

**Original citation:**

Legge, E. L. G., Madan, C. R., Spetch, M. L. and Ludvig, Elliot Andrew. (2016) Multiple cue use and integration in pigeons (*Columba livia*). *Animal Cognition*, 19 (3). pp. 581-591.

**Permanent WRAP URL:**

<http://wrap.warwick.ac.uk/77004>

**Copyright and reuse:**

The Warwick Research Archive Portal (WRAP) makes this work by researchers of the University of Warwick available open access under the following conditions. Copyright © and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable the material made available in WRAP has been checked for eligibility before being made available.

Copies of full items can be used for personal research or study, educational, or not-for profit purposes without prior permission or charge. Provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

**Publisher's statement:**

"The final publication is available at Springer via <http://dx.doi.org/10.1007/s10071-016-0963-8> "

**A note on versions:**

The version presented here may differ from the published version or, version of record, if you wish to cite this item you are advised to consult the publisher's version. Please see the 'permanent WRAP URL' above for details on accessing the published version and note that access may require a subscription.

For more information, please contact the WRAP Team at: [wrap@warwick.ac.uk](mailto:wrap@warwick.ac.uk)

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30

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

Eric L. G. Legge<sup>1</sup>, Christopher R. Madan<sup>1,2</sup>, Marcia L. Spetch<sup>1,†</sup>, and Elliot A. Ludvig<sup>3</sup>

<sup>1</sup> Department of Psychology, University of Alberta, Edmonton, AB, Canada

<sup>2</sup> Department of Psychology, Boston College, Chestnut Hill, MA, USA

<sup>3</sup> Department of Psychology, University of Warwick, Coventry, UK

† Corresponding author.  
Marcia L. Spetch  
Department of Psychology,  
P217-Biological Sciences  
University of Alberta  
Edmonton, AB Canada  
T6G 2E9  
[mspetch@ualberta.ca](mailto:mspetch@ualberta.ca)  
780 492-7548

31 **Abstract**

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

40

41 **Keywords:**

42 cue integration; spatial navigation; Bayesian; pigeons; hierarchical; win-shift; spatial cognition;  
43 cue-conflict; computational modeling

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

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

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

63           One method for coping with cue conflict used by animals is a *hierarchical* strategy  
64 whereby animals only use the cue at the top of a hierarchy for localizing a goal (also known as a  
65 winner-take-all or take-the-best strategy; Lea et al. 2009; Gigerenzer and Brighton 2009; Legge  
66 et al. 2009; Spetch and Edwards 1988). Though this strategy may be useful in some situations

67 due to its simplicity, relying on a single cue may be problematic because animals could discard  
68 relevant information from other nearby sources. Additionally, a strictly hierarchical strategy  
69 would cause an animal to search in an incorrect location if the cue at the top of the hierarchy was  
70 displaced.

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

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

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

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

## 111 **Methods**

### 112 *Subjects*

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

119

### 120 *Stimuli and Apparatus*

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

130           Pigeons started each trial in an opaque enclosed start box (0.49 m wide, 0.39 m deep,  
131 0.40 m high) that was built into the door to the testing room and contained a vertical sliding  
132 panel, which the experimenter opened to allow the pigeon into the room. After pigeons entered  
133 the testing room, the sliding panel was closed until the trial ended. The start box contained a food  
134 well that was baited while the pigeon was in the testing room. When the trial ended, the door to

135 the start box opened and the pigeon entered to eat from the food well. All test trials were video  
136 recorded and digitized before being scored.

137

138 *Procedure*

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

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

153         The next phase of training adapted the birds to receiving partial reinforcement. Food was  
154 available in the goal on 8/10 trials per day for 2 days and then on 6/10 trials per day for the  
155 remainder of this phase. During unreinforced trials, the goal container was removed and subjects  
156 were given a maximum of 2 min or until 30 search attempts were observed. When either of these  
157 limits was reached, the room lights were turned off and the start box door was opened to allow

158 pigeons to return to the baited start box. Trial order was pseudo-randomized each day with the  
159 restriction that the first trial was always reinforced and subjects could not receive more than two  
160 consecutive unreinforced trials. To progress to testing, subjects had to complete at least five days  
161 of this training and had to successfully locate the hidden goal on at least 5 out of 6 reinforced  
162 trials for three consecutive days.

163

164 **Testing.** There were two testing phases: (a) single-cue and (b) shift. In both phases, the position  
165 of the landmark array within the search space varied as in training. Additionally, as in the final  
166 phase of training, subjects received 10 trials per day, four of which were unreinforced, and the  
167 position of unreinforced trials in the trial sequence was pseudo-randomized as described above.  
168 Of these four unreinforced trials, two were control trials, with the same landmark arrangement as  
169 in training. The remaining two unreinforced trials each day were unique to each stage of testing  
170 (single-cue or shift testing). Subjects had a maximum of 2 min to find the goal (reinforced trials)  
171 or to search for the goal (unreinforced trials) before they could return to the start box. After 2  
172 min elapsed, the room lights were turned off, and the start box door was opened to allow pigeons  
173 to return to the baited start box.

174

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

180

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

190

191 **Scoring.** Data were scored by five research assistants who were unaware of the study's  
192 hypotheses. Prior to independently scoring data, each assistant received a minimum of 5 training  
193 sessions with an experienced rater. During these sessions, the trainee was instructed on how to  
194 score video data and s/he observed the trainer score several videos. The trainee was then  
195 monitored while scoring a new set of previously-scored video files and the scores obtained by  
196 the trainee were compared to those obtained previously to ensure scoring reliability. In all cases,  
197 scored data by the trainee closely matched the previous scores in number and location of  
198 recorded pecks, and therefore the trainee was then permitted to score new video files.  
199 Furthermore, to prevent any potential effects of across-rater variance from differentially  
200 influencing experimental conditions, research assistants were assigned to score trials across all  
201 shift tests for a given bird. When scoring video data, a transparency was overlaid on the  
202 computer monitor and the position of the cues and of each search location (beak sweep) were  
203 marked while playing the video in slow motion. During this process, each peck was numbered

204 sequentially. After scoring, the data from each transparency was digitized using in-house  
205 software such that clicking on each each cue and search location provided it with  $x$ - and  $y$ -  
206 coordinates that were later used in the computational modeling.

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

216

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

224

225 **Computational Models.** Three models were fit to the data, representing the three key  
226 hypotheses about how pigeons would combine the conflicting cue information (see Figure 2).

227           (i) *Hierarchical*. The first model predicted that subjects would cope with cue conflict by  
228 using a hierarchical search strategy. This *Hierarchical* model ( $M_H$ ) assumes that, when cues  
229 provide conflicting information, subjects only rely on a single, preferred cue to locate the goal.  
230 First, two sub-models were fit to the data, based on each possible hierarchical strategy, one  
231 representing preference for the large, blue cue ( $M_B$ ), and the other representing preference for the  
232 small, red cue ( $M_R$ ). Of these two models, the better-fitting model for each bird and test was used  
233 as the *Hierarchical* model. Note that this model has an additional degree of freedom relative to  
234 other models, and this was taken into account in the model comparison below.

235           (ii) *Independent-Source*. The second model predicts that animals will respond to each cue  
236 individually within a trial, adopting a win-stay/lose-shift strategy. Specifically, this *Independent-*  
237 *Source* model ( $M_{IS}$ ) predicts that subjects will search for the goal at the locations predicted by  
238 each cue individually, i.e., the same goal locations predicted by  $M_B$  and  $M_R$  above. Additionally,  
239 the *Independent-Source* model hypothesizes that the animal weights each cue according to the  
240 cue's reliability, which is measured as the inverse of the spatial variance of responding to that  
241 cue when presented alone (i.e., the variance of search locations observed when each cue is  
242 presented alone serves as an inverse indicator of the cue's functional reliability). The animal then  
243 allocates search attempts relative to each cue's predicted goal location according to this  
244 weighting. That is, if the blue cue had a weight of 0.30, and the red cue a weight of 0.70,  $M_{IS}$   
245 predicts that the animal would allocate 30% of its searches based exclusively on the large, blue  
246 cue, and the remaining 70% of its searches to the location based on the small, red cue (e.g., see  
247 Figure 2). Thus, this model uses Bayesian inference to determine each cue's weight (Cheng et al.  
248 2007; Friedman et al. 2012).

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

255

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

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

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

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

269           The predicted goal location for the *Integration* model  $M_{ITG}$  was calculated separately for  
 270 each subject. This goal location represented the weighted sum of the two landmarks, where the  
 271 weights corresponded to their relative reliability (inverse variance; see Cheng et al. 2007). The

272 reliability was estimated from the single-cue trials, separately for the  $x$ - and  $y$ -dimensions  
 273 (corresponding to the parallel and orthogonal dimensions, respectively). The weights were then  
 274 calculated using the following formula:

$$275 \quad w_B = \frac{\sigma_R^2}{\sigma_R^2 + \sigma_B^2}, \quad (1)$$

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

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

$$281 \quad G_M = w_B G_B + w_R G_R. \quad (2)$$

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

285 *Variance.* A pooled variance estimate was calculated for each bird separately for the  $x$ -  
 286 and  $y$ -dimensions:

$$287 \quad \sigma_P^2 = \frac{(n_B - 1)\sigma_B^2 + (n_R - 1)\sigma_R^2}{n_B + n_R - 2}, \quad (3)$$

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

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

294 
$$P(r|M) = N(r; G_M, \sigma_p^2). \quad (4)$$

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

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

301 
$$P(r|M_{IS}) = w_B P(r|M_B) + w_R P(r|M_R). \quad (5)$$

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

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

308 
$$LL(M|R) = \sum_{i=1}^n \ln P(r_i|M), \quad (6)$$

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

312 
$$BIC = -2 LL + k \ln (n), \quad (7)$$

313 where  $k$  is the number of parameters in the model (Raftery 1999; Schwarz 1978). This  $BIC$  value  
 314 represents the relative fit of a model to subjects' search accuracy data. For model comparison,  
 315 the pairwise difference in  $BIC$  values for each model was calculated by subtracting the best-  
 316 fitting model's  $BIC$  from each model's  $BIC$ , resulting in a  $\Delta BIC$  value for each model. Thus, the

317 best-fitting model always had a  $\Delta BIC$  of 0. By convention, a difference between two model fits  
318 of two or more ( $\Delta BIC > 2$ ) is taken as significant evidence in favour of the better model  
319 (Burnham and Anderson 2002; 2004). Note that the *Hierarchical* model had an additional degree  
320 of freedom relative to the *Independent-Source* and *Integration* models, and this was corrected for  
321 through the *BIC* calculations.

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

## 325 Results

### 326 *Single-cue tests*

327 On the single-cue tests, cues were presented to pigeons individually to obtain an unbiased  
328 estimate of pigeons' search variance relative to each cue. This search variance was then used to  
329 determine how strongly pigeons weighted each of the two cues, as described in Eq 1. Table 1  
330 displays the cue weights for each bird as derived from these single cue tests for the red cue; by  
331 definition, the blue cue weights are 1 minus the red cue weight. As shown in Figure 3, despite  
332 variability across birds in their overall preference for the red or blue cue, all birds weighted the  
333 red cue more heavily in the parallel axis than the orthogonal axis. Conversely, all birds weighted  
334 the blue cue more heavily in the orthogonal axis than the parallel axis. This difference likely  
335 reflects the physical properties of the two cues, with the large, blue cue providing edge or  
336 boundary information and the small, red cue serving as a discrete landmark. The pattern of  
337 results is consistent with previous studies that have found differences in control by edges and  
338 discrete landmarks in birds, with distance from an edge being more important than distance  
339 along that edge (Cheng & Sherry, 1992; Spetch, Cheng, & Mondloch, 1992).

340 *Near-shift tests*

341           On near-shift tests, in which the spatial information provided by the two cues conflicted  
342 by only a small amount, the birds generally searched at an intermediate location between the goal  
343 locations indicated by each cue. Figure 4 illustrates how on these near-shift tests, the *Integration*  
344 model best fits subjects' search behaviour, regardless of whether the red cue was shifted parallel  
345 or orthogonal to the blue cue (see Table 2). Additionally, pigeons' preference for using an  
346 integrative strategy was fairly consistent across subjects with the *Integration* model serving as  
347 the best-fitting model for individual subjects' data on 13 out of 16 near-shift tests (Table 3).  
348 Taken together, these findings indicate that when cues were only shifted by a small distance and  
349 thus provided only a small amount of cue conflict, the pigeons' search pattern integrated the  
350 information provided by each cue.

351 *Far-shift tests*

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

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

362 *Hierarchical models*



386 of cue conflict suggests that the cues are unrelated. Animals will still search relative to both cues  
387 if the cost of travelling between them is not prohibitive (i.e., no significant use of time or energy  
388 involved in travelling between cues). Pigeons exhibited this same behaviour on the far-shift tests.

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

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

409 individually, as long as the cost to travel between the cues is not prohibitive (Pfuhl et al. 2011).  
410 The point at which the cues are perceived as being unrelated may vary across individuals.  
411 Additional tests that provide a larger degree of separation between the two cues than in the far-  
412 shift tests would be required to validate this hypothesis by showing that at some point all pigeons  
413 switch to an independent-source strategy.

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

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

438

439  
440  
441  
442  
443  
444  
445  
446  
447

### **Acknowledgements**

The authors are thankful to Isaac Lank for help in designing and maintain the experimental apparatus and the many undergraduate research assistants who helped run daily experimental trials. We especially thank Carla Edgington and Andrea Nicole Savignac for their exceptional work scoring, coordinating subject run schedules, and running subjects. Funding was provided by a National Sciences and Engineering Research Council (NSERC) of Canada Discovery grant #38861 to MLS, and NSERC Alexander Graham Bell Canada Graduate Scholarships (Doctoral-level) to ELGL and CRM.

448

**Ethical Statement**

449

All procedures performed in studies involving animals were in accordance with the ethical

450

standards of the University of Alberta and the Canadian Council on Animal Care, and were

451

approved by the Bioscience Animal Care and Use Committee.

452

453

**Conflict of Interest**

454

The authors declare that they have no conflict of interest.

455

456

457

**Figure Captions**

458 **Figure 1.** Illustrations and photographs depicting landmark locations on training and testing  
459 trials. [A] A diagram depicting the position of the blue and red cues relative to each other in  
460 training. Note that while the distances by which the red and blue cues are separated are to scale  
461 relative to the size of the search space (figure panel), the width of the blue cue, and the diameter  
462 of the red cue have been expanded for illustrative purposes. In training, the red cue was located  
463 21 cm left of the blue cue, along the parallel axis, and 49 cm closer to the entrance to the room,  
464 along the orthogonal axis of the blue cue. The goal (diameter of 3 cm) was located 22 cm away  
465 from the red cue along the orthogonal axis, positioned between the blue and red cues as indicated  
466 by the letter “G” in the figure. [B] An overhead image of a pigeon relative to both cues during  
467 training. [C] A scale diagram depicting the position of the both cues relative to each other on  
468 shift tests. The dashed, unfilled circle depicts the location of the red cue during training. For each  
469 test, the red cue was shifted by the following distance and direction relative to the blue cue from  
470 its training position: Orthogonal-Near: 47 cm away along the orthogonal axis; Orthogonal-Far:  
471 98 cm away along the orthogonal axis, Parallel-Near: 35 cm away along the parallel axis;  
472 Parallel-Far: 83 cm away along the parallel axis. On all training and testing trials, the position of  
473 the two cues were varied within the room to prevent pigeons from using room features to help  
474 localize the goal as described in the main text.

475

476 **Figure 2.** Probability density function (PDF) plots for each model. Red and Blue denote the two  
477 *Hierarchical* models, based on the red or blue cue, respectively; IS denotes the *Independent-*  
478 *Source* model; ITG denotes the *Integration* model. Of the two *Hierarchical* models, the best-

479 fitting model for each bird and test was used as  $M_H$ . [A] Orthogonal-Near (O-Near) tests. [B]  
480 Orthogonal-Far (O-Far) tests. PDFs shown here are based on data from bird 887.

481

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

487

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

495

496 **Figure 5.** Graphical representation of model fits for pigeon responses on Far-shift tests. Of the  
497 two *Hierarchical* models, the best-fitting model for each bird and test was used as  $M_H$ .  
498 Responses (green dots) on far-shift tests plotted relative to the two cues. Contour plots in the  
499 background denote model likelihoods. Each ring of the contour plot captures 20% of the model's  
500 respective predicted responses. Plotted data is from bird 887. Response data are replicated in

501 each column to highlight model predictions. Note that the width of the blue cue and the diameter  
502 of the red cue were enlarged for illustrative purposes.

503  
504  
505  
506  
507  
508  
509  
510  
511  
512  
513  
514  
515  
516  
517  
518  
519  
520  
521  
522  
523

**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.), *Anim Cogn* (pp. 513–532). Hillsdale, NJ: Erlbaum.

Beierholm U, Shams L, Ma WJ, Körding, K (2007) Comparing Bayesian models for multisensory cue combination without mandatory integration. *Adv Neur In (NIPS-06)* 19:81-88.

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 ed.). New York, NY: Springer–Verlag.

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

- 524 Cheng K, Narendra A, Sommer S, Wehner R (2009) Traveling in clutter: Navigation in the  
525 Central Australian desert ant *Melophorus bagoti*. *Behav Process* 80:261–268. doi:  
526 10.1016/j.beproc.2008.10.015
- 527 Cheng K, Sherry DF (1992) Landmark-based spatial memory in birds (*Parus atricapillus* and  
528 *Columba livia*): The use of edges and distances to represent spatial positions. *J Comp*  
529 *Psychol* 106:331–341
- 530 Cheng K, Shettleworth SJ, Huttenlocher J, Rieser JJ (2007) Bayesian integration of spatial  
531 information. *Psychol Bull* 133(4):625–637. doi: 10.1037/0033-2909.133.4.625
- 532 Ernst MO, Banks MS (2002). Humans integrate visual and haptic information in a statistically  
533 optimal fashion. *Nature* 415:429–433.
- 534 Friedman A, Ludvig EA, Legge ELG, Vuong QC (2012) Bayesian combination of two-  
535 dimensional location estimates. *Behav Res Method* 45:98–107. doi: 10.3758/s13428-012-  
536 0241-x
- 537 Gaffan EA, Davies J (1981) The role of exploration in win-stay and win-shift performance on a  
538 radial maze. *Learn Motiv* 12:282–299. doi:10.1016/0023-9690(81)90010-2
- 539 Gigerenzer G, Brighton H (2009) Homo heuristicus: Why biased minds make better inferences.  
540 *Top Cogn Sci* 1:107–143. doi: 10.1111/j.1756-8765.2008.01006.x
- 541 Goto, K, Wills, AJ, Lea, SEG (2004). Global-feature classification can be acquired more rapidly  
542 than local-feature classification in both humans and pigeons. *Anim Cogn* 7: 109-113. doi;  
543 10.1007/s10071-003-0193-8
- 544 Grohn M, Lokki T, Takala T (2005) Comparison of auditory, visual, and audiovisual navigation  
545 in a 3D space. *ACM Transactions on Applied Perception* 2(4):564–570. doi: 1544-  
546 3558/05/1000-0564

- 547 Hodges CM (1985) Bumble bee foraging: The threshold departure rule. *Ecology* 66(1):179–187.  
548 DOI: 10.2307/1941318
- 549 Hosoi E, Rittenhouse LR, Swift DM, Richards RW (1995) Foraging strategies of cattle in a y-  
550 maze: Influence of food availability. *Appl Anim Behav Sci* 43(3):189–196. doi: 10.1016/  
551 0168-1591(95)00565-A
- 552 Kamil AC, Cheng K (2001) Way-finding and landmarks: The multiple-bearings hypothesis. *J*  
553 *Exp Biol* 204:103–113.
- 554 Kamil AC, Goodyear AJ, Cheng K (2001) The use of landmarks by Clarks nutcrackers: First  
555 tests of a new model. *J Navigation* 54(3):429–435. doi: 10.1017/S0373463301001436
- 556 Kearns MJ, Warren WH, Duchon AP, Tarr MJ (2002) Path integration from optic flow and body  
557 senses in a homing task. *Perception* 31(3):349–374. doi: 10.1068/p3311
- 558 Körding K, Beierholm U, Ma WJ, Quartz S, Tenenbaum JB, Shams L (2007) Causal inference in  
559 multi sensory perception. *PLoS ONE* 2(9):e943. doi: 10.1371/journal.pone.0000943
- 560 Körding KP, Wolpert DM (2004) Bayesian integration in sensorimotor  
561 learning. *Nature* 427(6971):244-247.
- 562 Lea SEG, Wills AJ (2008) Use of multiple dimensions in learned discriminations. *Comp Cogn &*  
563 *Behav Rev* 3: 115-133.
- 564 Lea SEG, Wills AJ, Leaver LA, Ryan CME, Bryant CML, Millar L (2009) Comparative analysis  
565 of the categorization of multidimensional stimuli: II. Strategic information search in  
566 humans (*Homo sapiens*) but not pigeons (*Columba livia*). *J Comp Psychol* 123: 406-420.  
567 doi: 10.1037/a0016851

- 568 Legge ELG, Wystrach A, Spetch ML, Cheng K (2014) Combining sky and earth: Desert ants  
 569 (Melophorus bagoti) show weighted integration of celestial and terrestrial cues. *J Exp*  
 570 *Biol* 217:4159-4166. doi: 10.1242/jeb.107862
- 571 Legge ELG (2013) Multiple Cue Use in Animals (Doctoral dissertation, University of Alberta).
- 572 Legge ELG, Spetch ML, Batty ER (2009) Pigeons (*Columba livia*) hierarchical organization of  
 573 local and global cues in touch screen tasks. *Behav Process* 80(2):128–139. doi:  
 574 10.1016/j.beproc.2008.10.011
- 575 Pfuhl G, Tjelmeland H, Biegler R (2011) Precision and reliability in animal navigation. *B Math*  
 576 *Biol* 73:951–977. doi: 10.1007/s11538-010-9547-y
- 577 Raftery AE (1999) Bayes factor and BIC. *Sociol Method Res* 27(3):411–427.
- 578 Rossier J, Haerberli C, Schenk F (2000) Auditory cues support place navigation in rats when  
 579 associated with a visual cue. *Behav Brain Res* 117:209–214. doi:10.1016/S0166-  
 580 4328(00)00293-X
- 581 Schwarz G (1978) Estimating the dimension of a model. *Ann Stat* 6:461-464.
- 582 Spetch ML, Cheng K, Mondloch MV (1992) Landmark use by pigeons in a touch-screen spatial  
 583 search task. *Anim Learn Behav* 20:281–292.
- 584 Spetch ML, Edwards CA (1988) Pigeons, *Columba livia*, use of global and local cues for spatial  
 585 memory. *Anim Behav* 36(1):293–296. doi: 10.1016/S0003-3472(88)80274-4
- 586 Spetch ML, Kelly DM (2006) Comparative spatial cognition: Processes in landmark- and  
 587 surface-based place finding. In E. A. Wasserman and T. R. Zentall (Eds.), *Comparative*  
 588 *cognition: Experimental explorations of animal intelligence* (pp. 210–228). Oxford, NY:  
 589 Oxford University Press.

- 590 Steck K, Hansson BS, Knaden M (2009) Smells like home: Desert ants, *Cataglyphis fortis*, use  
591 olfactory landmarks to pinpoint the nest. *Front Zool* 6(5). doi: 10.1186/1742-9994-6-5
- 592 Stephan KE, Penny WD, Daunizeau J, Moran RJ, Friston KJ (2009) Bayesian model selection  
593 for group studies. *NeuroImage*, 46(4):1004–1017. doi:10.1016/j.neuroimage.2009.03.025
- 594 Wallace DG, Gorny B, Whishaw IQ (2002) Rats can track odors, other rats, and themselves:  
595 Implications for the study of spatial behavior. *Behav Brain Res* 131:185–192.  
596 doi:10.1016/S0166-4328(01)00384-9