

Pigeons' (*Columba livia*) hierarchical organization of local and global cues in touch screen tasks

Eric L.G. Legge*, Marcia L. Spetch, Emily R. Batty

Department of Psychology, University of Alberta, BSP-217, Edmonton, Alberta, Canada T6G 2E9

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ABSTRACT

Redundant encoding of local and global spatial cues is a common occurrence in many species. However, preferential use of the each type of cue seems to vary across species and tasks. In the current study, pigeons (*Columba livia*) were trained in three experiments on a touch screen task which included redundant local positional cues and global spatial cues. Specifically, pigeons were required to choose the middle out of three choice squares, such that the position within the array provided local information and the location on the screen provided global information. In Experiment 1, pigeons were trained and tested on vertically aligned arrays. In Experiment 2, pigeons were trained and tested on horizontally aligned arrays, and in Experiment 3, pigeons were trained and tested with vertical, horizontal and diagonally aligned arrays. The results indicate that preference for cue type depends upon the type of spatial information being encoded. Specifically, on vertical and diagonally aligned arrays, pigeons preferred global cues, whereas on horizontally aligned arrays, pigeons preferred local cues.

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Spatial information is important for all animals that navigate through their environment, and can be critical for many activities including procuring food, returning to mates and locating suitable breeding sites (Gallistel, 1990). However, the type of spatial information used by animals for orientation and navigation can vary widely among species, the type of task to be performed and the environment in which the animal resides. The various types of spatial information animals use to orient and navigate can be broadly categorized as providing either local or global cues. The terms local and global are arbitrary and context-specific. In general, however, local cues are close to the goal and can include non-spatial visual features at or near the goal (e.g. a colour or pattern), spatial cues provided by objects near the goal (e.g. local landmark or beacon) or positional cues (e.g. position in an array of objects). Global cues are more distal and can include stable environmental cues such as a mountain ridgeline or the edge of a ravine (Hurly and Healy, 1996), an absolute location within an arena (Spetch and Edwards, 1988), or the geometry of an enclosure (Tommasi and Vallortigara, 2004). Many species have been shown to redundantly encode different kinds of spatial information, including many avian

species (e.g. black capped chickadees, Brodbeck, 1994; pigeons, Kelly et al., 1998; dark-eyed juncos, Brodbeck and Shettleworth, 1995; hummingbirds, Hurly and Healy, 1996; Clark's nutcrackers, Gibson and Kamil, 2001; marsh and blue tits, Clayton and Krebs, 1994), and several species of mammals (e.g. rats, Cheng, 1986; squirrels, Nesterova, 2007; dogs, Fiset et al., 2000).

Redundant encoding of local and global cues is thought to be an adaptive strategy for at least two reasons. First, encoding multiple cues allows animals to use both types of cues in tandem to more accurately pinpoint a location than is possible using only a single cue (e.g. Kamil and Cheng, 2001). Second, redundant information may provide a back-up source of information in the event that one cue is lost or changes suddenly (e.g. a sudden snowfall; a flash flood). Encoding both local and global information makes it more likely that at least one source will remain intact (i.e. a snowfall will obscure local cues on the ground, but not global cues such as the ridgeline of a mountain). For example food-storing birds living in Northern climates can still recover food-caches that they stored in the fall even after the land is covered in snow (Sherry, 1992; Vander Wall, 1982; Bossema, 1979).

Although redundancy in encoding of local and global cues has been demonstrated in many species, the hierarchical organization of these cues appears to vary across species. For example, in a study with pigeons by Spetch and Edwards (1988), the goal was redun-

* Corresponding author. Tel.: +1 780 492 7139; fax: +1 780 492 1768.
E-mail address: ellegge@ualberta.ca (E.L.G. Legge).

dantly defined by the location in the room (global cue) and the position of the goal in an array of containers (local cue). Both cues were encoded but when a conflict existed between local and global cue information, the local cue information was preferred. However, in similar kinds of tests, chickadees (Brodbeck, 1994), Clark's nutcrackers (Gould-Beierle and Kamil, 1996), hummingbirds (Hurly and Healy, 1996) and Columbian ground squirrels (Vlasak, 2006a, 2006b) seemed to prefer global cues over local cues when the cues were placed in conflict. Furthermore, Brodbeck found that dark-eyed juncos (a non-storing bird) showed no consistent preference between local and global cues, indicating species differences in preferred cue use. The hierarchical organization of preferential cue use can also vary by individual within species (adult humans, Steck and Mallot, 2000) and may change with age (squirrels, Nesterova, 2007).

In many recent studies, redundant cues for orientation have been provided by the geometry of an enclosure and features near the goal. With only a few exceptions (e.g. Gray et al., 2005), organisms readily encode geometric information, but species and developmental differences have been found in the extent to which local features are also used (see Cheng and Newcombe, 2005 for a review). Interestingly, the use of featural information also appears to depend on the size of the enclosure for young children (Learmonth et al., 2002), chicks (Vallortigara et al., 2005) and fish (Sovrano et al., 2005): in each of these species, features were more likely to be encoded or preferred in larger enclosures than in smaller enclosures. These results indicate that stimulus factors can play an important role in the hierarchy of cue use.

The present study was designed to investigate stimulus factors in pigeon's use of redundant local position cues and global location cues. In the study by Spetch and Edwards (1988), pigeons showed a strong preference for local positional cues over global room location cues. However, the more typical result in other species appears to be a preference for global location cues over local position cues. In the present study, we developed a touch screen analogue of Spetch and Edwards' open-field experiment to determine if pigeons' hierarchical organization of cue use would generalize to a different type of search task with a vertically oriented search space (i.e. a touch screen). We also varied the orientation of the positional information (vertically, horizontally or diagonally aligned arrays) to determine whether orientation of the array alters the hierarchy of cue use. In our experiments, pigeons were trained with different arrays of three yellow squares on a touch screen. In training, a peck to the middle square was reinforced. In this case, the positional information of the correct square within the array (i.e. the middle) was considered to be the local cue information because it was provided by nearby visual cues (i.e. the other choice locations in the array). The specific position of the goal square on the screen was considered to be the global cue information. This global information could be provided by any of a number of cues, including proprioceptive cues, distance from the edges of the screen, location relative to food hoppers, or geometric properties of the screen or operant chamber. Pigeons were given a variety of tests in which the position of the array on the screen was altered or local and global cues were placed in conflict, to determine whether the pigeons independently encoded both local and global information and which of the two types of information dominated.

Three experiments were conducted. In Experiment 1, pigeons were trained with only vertically aligned arrays. In Experiment 2, pigeons were trained with only horizontally aligned arrays. In Experiment 3, pigeons were trained with horizontal, vertical, and diagonally aligned arrays. These studies were designed to determine whether pigeon's hierarchical organization of cue use in an operant task would remain consistent with those reported by Spetch and Edwards (1988) in the open field (i.e. show a preference

for local information), and whether pigeons' preferences would change depending on the orientation of the array.

1. Experiment 1: Vertical array

1.1. Method

1.1.1. Subjects

The subjects were four adult pigeons (*Columba livia*) with varied previous experience in tasks conducted on computer screens. None had any previous training with tasks requiring a choice among discrete spatial locations. The birds were maintained between 85% and 90% of their free-feeding weights by pigeon pellets obtained during experimental sessions and supplemental feedings in the home cages. They were housed in large individual cages under a 12:12-h light:dark cycle (with light onset at 6:00 a.m.). Grit and water were freely available in the home cages.

1.1.2. Stimuli and apparatus

The choice stimuli were identical yellow squares, approximately 3 cm × 3 cm. The locations of the squares were selected using a 9 column × 7 row grid (not visible to subjects). In training, three choice squares were aligned vertically in the center of the computer screen (horizontal grid location five from left). The correct square was at vertical grid location four from the top of the screen (see Fig. 1). In testing, the number and location of the squares varied across trials. The experiment was conducted in custom-built operant chambers, equipped with a 15-in. colour LCD screen and an infrared touch frame that recorded the location of the pigeons' pecks. The touch frame was fitted to an opening of approximately 29 cm × 22 cm at the back wall of the chamber and the monitor was attached behind the frame. The chamber contained two solenoid-type bird feeders, one on each side of the monitor. Lamps within each feeder illuminated feeder presentations, and photocells measured head entries into the hoppers for timing of feeding durations. Food rewards consisted of 1–2 s of feeding duration, depending on the weight of the bird. Computers located in an adjacent room controlled the experimental contingencies and recorded the responses.

1.1.3. Training

The pigeons received one session per day, 5 or 6 days per week. A few of the birds required pretraining to establish reliable pecking at a yellow square. During pretraining sessions, a single yellow square was presented in a randomly selected location on the computer screen for 8 s or until the bird pecked at it, and then food was presented. Pretraining sessions were given until the bird pecked at the square on over 80% of the trials. During training, each trial began with the presentation of the three vertically aligned yellow squares against a grey background. The first peck in any of the three squares terminated all three stimuli, leaving a blank grey screen. A peck to the center stimulus was followed by a food reward, whereas a peck to the top or bottom square terminated the trial without food. The trial also ended without food if the bird failed to peck any of the stimuli within 2 min of stimulus onset. A 5 s intertrial interval with the grey screen preceded the start of the next trial. Each session contained 64 trials. Once pigeons reached an accuracy criterion of a minimum of 80% correct choices over 2 consecutive days, the percentage of reinforcement for correct choices was decreased over sessions to 75% and then to 50%. Non-reinforced correct choices resulted in termination of the trial without food. This was designed to encourage persistent choice behavior in the subsequent testing phase. The pigeon moved to testing when they reached an accuracy criterion of a minimum of 80% for five consecutive sessions on 50% reinforcement.

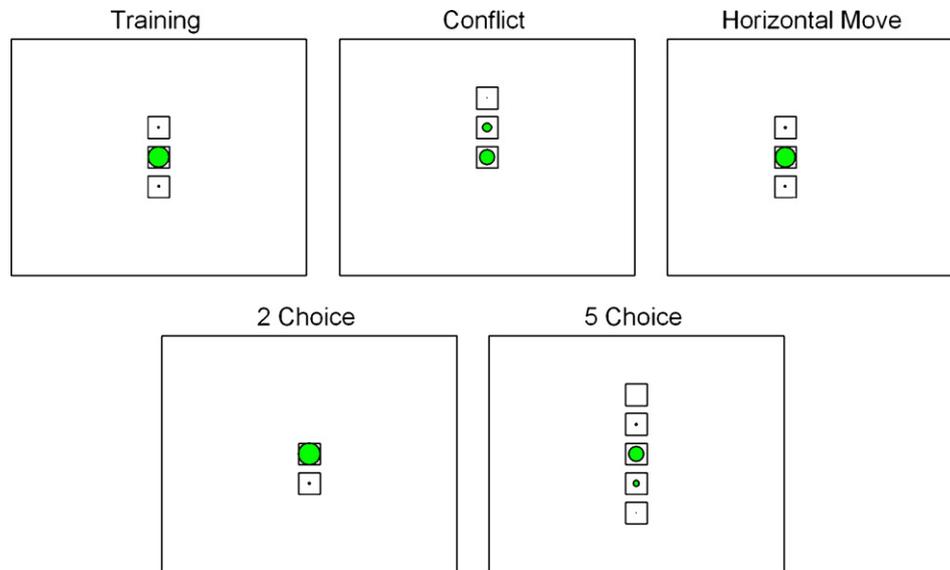


Fig. 1. Proportion plots for each type of test trial in Experiment 1. The small squares are the individual squares of each array and indicate where the array was located on the screen. The size of the shaded circle inside the squares indicates the proportion of choices birds made to that particular location across test trials.

1.1.4. Testing

Ten testing sessions were presented, each containing 36 training trials with reinforcement for correct responses, nine non-reinforced training trials, and 21 non-reinforced probe trials. The order of training and test trials was randomized within each block of 22 trials. There were four types of probe tests. In *Conflict Tests*, the three squares were moved down or up by one grid location; this produced a conflict between the local cues (middle position in the array) and the global cues (location on the screen). In *2-Choice Tests*, either the top or the bottom square was removed, thus eliminating the local cues provided by position in the array. In *Horizontal Move Tests*, the three squares were moved horizontally by one grid location either to the left or the right, but the vertical location of the array remained unchanged. Finally, in the *5-Choice Test*, an extra square was added to each side of the array. In this case, the middle square was still in the globally correct screen location. Depending on how the local information was encoded, any of the three center squares might serve as locally correct locations.

1.1.5. Data analyses

The data in these experiments are frequencies of pecks to each of the presented locations. Following the lead of Brodbeck (1994), we analyzed these frequencies using a replicated G -test of Goodness of Fit (Sokal and Rohlf, 1995), which is distributed as a chi-square but allows one to pool data from several subjects and separate variance due to individual subjects from variance due to choice locations. For each test condition, we report the pooled G -statistic (G_p : which tests whether choice frequencies differ from expected frequencies pooled across all subjects) and the G -statistic for heterogeneity (G_h : which tests for differences among birds). When inter-bird differences were significant, we also report G -statistics for individual birds. All statistics are presented in Appendices A–C. For between condition comparisons (e.g. training to test trials), we calculated the proportion of responses made by each bird to a particular location and then analyzed the results with a paired t -test.

For some test conditions (e.g. *2-Choice* and *Training*), we analyzed responding to all presented locations. However, for other conditions (e.g. *Conflict*) the comparison of interest was between a subset of the locations presented (e.g. globally or locally correct locations). In these cases, we graphically present the frequencies for all presented locations, but we report statistical comparisons

between only the relevant subset. Finally, we summed across tests that were functionally equivalent (e.g. *Conflict Tests* in which the locations were moved up or down) both for graphical presentation and statistical analyses.

1.2. Results

The four pigeons took between 31 and 59 session of training (mean = 42) to reach the criterion required to start testing. During test sessions, accuracy in selecting the middle location in training trials was high for all birds (78–90%, mean = 84%) and was significantly above chance (33%), $t(3) = 15.6$, $p < .01$.

Fig. 1 shows choice behavior on each type of test trial. The outlined squares indicate the particular choice locations available on a particular trial type, and the size of the filled square corresponds to the proportion of choices of that location.

In *Conflict Tests*, birds chose the globally correct location most frequently and the locally correct location with the next highest frequency. The location that was neither globally nor locally correct was never chosen by one bird and infrequently chosen by the remaining birds. A comparison of the frequencies to the globally or locally correct locations revealed that most choices were to the globally correct location, $G_p(1) = 19.6$, $p < .001$ but inter-bird differences were also significant, $G_h(3) = 8.7$, $p < .05$. Two of the four birds showed a significant preference for the globally correct location. The remaining two birds showed a non-significant preference for the globally correct location. In *2-Choice Tests*, the birds showed a significant preference for the globally correct location, $G_p(1) = 231.2$, $p < .001$ and there was no significant inter-bird variation. Moving the vertical array to the left or right in *Horizontal Move Tests* had little apparent effect on choice behavior: the birds continued to show highly significant choice of the middle location compared to the two outer locations, $G_p(1) = 319.8$, $p < .001$ and there was no significant variation among birds. Moreover, the proportion of choices in the vertically central location in *Horizontal Move* trials (82%) was not significantly different from that in training trials (84%), $t(3) = 1.56$, $p > .1$. The birds also continued to respond most frequently to the middle location in the *5-Choice Test* in which an extra location was added above and below the array. Comparison of choices to the middle location vs. the two inner locations revealed above chance choice of the middle location, $G_p(1) = 59.02$,

$p < .001$ with no significant inter-bird variation. However, choice of the center location (63%) was lower than in training trials and this decrease approached significance, $t(3) = 2.98$, $p < .06$. In summary, the birds appeared to be unaffected by a small horizontal shift in location but were slightly affected by the addition of two outside locations in the *5-Choice Test*.

1.3. Discussion

The results of Experiment 1 indicate stronger control by the global vertical location on the screen than by the local position in the array. Specifically, pigeons showed strong control by the globally correct vertical location in *2-Choice Tests* when only global information was available and control by the global location dominated when local and global cues were placed in conflict. This dominance of global over local cues contrasts with the results found by Spetch and Edwards (1988) for pigeons in an open room. It seems possible that global vertical location is highly salient to a pigeon pecking on a computer screen because distinct proprioceptive cues would be correlated with pecking at different heights. If so, then global location may be less dominant in the horizontal dimension. Experiment 2 was similar to Experiment 1 except that the training array was aligned horizontally rather than vertically, and some additional tests were included.

2. Experiment 2: Horizontal array

2.1. Method

2.1.1. Subjects

The subjects were seven adult pigeons (*C. livia*) with varied previous experience in tasks conducted on computer screens. None had any previous training with tasks requiring a choice among discrete spatial locations. The birds were maintained and housed as described in Experiment 1.

2.1.2. Stimuli and apparatus

The stimuli and experimental chambers were the same as described in Experiment 1. In training, three choice squares were aligned horizontally on the computer screen (see Fig. 2). The correct location was five grid locations from the left and three grid locations from the top of the screen. In testing, the number and location of the squares varied across trials.

2.1.3. Training

The procedure was identical to Experiment 1 except that during training the three yellow squares were aligned horizontally. A peck to the center square was followed by a food reward, whereas a peck to the left or right square terminated the trial without food. All other aspects of the procedure remained unchanged from Experiment 1.

2.1.4. Testing

Ten testing sessions were presented, each containing 36 training trials with reinforcement for correct responses, 12 non-reinforced training trials, and 30 non-reinforced probe trials. The order of training and test trials was randomized within each block of 26 trials. There were six general types of probe tests. In *Conflict Tests*, the three squares were moved left or right by one location; this produced a conflict between the local (middle position in the array) and global cues (location on the screen). In *2-Choice Tests*, either the left or the right square was removed, thus eliminating the local cues provided by position in the array. In *Vertical Move Tests*, the three squares were moved down by three locations, but the horizontal location of the array remained unchanged. In *Horizontal Move Tests*, the three squares were moved left or right by three locations, but

the vertical location of the array remained unchanged. In *5-Choice Tests*, an extra square was added to each side of the array. In this case, the middle square was still in the globally correct screen location. Finally, in *5-Choice Horizontal Move Tests*, five squares were presented but the horizontal location of the array was shifted left or right. In these tests, the middle square of the array was shifted by two locations left or right of the middle square in training so that the square on the edge of the array was in the globally correct screen location.

2.2. Results

The seven pigeons took between 16 and 93 session of training (mean = 41) to reach the criterion required to move to testing. During testing, accuracy in selecting the middle location in training trials was high for all birds (69–94%, mean = 78%) and was significantly above chance (33%), $t(6) = 12.4$, $p < .001$.

Test results are shown in Fig. 2. In *Conflict Tests*, birds chose the locally correct location most frequently and the globally correct location with the next highest frequency. The location that was neither globally nor locally correct was never chosen by one bird and infrequently chosen by the remaining birds. In trials in which the birds chose a globally or locally correct location, most choices were to the locally correct location, $G_p(1) = 65.5$, $p < .001$ but inter-bird differences were also significant, $G_h(6) = 20.7$, $p < .01$. Although all seven birds chose the locally correct location most frequently, the degree of preference varied and preference for the locally correct location was not significant for two of the birds.

In *2-Choice Tests*, in which local cues were removed, there was a significant overall preference for the globally correct location, $G_p(1) = 29.15$, $p < .001$. Inter-bird variation was not significant.

In the *5-Choice Tests*, the birds never (three birds) or infrequently (four birds) chose the added locations. Comparison of the middle location to the two inner locations revealed a significant preference for the middle location, $G_p(1) = 24.0$, $p < .001$ with no significant inter-bird variation. Nevertheless, the addition of the two outside locations affected pigeons' choice of the three center locations. Considering only the center three locations, the birds chose the middle location 50% of the time which was significantly lower than choice of the center location in training trials (78%), $t(6) = 7.3$, $p < .001$.

Moving all squares three locations down on the screen in the *Vertical Move Tests* had a substantial effect on the pigeons' behavior. Six of the seven birds failed to peck one of the squares on some of the trials; across all birds an average of 34% of the trials ended without a choice. In the trials in which a peck occurred, the middle square was not chosen significantly more than the two outer locations, $G_p(1) = 0.4$, $p > .05$ and inter-bird variation was also not significant, $G_h(6) = 9.9$, $p > .05$. Only one bird showed a significant preference for the middle location. Thus, the tendency to choose the horizontally middle location did not transfer to an array lower on the screen.

In the *Horizontal Move Test*, four pigeons never chose the square furthest from the training locations and three pigeons chose it only once. Therefore, we compared choice of the locally correct middle square to choice of the outer square that was closest to the training locations. The birds showed a significant preference for the globally closer outer location over the middle location, $G_p(1) = 107.8$, $p < .001$. Although inter-bird differences were also significant, $G_h(6) = 21.08$, $p < .01$ all birds chose the globally correct location more than the middle location and this preference was significant for all but one bird.

Finally, in the *5-Choice Horizontal Move Test*, pigeons rarely (two birds) or never (five birds) chose the two locations farthest from the training area. Choice of the location that was in the middle of the array was also very low (less than 7% of the trials on average with no bird choosing the middle square on more than 12% of the trials).

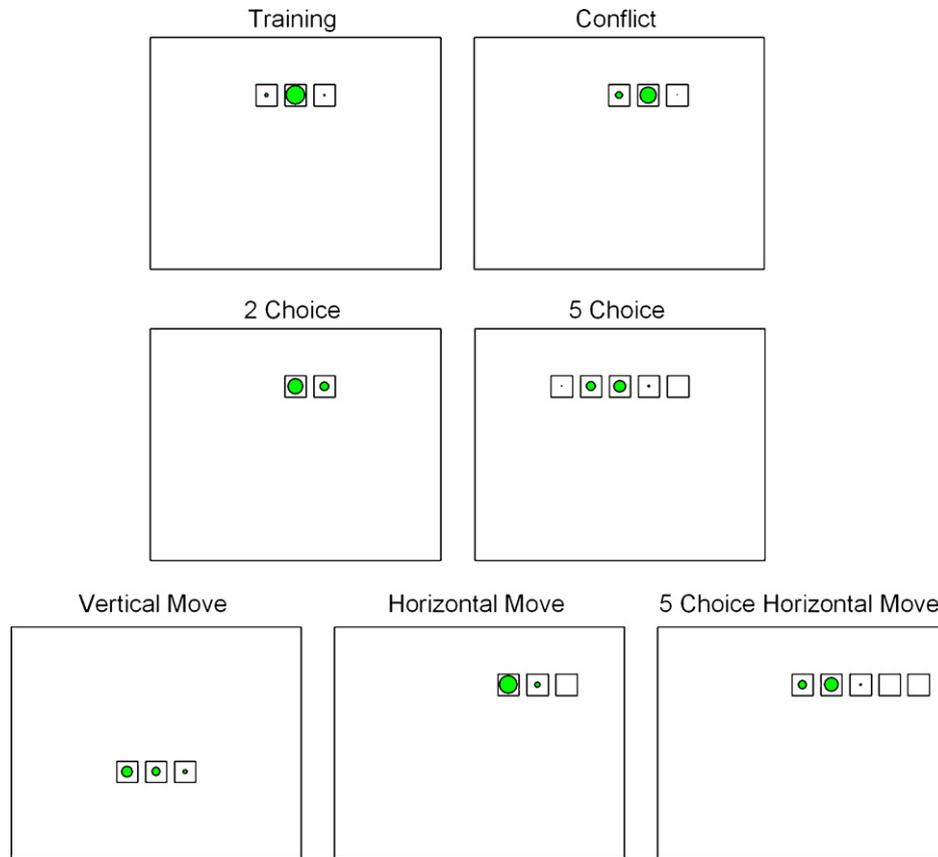


Fig. 2. Proportion plots for each type of test trail in Experiment 2. The small squares are the individual squares of each array and indicate where the array was located on the screen. The size of the shaded circle inside the squares indicates the proportion of choices birds made to that particular location across test trials.

We therefore compared the globally correct outer location to the closest inner location). The birds showed a significant preference for the inner location, $G_p(1) = 20.1, p < .001$. There was no significant inter-bird variability, $G_h(6) = 5.01, p > .05$.

2.3. Discussion

In summary, the results of the *Conflict* and *2-Choice Tests* are similar to those found by Spetch and Edwards (1988) for pigeons in an open room, and they contrast with those found in Experiment 1 with a vertical array. Specifically, pigeons showed hierarchical redundant control by local and global cues: the local position in the horizontal array dominated in *Conflict Tests*, but global location was also encoded. However, the remaining tests indicated that control by local position was constrained by global location cues. When the array was moved far from the correct global location, either in the vertical or horizontal dimension, pigeons did not continue to select the locally correct square. This latter result contrasts with the findings of Spetch and Edwards in the open field. In their study, pigeons continued to choose the locally correct training location even when the array was moved far from the global training location in the room.

In Experiment 3, we trained pigeons with vertical, horizontal and diagonal alignments of the array to provide a within-subject comparison of cue use at different array orientations. Experiment 3 was also designed to assess whether global cues would still exert control if they provided imprecise information in training. Specifically, each array orientation occurred in three different absolute locations on the screen so that, across all trials, the correct global location was a set of nine possible locations rather than single fixed location on the screen (see Fig. 3 for more detail).

Locally Correct Locations in Training

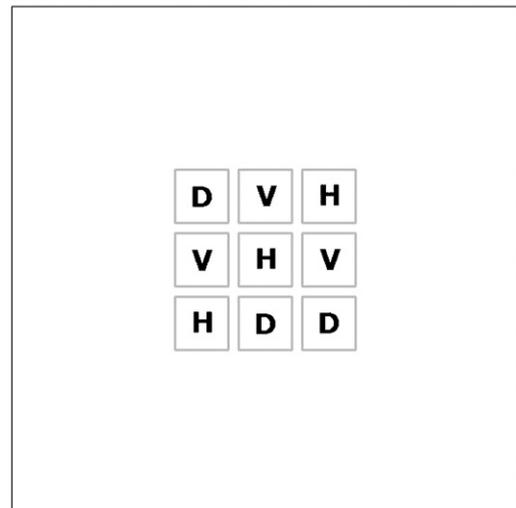


Fig. 3. This figure indicates where on the screen the center (reinforced) square was for each type of training array in Experiment 3. These locations made up the globally correct area of the screen in test trials. The letter inside each square indicates which type of training array had a central square in that particular location. A “D” corresponds to a diagonally oriented training array, a “V” to a vertically oriented training array, and a “H” corresponds to a horizontally oriented training array.

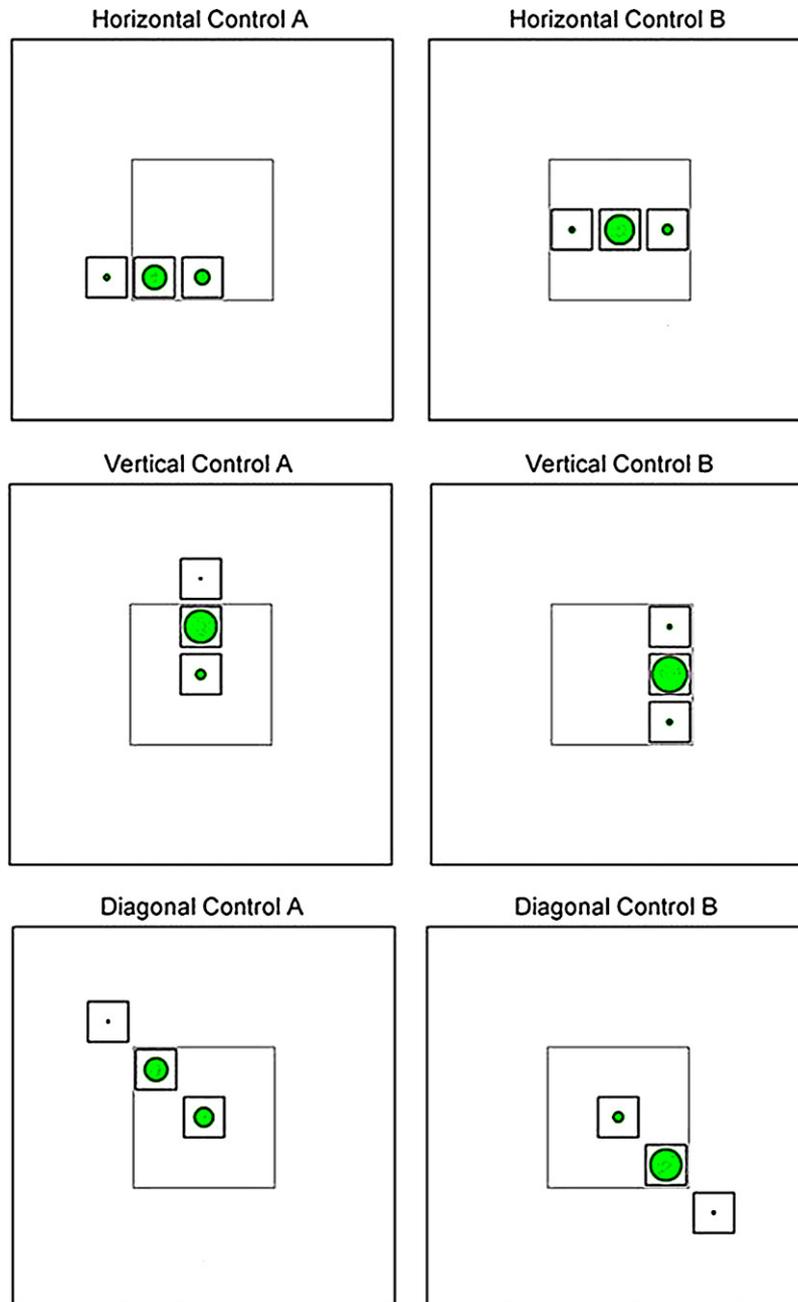


Fig. 4. Proportion plots for each type of control test trail in Experiment 3. The large, central square in all figures indicates the globally correct area of the screen. The small squares are the individual squares of each array and indicate where the array was located on the screen. The size of the shaded circle inside the smaller squares indicates the proportion of choices birds made to that particular location across test trials.

3. Experiment 3: Vertical, horizontal and diagonal arrays

3.1. Method

3.1.1. Subjects

The subjects were seven adult pigeons (*C. livia*) with varied previous experience in tasks conducted on computer screens. None had previously been trained to make a discrete spatial choice. The birds were housed and maintained as described in Experiment 1.

3.1.2. Stimuli and apparatus

Three birds were tested in the same experimental chambers described in Experiment 1. The chamber for the four remaining birds was equipped with a 19-in. monitor and had a 34 cm × 24 cm

opening for the touch frame. Trials began with a white circular (diameter = approximately 3 cm) start stimulus that appeared in a random screen location. The choice stimuli were smaller yellow squares (approximately 2.3 cm × 2.3 cm) than those used in the first two experiments. In training three squares were aligned either horizontally, vertically, or diagonally in a central area of a computer screen with a 3 mm space between each square. In testing, the number and location of the squares varied as described in the testing procedure. The locations of the squares were selected using a 7 × 7 square grid (not visible to subjects) that had a 4.88 cm border on the left and right sides of the screen and a 1.49 cm border on the top and bottom of the screen. This border prevented squares from appearing outside the visible screen area. The border was not visible to subjects.

3.1.3. Training

The pigeons received one session per day, 5 or 6 days per week. All birds first received pretraining to establish reliable pecking at a white circle which appeared randomly on the computer screen. After birds reached a criterion of pecking the white circle 80% of the time within 180 s of it being displayed for 2 consecutive days, subjects were moved to training. In training, the white circle appeared on the screen until the pigeon pecked it, at which time it disappeared and three choice stimuli (i.e. the yellow squares described above) appeared near the middle of the screen in either a vertical, horizontal, or diagonal orientation. For each orientation, the array of choice stimuli occurred equally often in three absolute screen locations. In all cases, the locally correct (middle) square was positioned within a central area of the screen. Across the three orientations, the locally correct square appeared in nine central locations of the 7×7 grid (see Fig. 3 for more detail). After pretraining, subjects received three phases of training, which differed in percentage of reinforcement. The initial training phase provided 100% reinforcement for correct pecks, whereas the second and third training phases provided 75% and 50% reinforcement, respectively. Subjects had to choose the center square in all orientations significantly more often than chance across a 5-day period in order to advance to the next training phase, and across a 10-day period to advance from the final phase of training to testing. Chi-square tests were conducted to determine if these criteria were met.

3.1.4. Testing

Testing consisted of 10 sessions of 72 trials. Each session had 36 training trials, 12 control trials (i.e. non-reinforced training trials; see Fig. 4), and 24 test trials, presented in a random order within blocks of 36 trials. For control tests, two of the three training arrays from each orientation were used. The test trials were novel displays of choice stimuli. For each orientation (i.e. horizontal, vertical and diagonal) there was a 2-Choice Test, a 4-Choice Test and a 5-Choice Test. In the horizontal orientation, there were also two distant array tests (*Far Horizontal A* and *Far Horizontal B*) in which the arrays of three squares were moved to the distant edges of the screen so that they were as far as possible from the globally correct area of the screen. Finally, there was a *Diagonal Rotation Test* in which the horizontal axis of a three square diagonal choice array was transposed so that it was in opposition to the orientation of the diagonal arrays used in training. All birds received all types of tests but the exact position of the array on the screen was as shown in Fig. 5 for four birds only. For the remaining three birds, the screen positions were transposed for tests to ensure that results were not due to specific screen position effects.

3.2. Results

The seven pigeons took between 57 and 102 session of training (mean = 82.42) to reach the criterion required to move to testing. Tests were divided into three categories: horizontally oriented arrays, vertically oriented arrays, and diagonally oriented arrays. Figs. 4 and 5 show choice behavior on each type of test trial. The outlined squares indicate the particular choice locations available in a particular trial type, and the size of the filled circle inside the square corresponds to the proportion of choices to that location. The proportion data is collapsed across all birds for each particular test type displayed.

3.2.1. Horizontally oriented arrays

Subjects received two different control tests. In *Control Test A*, birds chose the locally correct square (i.e. the middle square) sig-

nificantly more often than the two outside squares. The middle square and one of the outside squares were within the globally correct area of the screen. A comparison of frequencies between the middle square and the two outside squares revealed that birds significantly selected the locally correct location more often than the other two locations, $G_p(1) = 103.27$, $p < .001$, but there were significant differences among birds, $G_h(6) = 14.02$, $p < .01$. All but one of the birds showed a significant preference for the locally correct square; the remaining bird did not show a preference for either square.

In *Control Test B*, birds chose the locally correct square significantly more often than the two outside squares. All three squares were within the globally correct area of the screen. A comparison of frequencies between the middle square and the two outside squares revealed that birds significantly selected the locally correct location more often than the other two locations, $G_p(1) = 43.18$, $p < .001$, but there were significant differences among birds, $G_h(6) = 18.54$, $p < .05$. While the majority of birds significantly preferred the locally correct square, two of the birds did not display a preference for any square.

In *2-Choice Tests*, there was no locally correct location but one of the two squares was in the globally correct area of the screen. A comparison of frequencies between the two locations revealed that there was no significant difference between the selection of the globally correct square compared to the other square $G_p(1) = 1.38$, $p > .05$, but there were significant differences among birds, $G_h(6) = 28.32$, $p < .001$. Five of the birds did not show a preference for either square; the remaining two birds displayed a preference for the square that was not in the globally correct location of the screen.

In *4-Choice Tests*, there was once again, no locally correct location, and none of the four squares were within the globally correct area of the screen experienced during training. However, we thought it likely that, although there was no true locally correct location, birds may treat both of the inner two squares as locally correct. A comparison of frequencies between the inner two locations compared to the outside two locations revealed that birds significantly preferred the inner squares to the outer squares, $G_p(1) = 56.98$, $p < .001$. There were no significant differences among birds, $G_h(6) = 8.28$, $p > .05$.

In *5-Choice Tests*, there was a locally correct location (i.e. the middle square), and three globally correct locations (i.e. the inner three squares). The frequencies of choices to the outer two locations were very low, and thus were excluded from the analysis. A comparison of frequencies of the middle square to the other two inner squares revealed no significant difference, $G_p(1) = .67$, $p > .05$. There were no significant differences among birds, $G_h(6) = 4.34$, $p > .05$.

In the *Far Horizontal A* tests, none of the squares were in the globally correct area of the screen, but the middle square was locally correct. A comparison of the frequencies to the locally correct location compared to the other two locations revealed a significant preference for the locally correct location, $G_p(1) = 19.15$, $p > .001$. However, there were significant differences among birds, $G_h(6) = 26.01$, $p < .001$. Four of the seven birds significantly preferred the middle square, one bird significantly preferred the outer two squares, and two birds did not display a significant preference for any square.

In the *Far Horizontal B* tests, none of the three squares were in a globally correct area of the screen, but the middle square was locally correct. A comparison of the frequencies to the locally correct location compared to the other two locations revealed a significant preference for the locally correct location, $G_p(1) = 45.30$, $p < .001$. However, there were significant differences among birds, $G_h(6) = 31.78$, $p < .001$. Five of the seven birds displayed a significant

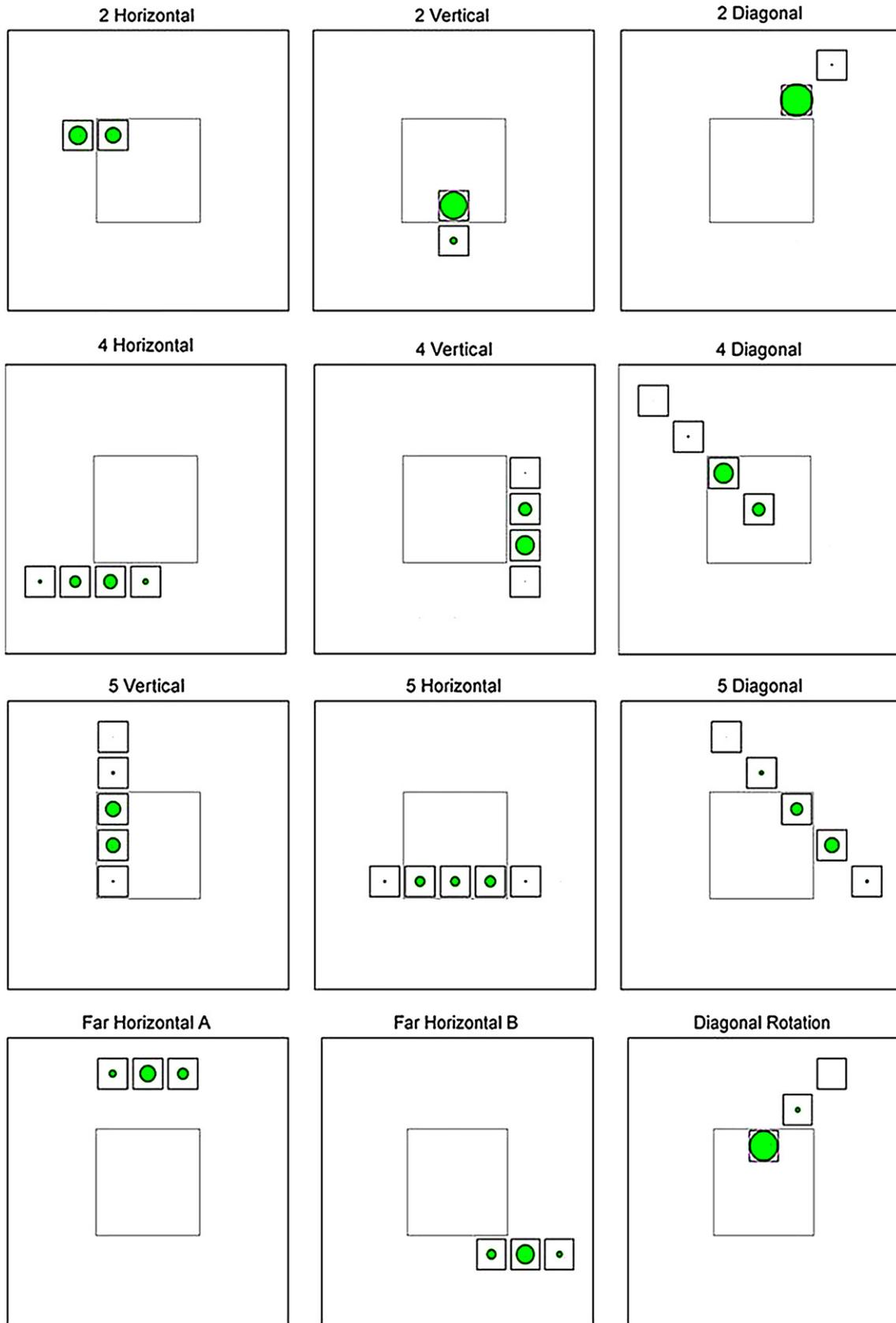


Fig. 5. Proportion plots for each type of test trial in Experiment 3. The large, central square in all figures indicates the globally correct area of the screen. The smaller squares indicate the individual squares of each array and indicate where the array was located on the screen for the first four birds. Arrays for the remaining three birds were transposed for all tests. However, because there was no significant difference among birds who received the arrays depicted above and those who received transposed arrays, data was collapsed. The size of the shaded circle inside the smaller squares indicates the proportion of choices birds made to that particular location across test trials.

preference for the middle square, while two of the birds did not display a significant preference for any square.

3.2.2. Vertically oriented arrays

In *Control Test A*, birds chose the locally correct square (i.e. the middle square) more often than the two outside squares. The middle square and one of the outside squares were inside the globally correct area of the screen. A comparison of frequencies between the middle square and the two outside squares revealed that birds significantly preferred the locally correct location more often than the two outside locations, $G_p(1) = 160.22$, $p < .001$, but there were also significant differences among birds, $G_h(6) = 24.28$, $p < .001$. Six of the seven birds preferred the locally correct square, while one bird did not display a significant preference for any square.

In *Control Test B*, birds chose the locally correct square more often than the two outside squares. All squares were within the globally correct area of the screen. A comparison of frequencies between the middle square and the two outside squares revealed that birds significantly selected the locally correct location more often than the other two locations, $G_p(1) = 221.66$, $p < .001$. There were no significant differences among birds, $G_h(6) = 12.04$, $p > .05$.

In *2-Choice Tests*, there was no locally correct location but one of the two squares was in the globally correct area of the screen. Overall, birds chose the globally correct square more often than the other, non-globally correct square. A comparison of frequencies between the two locations revealed that birds displayed a significant preference for the globally correct square, $G_p(1) = 100.18$, $p < .001$, but there were also significant differences among birds, $G_h(6) = 20.74$, $p < .01$. While six of the seven birds displayed a significant preference for the globally correct square, one bird did not display a significant preference for either square.

In *4-Choice Tests*, there was no locally correct location, and none of the four squares were within the globally correct area of the screen. However, the birds might treat both of the inner two squares as locally correct. A comparison of frequencies between the inner two locations compared to the outside two locations revealed that birds significantly preferred the inner squares to the outer squares, $G_p(1) = 223.38$, $p < .001$. There were no significant differences among birds, $G_h(6) = 8.05$, $p > .05$.

In *5-Choice Tests*, there was a clear locally correct location (i.e. the middle square), and three locations within the globally correct area of the screen (the middle square, one inner square and one outer square). The frequencies of choices to both outer locations were very low, and thus were excluded from the analysis. A comparison of frequencies between the middle location and to the two inner squares revealed that birds displayed a significant preference for the middle location, $G_p(1) = 18.49$, $p < .001$, but there were also significant differences among birds, $G_h(6) = 36.13$, $p < .001$. Only two of the seven birds displayed a significant preference for the middle location. Four birds did not display a significant preference for any square, while one bird displayed a significant preference for the inner squares. Due to this high level of inter-bird variability, two further comparisons were conducted.

First, we compared choices of the inner square that was outside the global area to choices of the inner square that was inside the global area. Birds significantly preferred the globally correct inner square to the non-globally correct inner square, $G_p(1) = 63.90$, $p < .001$, but there were significant differences among birds, $G_h(6) = 38.13$, $p < .001$. Five of the seven birds displayed a significant preference for the globally correct inner square, while two birds did not display a preference for any square.

Second, we compared choices of the globally correct inner square to the middle square, which was locally correct and within the globally correct area of the screen. Birds did not display a signif-

icant preference for either square, $G_p(1) = .11$, $p > .05$, but there were significant differences among birds, $G_h(6) = 53.98$, $p < .001$. Two out of seven birds displayed a significant preference for the middle square, two birds did not display a preference for either square, and three birds displayed a significant preference for the globally correct inner square.

3.2.3. Diagonally oriented arrays

In *Control Test A*, birds chose the locally correct square (i.e. the middle square) significantly more often than the two outer squares. The middle square, and one of the outside squares were inside the globally correct area of the screen. A comparison of frequencies between the middle square and the two outer squares revealed that birds displayed a significant preference for the locally correct location, $G_p(1) = 34.92$, $p < .001$, but there were significant differences among birds, $G_h(6) = 14.66$, $p < .05$. While six of the seven birds displayed a significant preference for the locally correct square, one bird did not display a preference for any square.

In *Control Test B*, birds chose the locally correct square significantly more often than the two outer squares. The middle square and one of the outside squares were inside the globally correct area of the screen. A comparison of frequencies between the middle square and the two outer squares revealed that birds displayed a significant preference for the locally correct location, $G_p(1) = 141.06$, $p < .001$, but there were significant differences among birds, $G_h(6) = 14.97$, $p < .05$. While six of the seven birds displayed a significant preference for the locally correct square, one bird did not display a preference for any square.

In *2-Choice Tests*, there was no locally correct location and neither square was in the globally correct area of the screen. However, one of the squares was closer to the globally correct area of the screen than the other. A comparison of frequencies between the two locations revealed that birds displayed a significant preference for the square closest to the globally correct area of the screen, $G_p(1) = 245.67$, $p < .001$, but there were also significant differences among birds, $G_h(6) = 54.93$, $p < .001$. While six of the seven birds significantly preferred the square closest to the globally correct area of the screen, one bird did not display a preference for either location.

In *4-Choice Tests*, there was once again, no locally correct location but birds may treat both of the inner two squares as locally correct. Two of the four squares (one inner and one outer square) were within the globally correct area of the screen. A comparison of frequencies between the two inner locations and the two outer locations revealed that birds displayed a significant preference for the inner squares, $G_p(1) = 13.97$, $p < .001$, but there were significant differences among birds, $G_h(6) = 35.73$, $p < .001$. Only two of the seven birds displayed a significant preference for the inner squares; the remaining five birds showed no significant preference. Only one of the inner squares was within the globally correct area of the screen. A comparison of frequencies between the globally correct inner square and the other inner square that was outside the globally correct area revealed that birds displayed a significant preference for the globally correct inner square, $G_p(1) = 136.54$, $p < .001$, but there were significant differences among birds, $G_h(6) = 15.97$, $p < .05$. All birds significantly preferred the globally correct inner square to the other inner square, but the magnitude of their preference varied.

In *5-Choice Tests*, the middle square was both locally and globally correct. None of the other squares were in the globally correct area of the screen. The frequencies of choices to the two outer squares were very low, and thus were excluded from the analysis. Therefore, we analyzed the middle square against the two inner squares.

A comparison of frequencies revealed that birds did not display a significant preference for the middle square which was both locally and globally correct, $G_p(1) = 3.63$, $p > .05$. However, there were significant differences among birds, $G_h(6) = 20.34$, $p < .01$. Only one of the seven birds displayed a significant preference for the middle square.

In *Diagonal Rotation Tests*, one of the outside squares was in the globally correct area of the screen. The other outside square was neither locally or globally correct. None of the birds ever selected the square that was neither globally or locally correct and thus it was excluded from the analysis. A comparison of frequencies between the locally (i.e. middle) and globally correct (i.e. outside) squares revealed that birds displayed a significant preference for the globally correct square, $G_p(1) = 143.38$, $p < .001$, but there were significant differences among birds, $G_h(6) = 38.19$, $p < .001$. Six out of the seven birds displayed a significant preference for the globally correct location, while one bird did not display a preference for either square.

3.3. Discussion

Clearly, hierarchical control by local and global cue information is variable and depends on the type of spatial information encoded. Specifically, when the local spatial cues were horizontally aligned, local cue information appeared to dominate and overshadow global cue information. This is best shown by results from the horizontal *2-Choice* and *4-Choice Tests* where local cues were absent or ambiguous and the pigeons did not seem to rely on global cues. However, when the local spatial cues were either vertically or diagonally aligned, global cue information seemed to dominate local cue information. This is evidenced by results from the vertical *2-* and *5-Choice Tests*, as well as the diagonal *2-Choice*, *4-Choice*, and *Rotation tests*. In sum, the results of Experiment 3 suggest that pigeons' hierarchical ordering of local and global cues for retrieval depends on the orientation of the information being encoded. When stimuli are horizontally aligned, local cues seem to be preferred to global cues. When stimuli are vertically or diagonally aligned, pigeons appear to prefer global cues to local cues, but they can use local cues when global information is not present or is ambiguous.

4. General discussion

Our experiments demonstrate that the hierarchical ordering of spatial information varies according to the type of spatial information being encoded. When arrays were horizontally aligned, pigeons primarily attended to and used local cues. In contrast to this, when arrays were vertically or diagonally aligned, pigeons primarily attended to and used global cues. These findings indicate that the hierarchical organization of spatial information is flexible and that the cues pigeons use depend in part upon environmental factors.

Our finding that pigeons rely on global cues much more when arrays are vertically aligned is interesting and could reflect the operation of a gravity-defined privileged axis. Results suggesting that gravity-defined axes may be privileged have been reported in various species (e.g. bees, Cartwright and Collett, 1982; ants, Rossel and Wehner, 1986; humans, Kelly and Spetch, 2004a; pigeons, Kelly and Spetch, 2004b). Vertically aligned arrays that were presented against a stable environmental background such as the computer screen may have encouraged orientation-specific encoding of global cue information. To determine if this was the reason for the enhanced control by global cues in vertically aligned arrays,

it would be interesting to test pigeons in an operant box in which a touch screen is horizontally positioned on the floor (e.g. Wright et al., 1988), thus alleviating the potential effects of gravity.

Alternatively, the stronger control by global cues in the vertical dimension could have been influenced by the orientation of the rectangular frame provided by the monitor. Specifically, pigeons may have used distance from an edge as a global cue. If so, they may have found it easier to judge the absolute goal location in the vertical dimension because distance to the nearest edge is smaller than in the horizontal dimension. Future tests that vary the orientation of the monitor and/or the absolute location of the goal on the screen (e.g. center of the screen or nearer to an edge) may help to reveal the type of global cues pigeons use.

A second notable finding of our experiments was that even with the horizontal arrays in which local cues were preferred in *Conflict Tests*, the control by local cues was constrained by global cues. Specifically, when the globally correct area of the screen was a single fixed location (i.e. Experiments 1 and 2), pigeons did not continue to prefer the locally correct square in tests in which the array was moved far from the globally correct area of the screen. This contrasts with the findings of Spetch and Edwards (1988) in which pigeons continued to choose the locally correct location even when the array was moved far from the global training location in the open field. It may be that global cues are more salient in touch screen tasks than in open-field tasks, perhaps due to inherent differences between the tasks such as the size of the search space and the type of movement required to reach the goal. When the globally correct area of the screen was a range of locations (Experiment 3), control by local cues appeared to be less constrained by global location in the horizontal dimension, but strong control by global cues still appeared in the vertical and diagonal dimensions.

Finally, we observed considerable individual variability among birds, even when the results were significant overall in many of the tests. Although this was not expected, it is consistent with other experiments investigating the hierarchical organization of local and global cues in spatial tasks (e.g. adult humans, Steck and Mallot, 2000). This potential for high levels of individual variability, coupled with evidence that the hierarchical organization of spatial information is pliable and depends upon environmental factors is evidence that researchers should carefully consider the types of tasks used when comparing spatial strategies across species.

There are several areas of future research that would be useful to conduct. One such area would be to further examine how lateralization of brain functioning influences the way in which spatial information is hierarchically organized. Several recent studies have begun to investigate the neurological bases of spatial navigation, especially in respect to encoding of local and global information (e.g. Tommasi and Vallortigara, 2004; Vallortigara et al., 2004). The avian visual system is strongly lateralized, thus most of what is seen by the left eye is processed by the contralateral hemisphere (i.e. right hemisphere) and vice versa (Cheng et al., 2006). Consequently, hemispheric control can be studied by occluding one eye during training and/or testing. Research in birds has indicated that the right hemisphere relies mainly on global cues and the left hemisphere relies on both global and local cues for navigation (Prior et al., 2002; Vallortigara et al., 2004). When birds are trained binocularly with both local and global cues, tests in which either the left or right eye is occluded can affect which cue is used most dominantly. Tommasi and Vallortigara (2004), for example, trained chicks to find food near a landmark in the center of a square arena. During monocular tests, the landmark was shifted to one corner of the arena.

Chicks tested with their left eye (right hemisphere), tended to use the global information and searched predominantly in the center of the arena. Conversely, chicks tested with their right eye (left hemisphere) relied on the local information provided by the landmark, searching mainly in the corner of the arena. However, there is some evidence that positional information is processed similarly to larger scale global information (Tommasi et al., 2000). Specifically, chicks were trained such that both colour and positional cues indicated the goal location. When the cues were placed in conflict, chicks tended to prefer the colour cue, but left-eyed chicks were more likely than right-eyed or binocular chicks to choose the positional location. Thus, further investigation into lateralization of local positional cues vs. global spatial cues is warranted. This line of research would be especially interesting in light of the differences we found between horizontal and vertical arrays. Specifically, are arrays of different orientations processed differently within the avian brain?

The malleability of preferential cue use is another interesting area for future research. A recent study by Brown et al. (2007) showed that rearing environment can alter preferential use of geometric and feature information in fish. In tests in which geometry and features were placed in conflict, fish that had been raised in a circular tank showed significantly less use of geometric information than fish that had been raised in a rectangular tank. It would be interesting to examine whether rearing conditions also affect

preferences for local position and global location cues. For example, if an animal was raised in an environment in which global cues were constantly changing, would that animal be more predisposed to rely on local cues in new situations?

In summary, the research presented in this paper adds to the literature suggesting that spatial information is hierarchically organized. Our findings also suggest that the hierarchical ordering of spatial information differs depending on the orientation of the spatial array. With horizontal arrays, pigeons strongly preferred local cues but they encoded global cues as well. With vertical or diagonal arrays, global cues dominated. The malleability and neural basis of the effect of orientation are interesting questions for future research.

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Appendix A

Experiment 1: Vertical orientation

Test	$G_h(df=3)$	$G_p(df=1)$	Individual birds			
			1	2	3	4
Training, <i>middle vs. outer</i>	59.02	2643.89	503.05 ^c	829.61 ^c	845.06 ^c	525.19 ^c
Conflict, <i>global vs. local</i>	8.69	19.58	20.12 ^c	0.80 ^{ns, c}	1.05 ^c	6.29 ^c
2 Choices, <i>global vs. other</i>	2.18 ^{ns}	231.20	54.63 ^c	73.50 ^c	54.63 ^c	50.62 ^c
Horizontal Move, <i>middle vs. outer</i>	5.58 ^{ns}	319.81	58.08 ^c	86.75 ^c	107.03 ^c	73.53 ^c
5 Choices, <i>middle vs. inner</i>	3.39 ^{ns}	59.02	25.59 ^c	14.17 ^c	5.97 ^c	16.69 ^c

This table reports all G -statistics from replicated G -tests for Goodness of Fit. Each replicated G -test for Goodness of Fit is reported for the most informative test we conducted for each array type. The specific comparison the replicated G -test for Goodness of Fit that we are reporting is specified in italicized text in the first column. In this table, G_h represents the G -statistic for heterogeneity among birds and G_p represents the pooled G -statistic for a particular test. G -statistics for individual birds are also reported. A superscript ns by a value indicates that it was not significantly different from chance ($p < .05$). When reporting G -statistics for individual birds, a superscript c indicates that performance was congruent with our hypothesis for that test, while a superscript r indicates it was not. A superscript e indicates that values were equal for all cells, thus showing no preference.

Appendix B

Experiment 2: Horizontal orientation

Test	$G_h(df=6)$	$G_p(df=1)$	Individual birds						
			1	2	3	4	5	6	7
Training, <i>middle vs. outer</i>	179.22	2803.26	281.09 ^c	396.98 ^c	823.59 ^c	394.10 ^c	262.49 ^c	250.48 ^c	573.74 ^c
Conflict, <i>global vs. local</i>	20.67	65.46	3.99 ^c	0.02 ^{ns, c}	23.13 ^c	22.15 ^c	16.30 ^c	3.41 ^{ns, c}	17.14 ^c
2 Choices, <i>global vs. other</i>	10.47 ^{ns}	29.15	2.42 ^{ns, c}	23.13 ^c	4.32 ^c	4.32 ^c	1.07 ^{ns, c}	3.30 ^{ns, c}	1.07 ^{ns, c}
5 Choices, <i>middle vs. inner</i>	1.75 ^{ns}	24.03	1.10 ^{ns, c}	3.53 ^{ns, c}	4.83 ^c	3.53 ^{ns, c}	2.28 ^{ns, c}	7.75 ^c	2.76 ^{ns, c}
Vertical Move, <i>middle vs. outer</i>	9.89 ^{ns}	0.41 ^{ns}	0.43 ^{ns, c}	4.16 ^c	0.00 ^{ns, e}	1.62 ^{ns, r}	1.30 ^{ns, c}	2.27 ^{ns, r}	0.53 ^{ns, r}
Horizontal Move, <i>global vs. middle</i>	21.08	107.79	2.89 ^{ns, c}	48.76 ^c	11.65 ^c	24.10 ^c	7.64 ^c	22.19 ^c	11.65 ^c
5 Choices Move, <i>inner vs. global</i>	5.01 ^{ns}	20.13	0.64 ^{ns, c}	0.86 ^{ns, c}	7.92 ^c	3.99 ^c	6.97 ^c	0.46 ^{ns, c}	4.30 ^c

This table reports all G -statistics from replicated G -tests for Goodness of Fit. Each replicated G -test for Goodness of Fit is reported for the most informative test we conducted for each array type. The specific comparison the replicated G -test for Goodness of Fit that we are reporting is specified in italicized text in the first column. In this table, G_h represents the G -statistic for heterogeneity among birds and G_p represents the pooled G -statistic for a particular test. G -statistics for individual birds are also reported. A superscript ns by a value indicates that it was not significantly different from chance ($p < .05$). When reporting G -statistics for individual birds, a superscript c indicates that performance was congruent with our hypothesis for that test, while a superscript r indicates it was not. A superscript e indicates that values were equal for all cells, thus showing no preference.

Appendix C

Experiment 3: Horizontal, vertical and diagonal orientations

Test	$G_h(df=6)$	$G_p(df=1)$	Individual birds							
			1	2	3	4	5	6	7	
Horizontal tests	Control A, <i>middle vs. outer</i>	14.02	103.27	33.48 ^c	8.62 ^c	34.78 ^c	17.42 ^c	7.58 ^c	0.00 ^{ns, e}	15.42 ^c
	Control B, <i>middle vs. outer</i>	18.54	43.18	5.02 ^c	2.83 ^{ns, c}	4.58 ^c	0.18 ^{ns, c}	28.31 ^c	14.42 ^c	5.39 ^c
	2 Choices, <i>global vs. other</i>	20.32	1.38 ^{ns}	0.02 ^{ns, c}	5.75 ^c	1.48 ^{ns, r}	1.10 ^{ns, r}	0.31 ^{ns, r}	20.72 ^c	0.33 ^{ns, c}
	4 Choices, <i>inner vs. outer</i>	8.28 ^{ns}	56.98	19.03 ^c	1.01 ^{ns, c}	9.22 ^c	9.64 ^c	11.56 ^c	1.10 ^{ns, c}	13.72 ^c
	5 Choices, <i>middle vs. inner</i>	4.34 ^{ns}	0.67 ^{ns}	0.14 ^{ns, c}	0.21 ^{ns, c}	1.39 ^{ns, r}	1.19 ^{ns, r}	0.30 ^{ns, c}	0.09 ^{ns, r}	1.69 ^{ns, r}
	Far Horizontal A, <i>middle vs. inner</i>	26.01	19.15	0.83 ^{ns, c}	11.11 ^c	6.98 ^c	6.27 ^c	3.06 ^{ns, c}	7.22 ^r	9.70 ^c
	Far Horizontal B, <i>middle vs. inner</i>	31.78	45.30	4.79 ^c	2.29 ^{ns, c}	0.07 ^{ns, r}	8.41 ^c	19.65 ^c	24.74 ^c	17.13 ^c
Vertical tests	Control A, <i>middle vs. outer</i>	24.28	160.22	43.24 ^c	11.09 ^c	61.50 ^c	23.74 ^c	5.81 ^c	38.22 ^c	0.91 ^{ns, c}
	Control B, <i>middle vs. outer</i>	12.04 ^{ns}	221.66	27.76 ^c	31.13 ^c	67.59 ^c	38.22 ^c	19.06 ^c	33.01 ^c	16.93 ^c
	2 Choices, <i>global vs. other</i>	20.74	100.18	7.14 ^c	19.50 ^c	38.92 ^c	20.72 ^c	23.17 ^c	1.84 ^{ns, c}	9.64 ^c
	4 Choices, <i>inner vs. outer</i>	8.50 ^{ns}	223.38	47.71 ^c	20.72 ^c	64.50 ^c	18.29 ^c	30.19 ^c	38.82 ^c	11.64 ^c
	5 Choices, <i>middle vs. inner</i>	36.13	18.49	27.76 ^c	1.23 ^{ns, c}	19.13 ^c	1.04 ^{ns, r}	4.79 ^r	0.38 ^{ns, r}	0.30 ^{ns, c}
Diagonal tests	Control A, <i>middle vs. outer</i>	14.66	34.92	2.79 ^{ns, c}	2.83 ^{ns, c}	36.32 ^c	2.29 ^{ns, c}	2.05 ^{ns, c}	3.30 ^{ns, c}	0.00 ^{ns, e}
	Control B, <i>middle vs. outer</i>	14.97	141.06	23.77 ^c	19.06 ^c	49.37 ^c	17.42 ^c	0.91 ^{ns, c}	33.01 ^c	12.50 ^c
	2 Choices, <i>closer to global vs. other</i>	54.92	245.67	85.95 ^c	37.43 ^c	88.72 ^c	33.27 ^c	23.17 ^c	31.88 ^c	0.17 ^{ns, c}
	4 Choices, <i>inner vs. outer</i>	33.73	13.97	0.00 ^{ns, e}	2.50 ^{ns, r}	11.20 ^c	0.18 ^{ns, r}	3.65 ^{ns, c}	30.19 ^c	1.99 ^{ns, c}
	5 Choices, <i>middle vs. inner</i>	20.34	3.63 ^{ns}	7.57 ^r	1.39 ^{ns, c}	3.00 ^{ns, c}	3.73 ^c	3.68 ^{ns, c}	4.60 ^c	0.00 ^{ns, e}
	Diagonal Rotation, <i>local vs. global</i>	38.19	143.38	18.84 ^c	26.26 ^c	67.09 ^c	12.97 ^c	14.78 ^c	41.59 ^c	0.04 ^{ns, c}

This table reports all G -statistics from replicated G -tests for Goodness of Fit. Each replicated G -test for Goodness of Fit is reported for the most informative test we conducted for each array type. The specific comparison the replicated G -test for Goodness of Fit that we are reporting is specified in italicized text in the first column. In this table, G_h represents the G -statistic for heterogeneity among birds and G_p represents the pooled G -statistic for a particular test. G -statistics for individual birds are also reported. A superscript ns by a value indicates that it was not significantly different from chance ($p < .05$). When reporting G -statistics for individual birds, a superscript c indicates that performance was congruent with our hypothesis for that test, while a superscript r indicates it was not. A superscript e indicates that values were equal for all cells, thus showing no preference.

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