Spatial Context Learning in Pigeons (Columba livia)
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CITATION
In a seminal paper in the cognitive sciences, Chun and Jiang (1998) described the contextual cueing paradigm in which they used artificial stimuli and showed that people became faster to locate a target when the background predicted the location of a target compared to when it did not. Here we examined contextual cueing in pigeons for the first time using artificial stimuli and procedures similar to those of Chun and Jiang. In the first test, we had pigeons search for a target among a display of seven distractors; during one condition, the position of the distractors predicted the location of the target, and in the second condition, there was no relationship between the two. In a second test, we presented the pigeons with the predictive displays from Test 1 and a second set of displays that also predicted the location of a target to see if learning about one set of predictive backgrounds disrupted learning about a second set. The pigeons were quick to acquire context-based knowledge and retain that information when faced with additional contexts. The results suggest that contextual cueing can occur for a variety of stimuli in nonhuman animals and that it may be a common mechanism for processing visual information across a wide variety of species.

Keywords: contextual cueing, visual search task, pigeons, predictive scene learning

When an animal moves through an environment, it may perceive a tremendous variety of colors, shapes, textures, and line orientations that comprise the elements of a visual scene. Yet, despite the complexity of an observed scene, animals are able to identify objects that are important for their survival (e.g., prey, mate) from the background features of the scene and respond appropriately. Animals use cognitive mechanisms such as perception, attention, and memory to help them efficiently identify these important stimuli (see Shettleworth, 2009, for a review).

The investigation of the cognitive mechanisms that animals use to visually search for targets such as cryptic prey has long been the basis for interdisciplinary work by both psychologists and evolutionary biologists. For instance, Tinbergen (1960) proposed that a foraging bird that repeatedly encountered the same prey type (more likely for populations with high densities) developed a search image—a remembered representation of the features of the prey—that allowed it to be more efficient during search. That is, the birds were more sensitive (primed) to the features of a prey after recently seeing similar conspecifics. Subsequent laboratory-based work using multiple avian species and methods confirmed the search image hypothesis (Blough, 1989, 1991, 1992; Bond, 1983; Langley, Riley, Bond, & Goel, 1996; Pietrewicz & Kamil, 1979, 1981; Reid & Shettleworth, 1992).

The emphasis of researchers studying the search image and related phenomena has largely been on the features of the prey/target and how they are encoded into memory. However, several sources of information may be available to a predator in an environment to indicate the presence and perhaps the location of prey. One additional source of information that might be used is the nature of the habitat comprising the background of the visual scene. The information in a background is not typically random and tends to show regularities (Gibson, 1963). Researchers have historically been less interested in the background of the search scene and have treated it more as “noise” that can be used to increase or decrease the crypticity of prey during the search process (but see Kono, Reid, & Kamil, 1998). Our knowledge about how the background or contextual information is acquired and how it can direct search in nonhuman animals, independent of the search image, is surprisingly limited.

In a seminal article in the cognitive sciences, Chun and Jiang (1998) described the contextual cueing paradigm in which they studied how visual background/context information is acquired and how that learning is expressed. Chun and Jiang employed a visual search task in which human participants searched for a rotated letter T, the bottom of which pointed to the left or right...
The target was surrounded by an array of distractors (letter Ls), which were each randomly rotated. Participants were asked to find the target and discriminate, via manual response, whether the T was rotated to the left or right. Chun and Jiang created conditions in which participants would learn that repeated spatial configurations of distractors were paired with target locations. For each participant, the investigators devised a set of 12 invariant or “old” context configurations in which the spatial locations of target and distractor locations were fixed. These 12 configurations were each assigned, in random order, into every block of 24 trials. For the remaining 12 trials in each block, the spatial locations of targets and distractors were generated randomly (“new” context). Chun and Jiang hypothesized that, after repeated exposure to the “old” configurations, participants would learn that each of these configurations reliably predicted the target location—and that the participants would use these associations to facilitate search compared to the “new” condition. Indeed, the results showed that participants became faster to locate the targets in the old context condition compared to the new context condition after a few exposures (although later tests indicated that participants had no explicit knowledge of the old context displays). Thus, contextual information provided by the spatial layout of a set of distractors can cue attention to a target and direct a behavioral response (see also Chun, 2000; Chun & Jiang, 1999, 2003; Chun & Phelps, 1999). The contextual cueing effect has also been extended to research with more naturalistic stimuli. For example, Brockmole and Henderson (2006) had participants search for a target in images of real-world scenes. The participants showed a steady decline in the amount of time it took to find the target during repeated images with the target but not for novel target-image configurations. Thus, regularities in background features of natural scenes also can produce contextual cueing.

Limited recent work on how context can direct search has been conducted with nonhuman primates and pigeons. Goujon and Fagot (2013) have explored contextual cueing in baboons using search task procedures comparable to Chun and Jiang (1998). Baboons, like the human participants reported by Chun and Jiang, were faster to respond to the target (T) when the background was predictive compared to when it was not predictive. Some researchers also have recently examined if nonhuman animals also show contextual cueing for more naturalistic stimuli. Wasserman, Teng, and Castro (2014) had pigeons find a target that was presented on a solid-color background or a colored image of a real-world photograph. The target could be located in one of the four corners of the display on the background. On 80% of the trials, the particular background (either color or real-world image) was paired with an invariant location; on the other 20% of the trials, the background-target location relationship was determined randomly. The birds were faster to respond to the target when it was predicted by the background (context) than when the target location was determined randomly, demonstrating a predictive effect of context. Additionally, the real-world background exerted higher rates of contextual cueing compared to the solid-color background.

In the current study, we used procedures comparable to those of Chun and Jiang (1999) in two separate tests to examine if pigeons show contextual cueing. We used Chun and Jian’s procedures so that we could isolate the spatial configuration information potentially driving contextual cueing, rather than other factors such as conspicuousness or scene categorization that might occur when using natural scenes (see Chun & Jiang, 1998). The distinction is similar to work in animal navigation. Some researchers examine navigation in the natural environment, but it can be difficult to isolate which cues control behavior. In contrast, other researchers study spatial cognition using laboratory-based tests such as the Morris water arena in which spatial cues presented to the animal can be better controlled (see Shettleworth, 2009, chap. 8). The current study is important for several reasons. As mentioned earlier, work on contextual cueing in nonhuman animal is limited. Contextual cueing is an important mechanism for people to effectively search visual scenes (Chun, 2000). Pigeons have an acute visual system that follows a different lineage than that of mammals, and they utilize it to search for food in a rich visual environment. Although mammals and their avian counterparts have different visual systems, both groups may demonstrate contextual cueing given common search demands in their respective environments. Researchers have successfully used pigeons in a variety of visual search tasks, and past work has shown that people and nonhuman animals such as pigeons may process visual information in qualitatively the same way. The same may be true for contextual cueing. The current work represents an important step in addressing these questions.

Method

Animals

We used seven individually housed adult white Carnoux pigeons. We restricted the weight of each pigeon during the course of the study to 85% of its ad lib value. During daily experimental sessions, the birds obtained mixed grain as reinforcement. The experimenter weighed the birds following the conclusion of an experimental session and provided a supplement of mixed grain if necessary to keep a bird at its target weight. The birds had free access to water and grit.

Apparatus

We trained and tested the pigeons in an operant chamber that had a 17-in. high-resolution (1,024 × 768) monitor inserted through the front wall. An infrared touchframe (Elotouch, Menlo Park, CA) surrounding the monitor recorded the Cartesian location of the birds’ responses to stimuli presented on the monitor. We used a feeder in the back wall of the chamber to deliver momentary (~2-s) access to mixed grain following selected responses. We paired a tone with the delivery of food to indicate its availability and to serve as a secondary reinforcer.

Discrimination Training

We presented a black letter T (40 × 40 pixels) on a light gray background on the monitor. The target was rotated on center so that the tail (i.e., bottom part) of the T was either to the left or the right (see Figure 1) during a trial. The direction of the tail of the target was block randomized. Following a peck to this stimulus, left and right rectangular choice keys appeared to the left and right side of the target, respectively. For half of the birds, a peck to the left key was considered a correct choice when the tail of the T was to the right, whereas a response to the right key was considered...
incorrect. When the tail of the T was to the left, the opposite relationship held true—that is, a response to the right key was correct and a response to the left incorrect. For the other half of the birds, the relationship between the direction of the tail of the target and the side of the key that was correct was reversed. Reinforcement was delivered following a correct response (always the tone, but food with 50% probability determined randomly). An incorrect response resulted in the screen going black for 5 s, followed by the initiation of a correction trial, which was a repetition of the same stimulus display used on the previous incorrect trial. The pigeon encountered correction trials until it made the correct response. Each daily session consisted maximally of 20 blocks of 16 trials for a total of 320 trials. Training continued until the birds made 80% correct responses to both the left- and right-tailed T during a single session. The birds were also presented with the target among a seven Os on the display that served as distractors. The procedures for the intermediate phase were identical to those described above and were designed to prepare the birds for encountering more challenging distractors during testing. Because the target was quite different from the distractors, the birds required only one or two sessions of this intermediate training before they reached the criterion and moved on to testing.

Test 1. Each bird was presented with the target (tail to the left or right) that had to be found in a group of seven L-shaped distractors (see Figure 1). During each block of 16 trials, we presented the birds with two different types of trials. During the eight Novel condition trials, we randomly positioned the seven distractors and the target in eight cells of a virtual 64-cell square grid overlaying the monitor. The position of the distractors and the target within a cell was adjusted slightly (~10 pixels) to the north, south, east, or west (randomly determined). The 64-cell grid was divided into four quadrants (up, down, left, and right); the position of the target was randomly assigned to a cell in one of the four quadrants. The position of the target was block randomized in each of the four quadrants across the trials of a daily session. The location of the seven distractors was randomly determined from the remaining 63 locations without restriction for each trial. To make the search task more challenging, we randomly rotated the L-shaped distractors by 0°, 90°, 180°, or 270°. For the eight Repeated condition trials, we created eight configurations of the target and the seven L distractors. The target location within each quadrant was randomly determined for each display, as well as the orientation of the target (i.e., ← or →). The target position was balanced across the four quadrants of the screen. The location of the seven distractors (also rotated on their center as described for the new context condition) was randomly determined from the remaining 63 locations without restriction for these eight displays. These eight repeated configurations then were randomly mixed with the eight new random condition trials to determine the presentation order of each block of the session. A peck of the target resulted in the appearance of the choice keys. A correct response to the target initiated the reward sequence, and errors prompted a correction trial as described above. Each daily session consisted of between 12 and 20 such blocks. We recorded the latency (ms) of the first peck to the target as a dependent measure. The median reaction time (RT) was calculated for each bird and then averaged across birds. These mean RT measures were log transformed prior to performing statistical analysis. We conducted a repeated-measures analysis of variance (ANOVA) using condition (Novel, Repeated) and block as within-subject variables and RT (ms) as a dependent measure. Confidence intervals are reported after the partial eta squared value (ƞ²) for each effect where appropriate.

Five birds encountered 800 trials during Test 1, one bird 544 trials, and one bird 256 trials. The performance of these latter two birds was comparable to the other five birds. These two birds were shifted into Test 2 more rapidly as they served as initial pilots through the Test 1 procedure.

Test 2. One goal of conducting Test 2 was to examine if whether learning about a context—if it occurred in Test 1—is continuous or if it stops once regularities about the background have been acquired. Five of the birds continued into Test 2, because some of the birds in the first study were used in a neural manipulation as part of another study and did not continue forward. Note that our choice of which birds continued in the following tests was not based on their performance in earlier tests but determined by randomization. As in Test 1, the birds encountered the same eight Repeated trials as in Test 1 and eight Novel trials during each block. We also presented the pigeons with a second set of eight repeated configurations (Repeated 2) of the seven distractors relative to the target (as described above) that they had not encountered previously. Thus, during each block of testing, the pigeons encountered eight Repeated trials (the same eight configurations from Test 1), eight Novel trials, and eight Repeated 2 configurations, for a total of 24 trials in each block. If the birds continued to learn about background regularities with new configurations, then the pigeons might be expected to show an RT advantage to the second population of repeated configurations. Likewise, because the pigeons may have already learned about contextual regularities in Test 1, learning about new contexts might be expected to be faster than in Test 1.

Each daily session consisted of approximately 10 blocks for a total of 240 trials. Four of the birds completed 432 trials, whereas one bird completed 96 trials (the bird that completed 256 trials in Test 1). We conducted a within-subjects ANOVA using block and condition (Novel, Repeated, Repeated 2) as variables and RT (ms) as a dependent measure to examine for differences between the conditions.
Results and Discussion

The birds became faster in finding the target during the course of Test 1, resulting in a significant effect of block, \( F(23, 92) = 9.324, p < .001, \eta^2 = 0.700, 117.038, 283.582 \) (Figure 2, top). The ANOVA also revealed a significant interaction between condition and block, \( F(23, 92) = 1.827, p = .23, \eta^2 = 0.314, 0.251, 49.819 \). The effect of the interaction appears to play out in two ways. First, response times for the Novel and Repeated conditions appeared comparable during the first two blocks but diverged after Block 3 until Block 16. We conducted simple planned comparisons examining response times for the first three blocks. As anticipated, there was no reliable difference in response times between the two groups during Block 1, \( t(6) = 1.170, p = .286, -0.059, 0.168 \), and Block 2, \( t(6) = 0.413, p = .694, -0.303, 0.426 \), but the responses times for the two groups started to diverge during Block 3, \( t(6) = 0.413, p = .694, -0.303, 0.426 \). The second phase of the interaction was that by Block 16, the response times for the two groups converged and appeared similar to each other, as at the start of testing. Indeed, comparisons indicated that there was no difference between the groups starting at Block 16, \( F(1, 4) = 0.435, p = .682, \eta^2 = 0.643, 0.000, 6.851 \). The ANOVA we conducted also revealed a marginally significant main effect of condition, \( F(1, 4) = 7.189, p = .055, \eta^2 = 0.643, 0.000, 27.626 \), with the Repeated group showing faster responses times compared to the Random condition when compared across all blocks. Notably, the five birds that were designated to continue on to Test 2 (see below) showed a similar pattern of performance to the entire set of birds used in Test 1 (Figure 2, middle).

When the birds were first introduced to the search task, they learned to search the display and locate the target, and their responses times across both conditions improved, as expected. The birds were also faster in finding the target during the Repeated compared to the Novel condition for the large balance of Test 1. Thus, the pigeons demonstrated the contextual cueing effect and were able to use the repeated arrangement of distractors in the displays (Repeated condition) to more effectively locate a target than when such contextual information was not present (Novel condition). The pigeons acquired knowledge about the target-background relationships rapidly, as the difference in RTs between the two conditions was apparent during the first block of trials. The faster RTs for the Repeated condition were observed both during the learning phase and continued when performance had stabilized. The fact that the pigeons had some intermediate training prior to Test 1 may have facilitated a familiarity of the procedures and resulted in a rapid acquisition of the cueing effect. Interestingly, the RT advantage for the Repeated compared to Novel condition disappeared during the final blocks of Test 1. We are uncertain why this occurred but discuss a few possibilities in more detail in the discussion below.

During Test 2, we presented pigeons with the same repeated displays as in Test 1 (Repeated 1), a new set of repeated displays (Repeated 2), and novel stimulus arrangements (Novel). As can be seen in Figure 2 (bottom), the RTs for the Novel displays were consistently longer across all blocks compared to either the Repeated 1 or Repeated 2 display conditions. Correspondingly, ANOVA revealed a significant main effect of condition, \( F(2, 6) = 15.452, p = .004, \eta^2 = 0.837, 2.654, 82.395 \). Least significant difference comparisons indicated that RTs for the Novel condition were significantly longer compared to the Repeated 1 condition \( (p = .008) \) and marginally significant compared to the Repeated 2 condition \( (p = .072) \). We subsequently performed comparisons of response times for the Novel and the Repeated 2 conditions during the first four blocks. The response times for the Novel and Repeated 2 conditions were comparable during Block 1, \( t(4) = 0.593, p = .585, -4.106,29, 633.657 \); Block 2, \( t(3) = 0.794, p = .485, -3.49,605, 582.089 \); Block 3, \( t(3) = 0.786, p = .489, -360.354, 596.843 \); but diverged at Block 4, \( t(3) = -8.557, p = .003, -169.115, -.77.421 \). Neither the effect of block, \( F(8, 24) = 1.051, p = .428, \eta^2 = 0.259, 0.000, 16.051 \), nor the interaction between condition and block, \( F(16, 48) = 0.359, p = .986, \eta^2 = 0.107, 0.000, 0.000 \), reached significance.

The pigeons were faster to respond to the Repeated 1 displays compared to the Novel displays, indicating that they retained their learning about the relationship between the distractors and the goal during Test 2. The pigeons also learned the new Repeated 2 displays and showed divergence with the Novel condition starting around Block 4, again demonstrating an effect of contextual cueing. Finally, the RTs for the Novel condition were comparable to those observed at the end of Test 1, but the RTs for the Repeated conditions were faster.

In the current study, we used procedures comparable to those of Chun and Jiang (1999) in two separate tests to examine if pigeons show contextual cueing. We used Chun and Jiang’s procedures so that we could isolate the spatial configuration information potentially driving contextual cueing, rather than other factors such as conspicuousness or scene categorization that might occur when using natural scenes. The results from our tests suggest that pigeons demonstrated contextual cueing and that the effect was due to the features of the distractors rather than other display features. Like people, pigeons were faster to respond to displays in which the position of the distractors predicted the target location, compared to displays in which there was no reliable spatial relationship between the two sets of items (e.g., Chun & Jiang, 1998). Pigeons, like people, also showed the contextual cueing effect early during testing (Chun, 2000; Chun & Jiang, 1998). Similar results have also been reported by Brooks, Rasmussen, Hollingworth, and Wasserman (2008) with pigeons and by Brooks, Dai, and Sheinberg (2011) with monkeys using procedures similar to that of Chun and Jiang. Knowledge about the configurations was retained over time across the tests by the pigeons in the current study, and the addition of new configurations did not appear to impair performance based on earlier contextual learning (Test 2), effects that have also been observed for people.

The current findings are also consistent with other work documenting contextual cueing–like effects in nonhuman animals. As mentioned previously, Goujon and Fagot (2013) have explored contextual cueing in baboons using search task procedures comparable to Chun and Jiang (1999). Baboons, like pigeons in the current study and people in past work, were faster to respond to the target (T) when the background was predictive compared to when it was not predictive.

In addition, the current results support other work on contextual cueing with pigeons that have used simple images or scenes. Wasserman, Teng, and Castro (2014) have explored contextual cueing–like effects using somewhat different procedures. These researchers had pigeons find a target (simple image) that was presented on a background that had a unique solid color or real-
Figure 2. The mean log response time (RT) in milliseconds to find the target across blocks of trails during the two tests. During Test 1 (top), the pigeons were presented with Novel and Repeated displays. The middle panel shows the results from the subset of the five birds that continued on to Test 2. Note that the performance of this subset of birds is comparable to the pattern for all seven birds shown in the top panel. During Test 2 (bottom), we presented the pigeons with Novel, Repeated, and Repeated 2 displays. Note that the HE (half-epoch) column on the far left indicates the scores for the first half-epoch of Epoch 1. Every other epoch contains a full 48 trials per epoch. Please see the text for a description of the stimulus conditions for each test. Error bars show SEMs.
world photograph. The birds were faster to respond to the target when it was predicted by the background (context) than when the target location was determined randomly. Additionally, Wasserman, Teng, and Brooks (2014), using similar procedures, recently found that contextual cueing could occur with up to an 8-s delay between the appearance of the scene and the target onset. These authors also found that more global features of the predictive scenes tended to control search rather than more local features of the context.

As mentioned previously, the contextual cueing effect disappeared at the end of Test 1 before reappearing again for the same displays during Test 2. This lapse in spatial cueing is somewhat surprising given that humans retain information about spatial context in memory for at least 1 week (e.g., Chun & Jiang, 2003). The lapse in cueing is unlikely to be due to a floor effect, because when cueing reappeared in Test 2, response times were faster than those observed when contextual cueing was present during Test 1. Also, it is unlikely that the birds failed to retain information about spatial context in memory because the effect returned quite prominently at the beginning of Test 2. Why, then, did the pigeons fail to demonstrate contextual cueing at the end of Test 1? There are several possible explanations. One possibility is that although the birds retained knowledge about the spatial context of the repeated displays, they had encountered a change in motivation toward the end of Test 1 that prevented them from expressing such knowledge. Another related possibility is that the pigeons had shifted their attention primarily to the Novel displays after having well learned the Repeated displays by the end of Test 1. Extended repeated testing with a small number of displays may have exacerbated the shift in attention. Ultimately, we have strong evidence that the spatial contexts were robustly learned and retained across sessions, but we remain puzzled about why the expression of this learning temporarily subsided at the end of Test 1 and hope to address this in future research.

One important facet of contextual cueing in humans is that the process is implicit. Participants do not report knowledge of the spatially correlated displays, even though they encounter them repeatedly in a session. Awareness in nonhuman animals is controversial and difficult to assess (see Shettleworth, 2009, for a review). Thus, although the performance of people and nonhuman animals appears quite comparable based on their performance, it is unclear whether nonhuman animals have knowledge of the repeated displays or whether the effects are operating in the same way.

Past work has revealed that participants show a decrement in learning about background relationships when natural scenes serving as the background are inverted compared to when the images are upright (Brockmole & Henderson, 2006). This suggests that semantic encoding of the background information may be important for people, particularly for natural scenes. Future work also might compare whether pigeons and other nonhuman animals might also show a similar effect or whether performance on a comparable contextual cueing task differs in only the nature of the background information (e.g., scenes vs. artificial stimuli) shows different rates of learning.

Finally, the fact that both nonhuman primates and now pigeons have been shown to demonstrate contextual cueing during a complex visual search task speaks to the ubiquitous nature of the effect. Using background information increases efficiency during the search processes that many animals engage in for survival. Given that pigeons have very different visual systems than do primates, different animals are likely using different neural architectures to solve the same search process. Future work exploring these possibilities would be of considerable interest.

**References**


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