, 5). For simplicity of exposition, we assume that only the red cue moved during shift tests (see Fig. 1c).

For the blue-only sub-model M_B, the predicted goal location (G_B) was the mean search location during blue-only single-cue trials. For the red-only sub-model M_R, the predicted goal location (G_R) was the mean search location during the red-only single-cue trials. Of these two sub-models, the best-fitting one was used as the *Hierarchical* model M_H.

For the *Independent-Source* model M_{IS}, the two predicted goal locations corresponded to the two goal locations predicted by M_R and M_B.

The predicted goal location for the *Integration* model M_{ITG} was calculated separately for each subject. This goal location represented the weighted sum of the two landmarks, where the weights corresponded to their relative reliability (inverse variance; see Cheng et al. 2007). The reliability was estimated from the single-cue trials, separately for the *x*- and *y*-dimensions (corresponding to the parallel and orthogonal dimensions, respectively). The weights were then calculated using the following formula:

$$w_B = \frac{\sigma_R^2}{\sigma_R^2 + \sigma_B^2},\tag{1}$$

where w_B is the weight on the blue cue for a particular dimension and σ^2 is the variance in that dimension on the corresponding single-cue trial (red or blue). The weights for the red cue (w_R) were calculated from the same formula with the opposite variances.

Using these weights, the goal location G_M was calculated by multiplying the weights of each landmark by the predicted goal location for the two single-cue sub-models:

$$G_M = w_B G_B + w_R G_R. \tag{2}$$

where w_B and w_R are the weights on the two cues and G_B and G_R are the goal locations as predicted by the individual cues, based on the single-cue trials as above. The same equation was applied separately to get the x and y-coordinates of the goal location.

Variance A pooled variance estimate was calculated for each bird separately for the x- and y-dimensions:

$$\sigma_P^2 = \frac{(n_B - 1)\sigma_B^2 + (n_R - 1)\sigma_R^2}{n_B + n_R - 2}, \tag{3}$$

where n denotes the number of search attempts made by a subject in the subscripted single-cue test (blue or red).

Model Likelihoods. To get model likelihoods, first the probabilities of each response r given that model were calculated. For the *Hierarchical* and *Integration* models, these probabilities were calculated assuming a normal distribution (N) using the predicted goal location for that model (G_M) as the mean and the pooled variance estimate (σ_p^2):

$$P(r|M) = N\left(r; G_M, \sigma_p^2\right). \tag{4}$$

This calculation was repeated separately for the x and y-dimensions, and the overall response probability was the product of these two probabilities.

For the *Independent-Source* model (M_{IS}), response probabilities were separately calculated given the blue-only (M_B) and red-only (M_R) models (as per Eq. 4). Then, a weighted average of these two probabilities was calculated based on the weights (w_B and w_R) from Eq. 1 as follows:

$$P(r|M_{IS}) = w_B P(r|M_B) + w_R P(r|M_R). \tag{5}$$

The calculation was repeated separately for the x- and y-dimensions, and the overall response probability was the product of these two probabilities. Note that the *Independent-Source* model predicts an equal proportion of pecks for each predicted goal location if w for both the blue and red cues, and in both the x- and y-dimensions, was 0.5.

To determine the model likelihoods, response probabilities were log-transformed and summed giving the log-likelihood (LL) for each model, given all the responses (R):

$$LL(M|R) = \sum_{i=1}^{n} \ln P(r_i|M), \tag{6}$$

where n is the number of responses emitted by each pigeon on that shift test. After determining the LLs for a given model for each subject, the Bayesian Information Criterion (BIC) was used to compare the different models:

$$BIC = -2LL + k \ln(n), \tag{7}$$

where k is the number of parameters in the model (Raftery 1999; Schwarz 1978). This BIC value represents the relative fit of a model to subjects' search accuracy data. For model comparison, the pairwise difference in BIC values for each model was calculated by subtracting the best-fitting model's BIC from each model's BIC, resulting in a ΔBIC value for each model. Thus, the best-fitting model always had a ΔBIC of 0. By convention, a difference between two model fits of two or more ($\Delta BIC > 2$) is taken as significant evidence in favor of the better model (Burnham and Anderson 2002, 2004). Note that the *Hierarchical* model had an additional degree of freedom relative to the *Independent-Source* and *Integration* models, and this was corrected for through the BIC calculations.

For group-level model comparisons, LLs were first summed across the subjects to produce a group LL (gLL; see Stephan et al. 2009). Group BIC values were computed for the sample by substituting this gLL into Eq. 7.

Results

Single-cue tests

On the single-cue tests, cues were presented to pigeons individually to obtain an unbiased estimate of pigeons' search variance relative to each cue. This search variance was then used to determine how strongly pigeons weighted each of the two cues, as described in Eq. 1. Table 1 displays the cue weights for each bird as derived from these single cue tests for the red cue; by definition, the blue cue

Table 1 Cue weights based on Bayesian inference

Bird	Red cue	
	Orthogonal	Parallel
61	0.22	0.35
85	0.36	0.87
473	0.11	0.40
887	0.64	0.76
943	0.51	0.78
948	0.53	0.59
975	0.37	0.44
2767	0.36	0.70

weights are 1 minus the red cue weight. As shown in Fig. 3, despite variability across birds in their overall preference for the red or blue cue, all birds weighted the red cue more heavily in the parallel axis than the orthogonal axis. Conversely, all birds weighted the blue cue more heavily in the orthogonal axis than the parallel axis. This difference likely reflects the physical properties of the two cues, with the large, blue cue providing edge or boundary information and the small, red cue serving as a discrete landmark. The pattern of results is consistent with previous studies that have found differences in control by edges and discrete landmarks in birds, with distance from an edge being more important than distance along that edge (Cheng and Sherry 1992; Spetch et al. 1992).

Near-shift tests

On near-shift tests, in which the spatial information provided by the two cues conflicted by only a small amount, the birds generally searched at an intermediate location between the goal locations indicated by each cue. Figure 4 illustrates how on these near-shift tests, the *Integration* model best fits
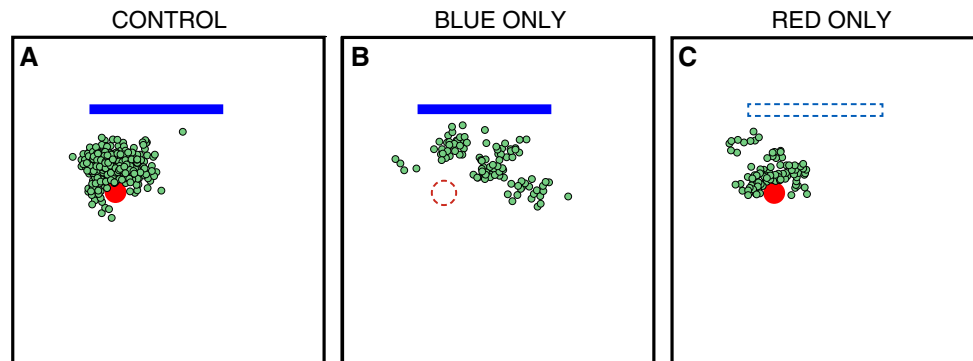

Fig. 3 Graphical representation of pigeon responses on the single cue tests with each landmark and on control trials with both cues. Responses (*green dots*) on near-shift tests plotted relative to the two cues. The *dashed, unfilled circle* and *rectangle* depicts the location of the red and blue cues, respectively, during training. Note that the width of the blue cue and the diameter of the red cue were enlarged for illustrative purposes (color figure online)
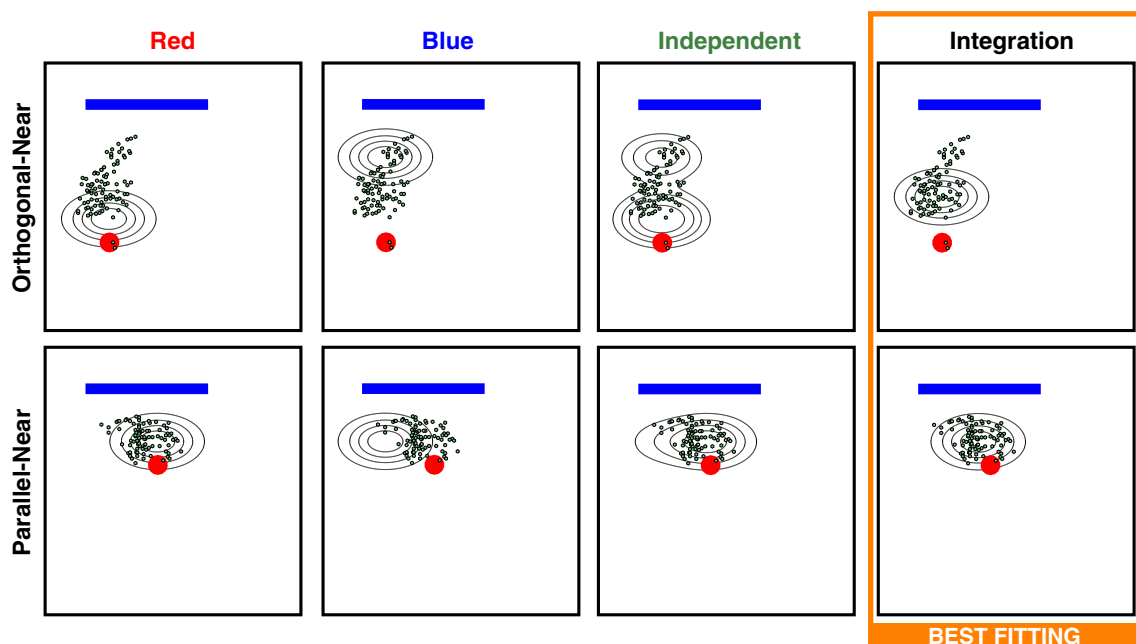

Fig. 4 Graphical representation of model fits for pigeon responses on Near-shift tests. Of the two *Hierarchical* models, the best-fitting model for each bird and test was used as M_H. Responses (*green dots*) on near-shift tests plotted relative to the two cues. Contour plots in the background denote model likelihoods. Each ring of the contour plot captures 20 % of the model's respective predicted responses. Plotted data is from bird 887. Response data are replicated in each column to highlight model predictions. Note that the width of the blue cue and the diameter of the red cue were enlarged for illustrative purposes (color figure online)

Table 2 ΔBIC values for each model and shift test on the pooled subject dataset

Model	Near shift		Far shift	
	Orthogonal	Parallel	Orthogonal	Parallel
Hierarchical	89.17	12.50	322.75	130.18
ITG	**0.00**	**0.00**	157.91	65.70
IS	43.78	16.43	**0.00**	**0.00**

Bolded values denote the best performing models. Hierarchical corresponds to the better-fitting of the two hierarchical models, based on the red or blue cue, respectively; IS denotes the independent-source model; ITG denotes the integration model

subjects' search behavior, regardless of whether the red cue was shifted parallel or orthogonal to the blue cue (see Table 2). Additionally, pigeons' preference for using an integrative strategy was fairly consistent across subjects with the *Integration* model serving as the best-fitting model for individual subjects' data on 13 out of 16 near-shift tests (Table 3). Taken together, these findings indicate that when cues were only shifted by a small distance and thus provided only a small amount of cue conflict, the pigeons' search pattern integrated the information provided by each cue.

Far-shift tests

In the far-shift tests, where the two cues were widely separated, the birds generally showed two locations of search, one appropriate to the goal location specified by each cue. As seen in Fig. 5, the *Independent-Source* model best fit subjects' search behavior on these far-shift tests, regardless of whether the red cue was parallel or orthogonal to the blue cue (see Table 2). Thus, on far-shift tests, pigeons searched relative to each cue independently and allocated the number of searches made to each location as a function of each cue's subjective reliability.

Note, however, that there was a larger degree of inter-individual variability on far-shift tests in terms of which model best fit each subjects' data. At an individual level, the *Independent-Source* model best fit subjects' data in only 7 out of 16 cases, which is the same number of cases in which the *Integration* model was the best fit to the data (Table 3).

Hierarchical models

When pooled-subject analyses were conducted on pigeons' search distributions, the *Hierarchical* model performed poorly on all tests (see Table 2). With the exception of the Parallel-Near test, the *Hierarchical* model was the worst model fit for every shift test. Thus, while the *Hierarchical* model represented the simplest strategy pigeons could use to search for a goal when cues provided conflicting information,

Table 3 ΔBIC values for each model and shift test for each individual bird

Bird	Model	Near shift		Far shift	
		Orthogonal	Parallel	Orthogonal	Parallel
61	Hierarchical	24.79	**0.00**	33.68	191.86
	ITG	**0.00**	20.45	**0.00**	24.08
	IS	23.97	25.05	6.65	**0.00**
85	Hierarchical	175.66	9.18	403.46	60.96
	ITG	**0.00**	**0.00**	**0.00**	302.06
	IS	151.51	21.64	8.05	**0.00**
473	Hierarchical	23.52	7.27	23.14	**0.00**
	ITG	**0.00**	**0.00**	10.16	22.04
	IS	**0.07**	4.31	**0.00**	22.10
887	Hierarchical	256.25	22.88	1863.10	514.34
	ITG	**0.00**	**0.00**	1176.80	232.11
	IS	16.64	32.07	**0.00**	**0.00**
943	Hierarchical	42.02	26.49	135.49	25.48
	ITG	**0.00**	**0.00**	**0.00**	**0.00**
	IS	27.79	18.32	46.02	17.82
948	Hierarchical	91.78	21.72	112.07	105.85
	ITG	**0.00**	**0.00**	169.07	14.00
	IS	64.58	8.39	**0.00**	**0.00**
975	Hierarchical	28.55	**0.32**	153.36	57.42
	ITG	**0.00**	**0.00**	**0.00**	**0.00**
	IS	23.96	20.46	66.23	8.50
2767	Hierarchical	70.81	32.60	**0.00**	154.19
	ITG	**0.00**	**0.00**	49.57	**0.00**
	IS	41.75	21.68	15.34	20.25

Bolded values denote the best performing models. Hierarchical corresponds to the better-fitting of the two hierarchical models, based on the red or blue cue, respectively; IS denotes the independent-source model; ITG denotes the integration model

the model fits reveal that pigeons were very unlikely to use this strategy on either the near- or far-shift tests.

Discussion

These results show that pigeons can use both integrative and independent-source strategies for coping with spatial cue conflict. Moreover, the preferred strategy is context dependent in a systematic way: When the amount of cue conflict was small (near-shift tests), pigeons integrated the information from the conflicting cues. Conversely, when the amount of cue conflict was large (far-shift tests), pigeons treated the conflicting cues as independent sources of information. This pattern of results is consistent with the Bayesian optimal use of sensory information, when that information can come from single or multiple sources (e.g., Beierholm et al. 2007; Körding et al. 2007).
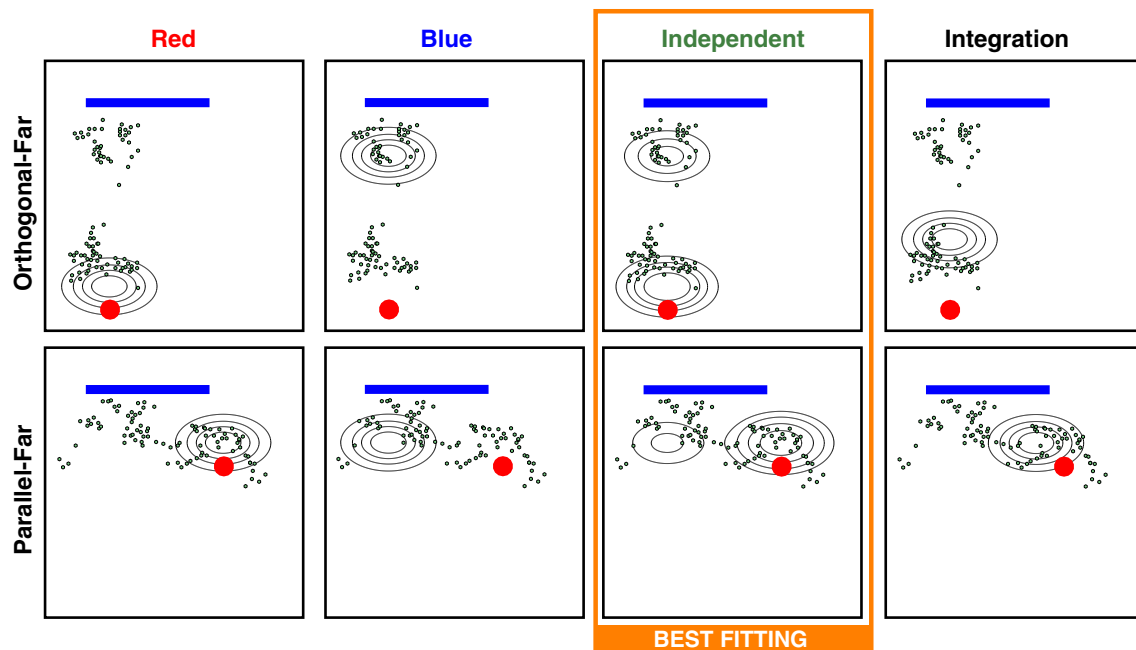
Fig. 5 Graphical representation of model fits for pigeon responses on far-shift tests. Of the two *Hierarchical* models, the best-fitting model for each bird and test was used as M_H. Responses (*green dots*) on far-shift tests plotted relative to the two cues. Contour plots in the background denote model likelihoods. Each ring of the contour plot captures 20 % of the model's respective predicted responses. Plotted data are from bird 887. Response data are replicated in each column to highlight model predictions. Note that the width of the blue cue and the diameter of the red cue were enlarged for illustrative purposes (color figure online)

These results are also congruent with recent theoretical discussions as to how animals cope with cue conflict (Cheng et al. 2007; Körding et al. 2007; Pfuhl et al. 2011). One such model explicitly predicts that animals will change their strategy for coping with cue conflict as the amount of conflict increases (Pfuhl et al. 2011). Specifically, the model predicts that when the amount of cue conflict is small, animals will attempt to integrate the information from all cues to identify a single goal location, as observed in the near-shift tests. The model also predicts that as the amount of cue conflict increases, animals will switch from an integrative strategy to one where both cues predict individual goal locations. This switch occurs because a large amount of cue conflict suggests that the cues are unrelated. Animals will still search relative to both cues if the cost of traveling between them is not prohibitive (i.e., no significant use of time or energy involved in traveling between cues). Pigeons exhibited this same behavior on the far-shift tests.

Finally, as the amount of conflict increases further, Pfuhl et al. (2011) predicted that animals would eventually switch to searching relative to only a single, preferred cue, as would be predicted by the *Hierarchical* model. This switch would occur because, when the cues are separated by such a degree that there would be a significant cost to travel between them, searching relative to both cues is no longer a viable option. While such a final strategy makes functional sense, we did not observe any evidence of this strategy in our experiment. This non-observation might arise because the cues were never separated by a large enough distance to incur a significant travel cost (i.e., the search space was only 2 m²).

Although pigeons were fairly consistent in their strategy use on near-shift tests, there was considerable inter-individual variability in the pigeons' preferred strategy on the far-shift tests. On far-shift tests, some birds appeared to use an independent-source strategy, whereas others used an integration strategy for coping with cue conflict. The conflict present in far-shift tests might have been close to the boundary where subjects would switch from using an integrative strategy that predicts a single, intermediate goal location, to using an independent-source strategy that predicts two unique goal locations, each relative to a single cue. Such a boundary is expected to exist because as the amount of cue conflict increases, it will eventually reach a point where the better inference is that the cues are not indicating the same location (e.g., Körding et al. 2007). In such cases, an integrative strategy would no longer be viable, as integrating the information provided by unrelated cues would lead an animal to search in an erroneous location. Instead animals should switch to an independent-source strategy and search relative to each cue individually, as long as the cost to travel between the cues is not prohibitive (Pfuhl et al. 2011). The point at which the cues are

perceived as being unrelated may vary across individuals. Additional tests that provide a larger degree of separation between the two cues than in the far-shift tests would be required to validate this hypothesis by showing that at some point all pigeons switch to an independent-source strategy.

Our results provided no evidence for the use of a pure hierarchical strategy. On the surface, this appears to be inconsistent with previous studies where pigeons demonstrated hierarchical strategy use (e.g., Lea et al. 2009; Legge et al. 2009; Spetch and Edwards 1988). These previous studies, however, used discrete choice locations rather than continuous search spaces, so integrative strategies were not possible. In addition, pigeons made only a single choice on each test trial, which prevented them from using an independent-source strategy, at least within a single trial. Thus, in such situations, pigeons may have used hierarchical strategies because more preferred strategies were not possible. Our results do not preclude the possibility that hierarchical strategies may still be used by animals in other situations due to their computational simplicity. For example, it is an open question whether animals might use hierarchical strategies for goal localization when they have a very short window of time to search, or when trying to escape a predator. In these situations, the computational simplicity of hierarchical strategies may allow animals to make a decision more quickly than more computationally complex strategies (e.g., an integrative strategy) and thus provide a survival advantage when a delay may be deadly (Pfuhl et al. 2011). Thus, though hierarchical strategies did not control pigeons' search behavior in this study, they may be used by pigeons or other animals in circumstances where a quick response provides a large survival advantage.

In sum, these results show that pigeons can use both integration and independent-source strategies to resolve spatial cue conflict. They can switch between these strategies pending the context, deploying the more appropriate strategy according to the degree of evidence that the shifted cues represent separate sources of information as to the goal location (i.e., how far apart the shifted cues are). These results provide confirmatory evidence for recent theoretical work on how animals cope with cue conflict (e.g., Cheng et al. 2007; Pfuhl et al. 2011) and highlight the context-dependent nature of pigeon search strategies.

Compliance with ethical standards

Ethical statement All procedures performed in studies involving animals were in accordance with the ethical standards of the University of Alberta and the Canadian Council on Animal Care and were approved by the Bioscience Animal Care and Use Committee.

Conflict of interest The authors declare that they have no conflict of interest.

References

Alais D, Burr D (2004) The ventriloquist effect results from near-optimal bimodal integration. Curr Biol 14(3):257–262. doi:10.1016/j.cub.2004.01.029

Balda RP, Turek RJ (1984) The cache recovery system as an example of memory capabilities in Clark's nutcrackers. In: Roitblat HL, Bever TG, Terrace HS (eds) Animal cognition. Erlbaum, Hillsdale, pp 513–532

Brodbeck DR (1994) Memory for spatial and local cues: a comparison of a storing and a nonstoring species. Anim Learn Behav 22(2):119–133. doi:10.3758/BF03199912

Burnham KE, Anderson DR (2002) Model selection and multimode inference, 2nd edn. Springer, New York

Burnham KE, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Method Res 33:261–304. doi:10.1177/0049124104268644

Cartwright BA, Collett TS (1983) Landmark learning in bees. J Comp Physiol A 151:521–543

Chalfoun AD, Martin TE (2010) Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? Oecologia 163(4):885–892. doi:10.1007/s00442-010-1679-0

Cheng K (2005) Behavioral ecology of odometric memories in desert ants: acquisition, retention, and integration. Behav Ecol 17(2):227–235. doi:10.1093/beheco/arj017

Cheng K, Sherry DF (1992) Landmark-based spatial memory in birds (*Parus atricapillus* and *Columba livia*): the use of edges and distances to represent spatial positions. J Comp Psychol 106:331–341

Cheng K, Shettleworth SJ, Huttenlocher J, Rieser JJ (2007) Bayesian integration of spatial information. Psychol Bull 133(4):625–637. doi:10.1037/0033-2909.133.4.625

Cheng K, Narendra A, Sommer S, Wehner R (2009) Traveling in clutter: navigation in the Central Australian desert ant *Melophorus bagoti*. Behav Process 80:261–268. doi:10.1016/j.beproc.2008.10.015

Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415:429–433

Friedman A, Ludvig EA, Legge ELG, Vuong QC (2012) Bayesian combination of two-dimensional location estimates. Behav Res Method 45:98–107. doi:10.3758/s13428-012-0241-x

Gaffan EA, Davies J (1981) The role of exploration in win-shit and win-stay performance on a radial maze. Learn Motiv 12:282–299. doi:10.1016/0023-9690(81)90010-2

Gigerenzer G, Brighton H (2009) Homo heuristicus: why biased minds make better inferences. Top Cogn Sci 1:107–143. doi:10.1111/j.1756-8765.2008.01006.x

Goto K, Wills AJ, Lea SEG (2004) Global-feature classification can be acquired more rapidly than local-feature classification in both

humans and pigeons. Anim Cogn 7:109–113. doi:10.1007/s10071-003-0193-8

Grohn M, Lokki T, Takala T (2005) Comparison of auditory, visual, and audiovisual navigation in a 3D space. ACM Trans Appl Percept 2(4):564–570

Hodges CM (1985) Bumble bee foraging: the threshold departure rule. Ecology 66(1):179–187. doi:10.2307/1941318

Hosoi E, Rittenhouse LR, Swift DM, Richards RW (1995) Foraging strategies of cattle in a y-maze: influence of food availability. Appl Anim Behav Sci 43(3):189–196. doi:10.1016/0168-1591(95)00565-A

Kamil AC, Cheng K (2001) Way-finding and landmarks: the multiple-bearings hypothesis. J Exp Biol 204:103–113

Kamil AC, Goodyear AJ, Cheng K (2001) The use of landmarks by Clark's nutcrackers: first tests of a new model. J Navig 54(3):429–435. doi:10.1017/S0373463301001436

Kearns MJ, Warren WH, Duchon AP, Tarr MJ (2002) Path integration from optic flow and body senses in a homing task. Perception 31(3):349–374. doi:10.1068/p3311

Beierholm U, Shams L, Ma WJ, Körding K (2007) Comparing Bayesian models for multisensory cue combination without mandatory integration. Adv Neural Inf 19:81–88

Körding KP, Wolpert DM (2004) Bayesian integration in sensorimotor learning. Nature 427(6971):244–247

Körding K, Beierholm U, Ma WJ, Quartz S, Tenenbaum JB, Shams L (2007) Causal inference in multi sensory perception. PLoS ONE 2(9):e943. doi:10.1371/journal.pone.0000943

Lea SEG, Wills AJ (2008) Use of multiple dimensions in learned discriminations. Comp Cogn Behav Rev 3:115–133

Lea SEG, Wills AJ, Leaver LA, Ryan CME, Bryant CML, Millar L (2009) Comparative analysis of the categorization of multidimensional stimuli: II. Strategic information search in humans (Homo sapiens) but not pigeons (Columba livia). J Comp Psychol 123:406–420. doi:10.1037/a0016851

Legge ELG (2013) Multiple Cue Use in Animals. Doctoral dissertation, University of Alberta

Legge ELG, Spetch ML, Batty ER (2009) Pigeons (Columba livia) hierarchical organization of local and global cues in touch screen tasks. Behav Process 80(2):128–139. doi:10.1016/j.beproc.2008.10.011

Legge ELG, Wystrach A, Spetch ML, Cheng K (2014) Combining sky and earth: desert ants (Melophorus bagoti) show weighted integration of celestial and terrestrial cues. J Exp Biol 217:4159–4166. doi:10.1242/jeb.107862

Pfuhl G, Tjelmeland H, Biegler R (2011) Precision and reliability in animal navigation. B Math Biol 73:951–977. doi:10.1007/s11538-010-9547-y

Raftery AE (1999) Bayes factor and BIC. Sociol Method Res 27(3):411–427

Rossier J, Haeberli C, Schenk F (2000) Auditory cues support place navigation in rats when associated with a visual cue. Behav Brain Res 117:209–214. doi:10.1016/S0166-4328(00)00293-X

Schwarz G (1978) Estimating the dimension of a model. Ann Stat 6:461–464

Spetch ML, Edwards CA (1988) Pigeons, Columba livia, use of global and local cues for spatial memory. Anim Behav 36(1):293–296. doi:10.1016/S0003-3472(88)80274-4

Spetch ML, Kelly DM (2006) Comparative spatial cognition: processes in landmark- and surface-based place finding. In: Wasserman EA, Zentall TR (eds) Comparative cognition: experimental explorations of animal intelligence. Oxford University Press, Oxford, pp 210–228

Spetch ML, Cheng K, Mondloch MV (1992) Landmark use by pigeons in a touch-screen spatial search task. Anim Learn Behav 20:281–292

Steck K, Hansson BS, Knaden M (2009) Smells like home: desert ants, Cataglyphis fortis, use olfactory landmarks to pinpoint the nest. Front Zool. doi:10.1186/1742-9994-6-5

Stephan KE, Penny WD, Daunizeau J, Moran RJ, Friston KJ (2009) Bayesian model selection for group studies. NeuroImage 46(4):1004–1017. doi:10.1016/j.neuroimage.2009.03.025

Wallace DG, Gorny B, Whishaw IQ (2002) Rats can track odors, other rats, and themselves: implications for the study of spatial behavior. Behav Brain Res 131:185–192. doi:10.1016/S0166-4328(01)00384-9