WARWICK
THE UNIVERSITY OF WARWICK

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

warwick.ac.uk/lib-publications

1

2

3

4

5

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

7

8

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

10

11

12 [1] Department of Psychology, University of Alberta, Edmonton, AB, Canada
13 [2] Department of Psychology, Boston College, Chestnut Hill, MA, USA
14 [3] Department of Psychology, University of Warwick, Coventry, UK
15
16

17

18

19

20

21 [†] Corresponding author.
22 Marcia L. Spetch
23 Department of Psychology,
24 P217-Biological Sciences
25 University of Alberta
26 Edmonton, AB Canada
27 T6G 2E9
28 mspetch@ualberta.ca
29 780 492-7548
30

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

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

276   where w_B is the weight on the blue cue for a particular dimension and σ^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
$$G_M = w_B G_B + w_R G_R.$$
(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
$$\sigma_P^2 = \frac{(n_B - 1)\sigma_B^2 + (n_R - 1)\sigma_R^2}{n_B + n_R - 2},$$
(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 (σ_p^2):

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

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

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

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

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 *ΔBIC* value for each model. Thus, the

317   best-fitting model always had a *ΔBIC* of 0. By convention, a difference between two model fits

318   of two or more (*ΔBIC* > 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, *LL*s 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*

363   When pooled-subject analyses were conducted on pigeons' search distributions, the

364 *Hierarchical* model performed poorly on all tests (see Table 2). With the exception of the

365 Parallel-Near test, the *Hierarchical* model was the worst model fit for every shift test. Thus,

366 while the *Hierarchical* model represented the simplest strategy pigeons could use to search for a

367 goal when cues provided conflicting information, the model fits reveal that pigeons were very

368 unlikely to use this strategy on either the near- or far-shift tests.

369   **Discussion**

370   These results show that pigeons can use both integrative and independent-source

371 strategies for coping with spatial cue conflict. Moreover, the preferred strategy is context

372 dependent in a systematic way: When the amount of cue conflict was small (near-shift tests),

373 pigeons integrated the information from the conflicting cues. Conversely, when the amount of

374 cue conflict was large (far-shift tests), pigeons treated the conflicting cues as independent

375 sources of information. This pattern of results is consistent with the Bayesian optimal use of

376 sensory information, when that information can come from single or multiple sources (e.g.,

377 Beierholm et al. 2007; Körding et al. 2007).

378   These results are also congruent with recent theoretical discussions as to how animals

379 cope with cue conflict (Cheng et al., 2007; Körding et al. 2007; Pfuhl et al. 2011). One such

380 model explicitly predicts that animals will change their strategy for coping with cue conflict as

381 the amount of conflict increases (Pfuhl et al. 2011). Specifically, the model predicts that when

382 the amount of cue conflict is small, animals will attempt to integrate the information from all

383 cues to identify a single goal location, as observed in the near-shift tests. The model also predicts

384 that as the amount of cue conflict increases, animals will switch from an integrative strategy to

385 one where both cues predict individual goal locations. This switch occurs because a large amount

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^2).

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

Acknowledgements

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   **References**

504   Alais D, Burr D (2004) The ventriloquist effect results from near- optimal bimodal integration.

505   Curr Biol 14(3):257–262. doi: 10.1016/j.cub.2004.01.029

506   Balda RP, Turek RJ (1984) The cache recovery system as an example of memory capabilities in

507   Clark's nutcrackers. In Roitblat HL, Bever TG, Terrace HS (Eds.), Anim Cogn (pp. 513–

508   532). Hillsdale, NJ: Erlbaum.

509   Beierholm U, Shams L, Ma WJ, Körding, K (2007) Comparing Bayesian models for

510   multisensory cue combination without mandatory integration. Adv Neur In (NIPS-06)

511   19:81-88.

512   Brodbeck DR (1994) Memory for spatial and local cues: a comparison of a storing and a

513   nonstoring species. Anim Learn Behav 22(2): 119-133. Doi: 10.3758/BF03199912

514   Burnham KE, Anderson DR (2002) Model selection and multimode inference (2nd ed.). New

515   York, NY: Springer–Verlag.

516   Burnham KE, Anderson DR (2004) Multimodel inference: Understanding AIC and BIC in model

517   selection. Sociol Method Res 33:261–304. doi: 10.1177/0049124104268644

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

519   Chalfoun AD, Martin TE (2010) Facultative nest patch shifts in response to nest predation risk in

520   the brewer's sparrow: A "win-stay, lose-switch" strategy? Oecologia, 163(4):885–892.

521   doi: 10.1007/s00442 -010-1679-0

522   Cheng K (2005) Behavioral ecology of odometric memories in desert ants: Acquisition,

523   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-shit and win-stay 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, Haeberli 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