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Visual Search and Attention in Blue Jays (*Cyanocitta cristata*): Associative Cuing and Sequential Priming

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Abstract

Visual search for complex natural targets requires focal attention, either cued by predictive stimulus associations or primed by a representation of the most recently detected target. Because both processes can focus visual attention, cuing and priming were compared in an operant search task to evaluate their relative impacts on performance and to determine the nature of their interaction in combined treatments. Blue jays were trained to search for pairs of alternative targets among distractors. Informative or ambiguous color cues were provided before each trial, and targets were presented either in homogeneous blocked sequences or in constrained random order. Initial task acquisition was facilitated by priming in general, but was significantly retarded when targets were both cued and primed, indicating that the two processes interfered with each other during training. At asymptote, attentional effects were manifested mainly in inhibition, increasing latency in miscued trials and decreasing accuracy on primed trials following an unexpected target switch. A combination of cuing and priming was found to interfere with performance in such unexpected trials, apparently a result of the limited capacity of working memory. Because the ecological factors that promote priming or cuing are rather disparate, it is not clear whether they ever simultaneously contribute to natural predatory search.

Keywords: animal cognition, aves: corvidae, interference, search image

A successful search for complex, natural stimuli usually requires focal visual attention. Subjects can locate any number of conspicuous items without much attentional investment, but camouflaged targets can seldom be detected with a nonattentive search (Wolfe, 1994; Wolfe, Oliva, Horowitz, Butcher, & Bompas, 2002). Attention can be drawn to particular stimulus features through a variety of cognitive processes (Pashler, 1998; Wolfe, 2007). Studies of human visual search have traditionally concentrated on associative cuing. Instructing a subject to search for a green “T” in the next display, for example, cues his attentional focus to a particular combination of shape and color and causes distracting alternatives to be ignored. This process depends on semantic memory for the association between the cuing stimulus (i.e., the words “green T”) and the focal features of the target (Wolfe, 1998). Attention can also be influenced from aspects of the sought-for stimulus and the surrounding environment. In sequential priming (Blough, 1991; Kristjánsson & Campana, 2010), subjects remember features of the last stimulus they discovered. Encoded in working memory, this recent experience provides a template to which subsequent visual input can be compared (Bravo & Farid, 2009).

Sequential priming is pervasive among animals. Tinbergen (1960) first suggested the use of a search template (classically called a “searching image”) to explain the pattern of predation by European tits on woodland insects. He re-

marked that the tits tended to take prey items in nonrandom sequences (Dawkins, 1971). This suggested that the birds were limiting their search to the features of only one of their possible prey types at a time, thereby filtering out alternative stimuli and increasing their ability to detect the focal prey species. Pietrewicz and Kamil (1979) subsequently tested Tinbergen's hypothesis using an operant procedure in blue jays. The jays were trained to peck photographs of camouflaged moths on tree trunks, discriminating them from similar images without moths. Birds were more accurate and faster when the trial sequence included runs of a single moth type than when two moth types were intermixed. Evidence of sequential priming has since been obtained both in pigeons (Blough, 1989, 1991; Bond, 1983; Bond & Riley, 1991; Langley, 1996; Langley, Riley, Bond, & Goel, 1996) and in blue jays (Bond & Kamil, 1999, 2002, 2006). The effect is most apparent when targets are difficult to detect, diverse in appearance, and displayed on complex, textured backgrounds (Bond, 2007). Under these circumstances, attending to the features of the most recently detected target is a fundamental component of visual search for natural stimuli in birds.

Associative cuing has also been thought to play a role in animal visual search. If distinctively different prey occur on characteristic backgrounds or in specific habitats, a visual predator could learn this association and come to anticipate

the features of a particular prey type when it enters an appropriate area (Curio, 1976). In his field study of foraging in carrion crows, Croze (1970) trained his birds to look for red-painted mussel shells in particular areas of ocean beach. When the birds were subsequently offered red shell targets of a novel size and shape, they were most successful in areas where they had previously found red shells. In other locations, the novel red shells were often overlooked. Croze surmised that features of the familiar foraging area associatively cued a search for red targets, a process analogous to contextual cuing in human subjects (Chun, 2000). Similar findings have been reported from the responses of insectivorous birds to visual indications of leaf damage (Heinrich & Collins, 1983; Real, Ianazzi, Kamil, & Heinrich, 1984).

Two operant studies have demonstrated associative cuing in birds. Blough (1989) tested for cuing effects in a discrimination study with pigeons. She used alphanumeric distractors and targets that were cued by particular screen colors. All trials included one of two targets (D or U), but on half the trials, the color cue was uninformative as to which target would be presented. Response time increased with the number of distractors, and the birds took significantly longer to detect ambiguously cued targets, thereby confirming an attentional effect. Belik (2002) subsequently reproduced Blough's results in a detection design using blue jays. The birds were given prior cues—informative, ambiguous, or miscues—to guide a search for dark or light digital moths on a fractal, naturalistic background. There was no effect on accuracy, but the subjects were much slower to detect miscued targets than informatively cued ones. As predicted by studies of natural foraging, avian attention can thus be influenced by both priming and cuing.

If either mechanism can enhance natural visual search, it is reasonable to ask whether priming and cuing produce a similar improvement in target detection. In the strongest form of the template hypothesis (Bravo & Farid, 2009, 2012; Langley, 1996), sensory input is matched against a representation that encodes features of the sought-for stimulus. Focal attention is viewed as a process of activating a particular template, bringing it into working memory as the current attentional filter (Langley, 1996). There is a constraint, however: In a perceptually demanding search only one template can apparently be used at a time (Kristjánsson & Campana, 2010; Langley, 1996). This has been well established in the human visual search literature. It was confirmed, for example, in a thorough signal detection analysis by Gorea and Sagi (2000), and Zhang and his associates (Zhang, Zhang, Huang, Kong, & Wang, 2011) have demonstrated that it is almost certainly attributable to the limited capacity of working memory.

This implies that any cognitive representation corresponding to a particular target type could be recalled to working memory and could guide a comparable attentional search (Wolfe, Butcher, Lee, & Hyle, 2003; Wolfe, Horowitz, Kenner, Hyle, & Vasan, 2004). Do cuing and priming in fact produce similar effects on visual attention? And, because all representations must compete for the same working memory space, do multiple representations result in additive effects on detectability, or do they overwrite or otherwise interfere with one another? In animal research, at least, the question has not proved to be easily addressed. When priming and cuing have been combined in visual searches for naturalistic stimuli, the results have generally been problematic.

Belik's (2002) second experiment with blue jays and digital moths used cuing, priming, both, or neither in a factorial design. She found that sessions involving both forms of attentional guidance showed significantly improved performance, but neither cuing nor priming alone appeared to have any effect. Other blue jay studies of priming and cuing have come to similar conclusions: Priming was most effective when the target was also associatively cued, but no single form of guidance had a significant influence on attention (Dukas & Kamil, 2001; Kono, Reid, & Kamil, 1998). The absence of effects from the single-guided treatments in these studies—in contrast to much of the previous literature—is especially perplexing. Effectively combining priming and cuing on complex, naturalistic backgrounds is apparently very difficult, at least in part for methodological reasons. Performance in a factorial design with two alternative targets is very sensitive to both the similarity between the targets and the asymmetry in their resemblance to the background (Bond & Kamil, 1999). In addition, changing guidance factors between successive daily sessions may produce confounding carry-over effects that disrupt normal performance (Kamil & Bond, 2006).

To explore the relationship between priming and cuing under stable experimental conditions, we trained blue jays to search for complex, naturalistic targets (as in Bond & Kamil, 1999, 2002, 2006), but we adopted Blough's (1989, 1991) discrimination design, presenting targets and comparable distractors on a flat gray background against which all stimuli were clearly visible. The targets were maximally distinctive from one another, while maintaining a sufficient resemblance to the distractors to make discrimination challenging. Most importantly, we divided the study into two successive phases—one with and one without sequential priming—to minimize carry-over effects from prior sessions. Cuing stimuli were presented before the search display, and infrequent probe trials in which the pretrial signal miscued the target type were inserted in each test session. We elicited sequential priming by presenting uniform blocks of the same target type and contrasted the results to sessions in which the targets were presented in randomized order. Combining all sessions within subjects across both phases yielded a full factorial design, enabling us to evaluate the relative effects of priming and cuing and to determine the nature of their interaction in combined treatments.

Method

Subjects

Twelve blue jays (*Cyanocitta cristata*), captured in the field as nestlings and hand-reared in the laboratory, served as subjects. They were housed individually in environmentally controlled rooms (22 °C; 14:10 hr light:dark) and maintained at 85% of their free-feeding weight on a diet of turkey starter, cockatiel pellets, and a vitamin supplement. All subjects were at least three years of age and were initially naïve to operant procedures.

Apparatus

The study was conducted in two identical operant chambers, each with an LCD monitor installed in a 28×21-cm window in the center of the front panel. The monitors were framed with Elotouch infrared touch screens to record peck responses and were protected with foam-padded transparent

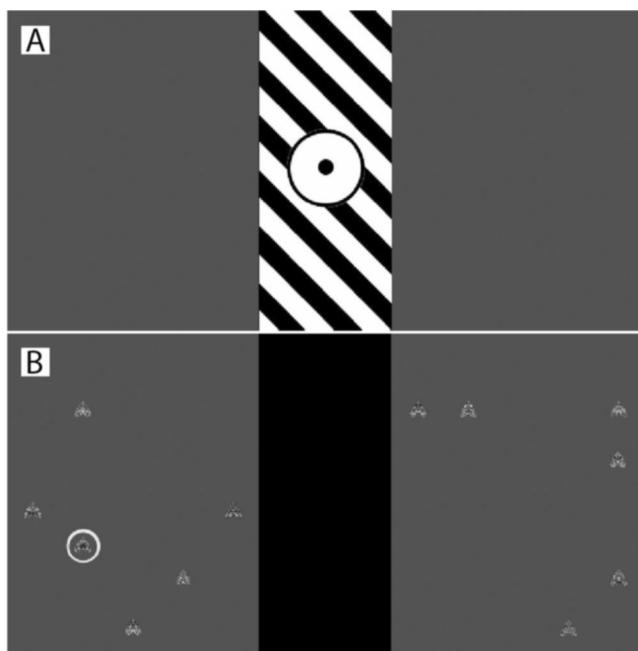


Figure 1. Trial event sequence: A trial begins with the display of a cue strip (A). In this illustration, it is the ambiguous black-and-white strip with oblique lines. When the bird pecks the cue strip three times, it disappears and the lateral search fields are displayed (B). To indicate the difficulty of the discrimination task, the B2 target moth for Subject 2 (see Figure 2) is shown circled in white, along with 11 distractors.

polycarbonate, which provided a resilient pecking surface. Custom-made 45-mg Noyes pellets synthesized from the jays' standard diet served as rewards. The pellets were released from Med Associates dispensers into magazines centered below the screen, where reward delivery was signaled with a food light. Data acquisition and device control were handled using custom software written in C and running on DOS computers. The box interior was diffusely lit, and ambient sounds were attenuated with white noise. Each subject was assigned to a specific operant chamber for all stages of the experiment.

Stimuli

Targets and distractors were bilaterally symmetrical, gray-scale images, originally based on the wing patterns of owl moth (Bond & Kamil, 1999). Onscreen, they appeared as 6.6-mm triangles, about the size and shape of a housefly (Figure 1B). We generated large numbers of these "moth" stimuli by sampling from pixel distributions of images of real moths, and we selected 200 of them for use in the study on the basis of their similar average detectability across a range of fractal backgrounds (Bond & Kamil, 2002). All stimuli were, therefore, roughly equally detailed and complex in appearance. We quantified the visual disparity among all possible pairs of moths using Sneath and Sokal's (1973) measure of phenotypic distance, and we chose 12 unique pairs that were most disparate in appearance to use as targets (Figure 2). Target moths could be confused with some of the distractors but were unlikely to be mistaken for one another. To establish reliable associations between cues and target types, two pairs of targets

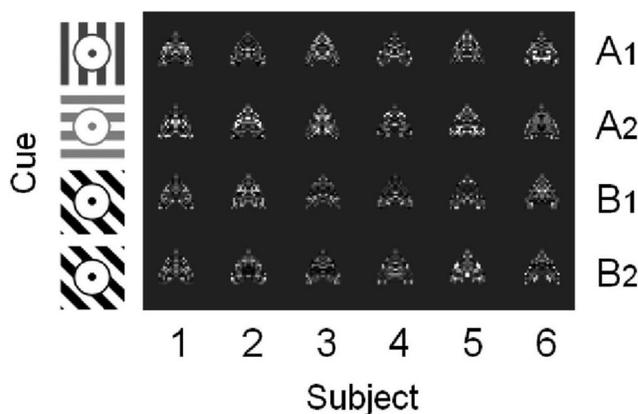


Figure 2. Target and cue assignments. There were six defined sets of four targets, each of which was assigned to two of the 12 subjects. (Two subjects were later dropped prior to their test sessions due to inability to meet the training criterion.) Within subjects, the four targets were chosen to maximize their distinctiveness. Targets in rows A1 and A2 were associatively cued by red vertical or green horizontal cue strips; targets in B1 and B2 were ambiguously cued by the black oblique pattern. Both the A and the B target sets were sequentially primed in half of the experimental sessions.

were assigned to each bird: one for associative cuing and one for sequential priming (target sets A and B in Figure 2). Each of the sets of targets was assigned to two of the birds, one from each of the two operant chambers. The remaining 188 stimuli were used as a pool of potential distractors.

Pre-Training

Jays were habituated to the operant chamber and trained to peck a simple, black-and-white moth centered in a medium-gray, 34×34-mm square. They then learned to peck a central "start" key (a 27-mm white disk with a black spot in the center) to initiate trials of the training moth. We introduced the full test display in stages. First, the training moth was presented somewhere in one of two 9.5×12.2-cm fields of medium-gray background that were displayed on each side of the start-key area. Subsequently, the start key was switched to a cue strip, a 5.0×12.2 cm rectangle with the original start key in the center surrounded with oblique black lines (Figure 1A). One peck to the cue strip brought up the background fields on either side of it (Figure 1B). Initially, the strip remained present, though unresponsive, after the target fields were shown. In the final training stage, three pecks had to be delivered to the cue strip alone to bring up the background fields, and the cue disappeared prior to the target display (Figure 1). At this point, we began discrimination training with target and distractor moths.

Trial Event Sequence

Each trial displayed one target and from 0 to 11 distractors. Distractor moths were a random sample from the pool of alternative stimuli, and the target and distractors were randomly distributed across the background fields (Figure 1B). There were 30 equally spaced locations in each field to which a stimulus could be assigned, so the minimum spac-

ing between any two items was 14 mm. The birds were given daily sessions of discrimination trials, each beginning with the presentation of one of three cue strips— either red with vertical bars, green with horizontal bars, or black with oblique bars (Figure 2)—in the start-key area. Except during later probe tests, cue strips with green horizontal lines or red vertical lines were fully predictive of the target type in the subsequent display. The black oblique configuration was ambiguous, in that it did not predict which of two possible targets would be presented. If the bird did not peck the cue strip within 30 s after onset, the cue would blink on and off every 3 s until a response was made. A single peck to one of the background fields cleared the screen. If the peck was directed at the target, a food light was illuminated for 5 s while a reward was delivered to the magazine. The screen was then cleared for a 5-s intertrial interval (ITI). If the bird pecked an area other than the target, the ITI was 45 s. If the bird did not respond to the display at all within 20 s, the ITI was 12 s. Each daily session ended when the bird either completed 60 trials or when 60 min had elapsed.

Treatment Design

The four experimental treatments comprised a 2×2 design, with sequential priming and associative cuing (each either present or absent) as independent variables.

- 1) The “Neither” Treatment provided neither priming nor cuing. The black oblique cue strip (Figure 2) was used in each trial of the session, giving no indication which of the two targets would be presented. Target types were presented equally often, but in random order, with the constraint that the same target could not appear in more than three successive trials. This procedure does not fully eliminate either form of guidance, of course. Sequential priming effects are apparent in difficult discriminations following even a single prior stimulus presentation (Bond, 2007), and the ambiguous cue strip still indicates that one of only two specific targets will follow. But this control minimizes the influence of both factors relative to the experimental treatments (Blough, 1989, 1991).
- 2) The “Primed” treatment emphasized sequential priming without predictive associative cuing. The black oblique cue strip was again used throughout the session. In this case, however, the trial sequence consisted of two contiguous blocks of the same target type, switching from one target to the other at a point near the middle of the session. Each of the two target types was randomly assigned to the initial block on half of the sessions, and the location of the switch point was randomized across sessions, producing contiguous sequences that ranged unpredictably from 26 to 34 trials. Previous studies have established that extended repetitions of trials with the same target produce much stronger facilitative effects (Dukas & Kamil, 2001; Goto, 2013).
- 3) The “Cued” treatment provided only predictive associative cuing. The green horizontal and red vertical cue strips (Figure 2) reliably predicted the target type in the following display. Trials were presented in randomized order, as in the Neither treatment.

- 4) The “Both” treatment enabled both forms of attentional guidance. The cue strip was reliably associated with the following target type (as in the Cued treatment), but in addition the trial sequence was contiguously blocked, facilitating sequential priming (as in the Primed treatment).

Previous attempts to explore the interaction of priming and cuing in blue jays used a similar factorial design (Belik, 2002; Kono, Reid, & Kamil, 1998). Their problematic results suggested that carry-over between primed and nonprimed sessions with the same target types may have obscured treatment relationships (Kamil & Bond, 2006). To limit carry-over effects, we conducted discrimination training and interference testing with two of the four treatments in each of two successive phases. Half of the subjects (the “Random First” group) were initially trained on the Cued and Neither treatments in alternating sessions. When all of the subsequent test sessions for these two treatments were completed, the birds were brought to criterion on the Primed and Both treatments and then tested on them. The second group of subjects (the “Blocked First” group) experienced the opposite order of treatment: They were first trained and tested on the Primed and Both treatments in alternating sessions, and were subsequently given the Cued and Neither conditions. So in both groups, successive sessions always used distinctive target sets— sessions with stimulus set A were always alternated with sessions of stimulus set B (Figure 2). The only difference between the groups was whether associative priming was emphasized or minimized in initial training.

Training and Testing Procedures

At the start of training, only the target moth was presented on the search display. The number of distractors was increased in subsequent sessions of a given treatment whenever the bird’s accuracy exceeded 80%. Training continued until the bird reached the 80% criterion on a search display with 11 distractors for both of their initial treatment types. Ten of the 12 subjects acquired all four treatments. Neither of the other birds was able to reach criterial performance with more than two distractors, even after 100 sessions. They were dropped from subsequent analyses.

When each subject had been fully trained, we conducted a series of test sessions to contrast the facilitative and inhibitory effects of priming and cuing (Posner & Snyder, 1975). Sessions using ambiguous cue strips (Primed or Neither treatments) were unchanged from the training configuration, but the interleaved sessions with predictive associative cues (Cued or Both treatments) included miscued probes in which the cue strip did not match the subsequent target type. Each test session of 60 trials included a probe trial of each target type interpolated in a random location, one in the first half and the other in the second half of the session. In sessions with both cuing and priming, the miscued trials used the same target type as the surrounding block (thereby avoiding disruption of an existing sequential prime), but were preceded by the incorrect cue strip. Tests were continued until each bird had completed at least 26 miscued probes for each target type.

Analysis Methods

The experimental results were subjected to four statistical analyses. We first examined the training trials to characterize changes over the course of acquisition, contrasting the Blocked First and Random First subjects. We then examined treatment effects for evidence of differences in the elicited attentional processes. Attention can have both facilitative and inhibitory effects, which are to some extent independent of each other (Milliken & Tipper, 1998; Posner & Snyder, 1975). Focal attention generally enhances detection of the sought-for target, but it can also impair performance on competing tasks and alternative stimuli (Dukas, 2002; Dukas & Kamil, 2000, 2001). We therefore conducted an initial analysis of the facilitative consequences of priming and cuing, comparing trials from Neither test sessions to Cued and Primed sessions from which miscues and sequential target switches had been eliminated. Subsequently, inhibitory attentional effects were sought in the responses to miscued trials in cued sessions and to trials following the sequential switch point in primed sessions.

We used repeated-measures analysis of variance of response accuracy and log latency within subjects, using a criterion of $p < 0.05$ to assess statistical significance. For significant effects, the effect size is given as Cohen's d_c (Cumming, 2012). Contrasts with $d_c < 3$ include confidence intervals. Symbols in the accompanying data displays (Figures 3–5) are least-squared means across subjects within treatments. Error bars indicate one SEM within treatment combinations, adjusted for the between-subjects error variance (Bakeman, 2006; Bakeman & McArthur, 1996).

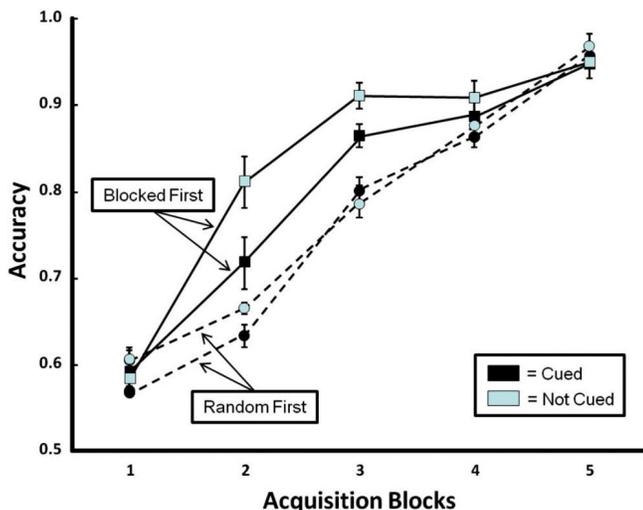


Figure 3. Task acquisition over initial training sessions in 200-trial blocks. Square symbols and solid lines indicate response accuracy across the five Blocked First subjects, which learned the task in primed sessions; circles and dashed lines indicate accuracy for Random First subjects, which learned the task with randomly sequenced trials. Black symbols indicate treatments with predictive cuing; gray symbols indicate treatments with ambiguous cues. Error bars delimit one SEM, adjusted for between-subjects error variance.

Results

Acquisition

Birds in the Blocked First group (Primed/Both) required 1584 ± 115 trials to reach criterion in initial training; those in the Random First group (Cuing/Neither) required 1956 ± 432 trials. The totals were not significantly different, but there were suggestions of a difference in sequential pattern: The Blocked First birds appeared to improve more rapidly in early sessions (see Figure 3). To test this hypothesis, we compared the changes in response accuracy and log latency across five successive 200-block trials per subject in their initial training sessions on each of the four treatments. The overall test contrasted the Blocked First group (square symbols in Figure 3) with the Random First group (circles in Figure 3) using a mixed two-factor ANOVA. As expected, the accuracy increased significantly across trial blocks in both groups, $F(4, 32) = 151, p < 0.0001, d_c > 3.0$. There was also a nonsignificant trend in the difference between the training groups, $F(1,8) = 4.67, p = .063$, with the Blocked First birds achieving somewhat higher mean accuracies. This result probably mirrored the significant group \times training block interaction, $F(4, 32) = 5.56, p < 0.002, d_c = 0.55, 95\% \text{ CI} = (0.35, 0.75)$. The two groups displayed similar accuracies in the first block of training, but the Blocked First birds apparently improved more rapidly in early sessions. This group difference eventually disappeared as the birds' response accuracies converged on a common asymptote (see Figure 3). Response latencies in both groups were slowed in later training blocks, $F(4,32) = 5.36, p < 0.0025, d_c = 2.21, 95\% \text{ CI} = (2.17, 2.26)$, probably because of the progressive increase in numbers of distractors. There was no significant effect of training group on latency, $F(1,8) = 1.43, p > 0.2$, and no group \times block interaction, $F(4,32) \leq 1.0, ns$.

To evaluate the interaction of cuing and priming during acquisition, we conducted component analyses of response accuracy within the two training groups separately, using two-way (treatment vs. trial block) repeated-measures ANOVA. For the Blocked First group, there was no main effect of treatment, $F(1,4) = 2.19, p > 0.2$, and there was the expected main effect of acquisition block, $F(4,16) = 52.9, p < 0.0001, d_c > 3.0$, but there was also a significant treatment \times block interaction, $F(4,16) = 3.13, p < 0.045, d_c = 1.52, 95\% \text{ CI} = (1.46, 1.58)$: In the Primed treatment, the birds' performance improved more rapidly in the early acquisition sessions than in the Both treatment (Figure 3). Cuing had no apparent impact on acquisition in the absence of priming, however: For the Random First group, there was only a significant effect of acquisition block, $F(4,16) = 134, p < 0.0001, d_c > 3.0$. Neither the treatment main effect nor the interaction was significant, $F(1,4) \leq 1.0, ns$.

In the second phase of the experiment, the treatments were reversed: Blocked First birds now received random sequence training, and Random First birds received blocked trials. No noticeable performance decrement was observed in any of the subjects as a result of reversing the sequential priming conditions: A group \times training phase ANOVA comparing mean accuracy during the final test sessions of the first phase and the first training sessions of the second phase revealed no significant main effects or interaction, $F(1,8) \leq 1.0, ns$. Given that neither the treatment stimuli nor the associated cues were changed between phases, this is not particularly surpris-

ing. The data from the first and second phases were therefore treated as a single, four-treatment experiment in subsequent analyses.

Facilitation

To test for facilitative attentional effects, we formed a database of all test trials from all 10 subjects in Cued, Primed, and Neither treatments. From these data, we deleted all miscued probes and sequential switches, in addition to the five trials that followed miscues or switches (to avoid possible carry-over effects of the disruption). We analyzed the remaining data (roughly 900 trials per bird per treatment) for evidence of facilitation, separately comparing Primed versus Neither and Cued versus Neither. During these sessions subjects displayed nearly the maximum possible levels of performance: mean accuracy in all treatments was above 98%. ANOVA revealed no significant treatment effects on accuracy (both treatment comparisons: $F(1,9) \leq 1.0$, *ns*). Mean response time was roughly 400 ms faster in Primed trials than in Neither trials, and 100 ms faster in Cued trials than in Neither, but ANOVA of log latency showed no significant main effects (both $F(1,9) \leq 1.0$, *ns*).

Miscuing

The inhibitory effects of associative cuing were analyzed in miscued trials in Cued versus Both treatments. For comparison, we used the five preceding correctly cued trials in each session as controls. Mean discriminative accuracy in both treatments was as high in miscued trials as in the preceding correctly cued trials. A treatment versus trial type ANOVA of accuracy found no significant effects: trial type: $F(1,9) \leq 1.0$; treatment: $F(1,9) \leq 1.0$; interaction: $F(1,9) = 1.64$; all $p > 0.2$ (Figure 4A). Miscuing did, however, result in longer latencies. ANOVA of log latency showed a significant main effect of trial type, $F(1,9) = 18.9$, $p < 0.002$, $d_c = 0.26$, 95% CI = (0.06, 0.46). The difference in mean response time between miscued and control trials, across both treatments, was 311 ms. There was no significant effect of treatment, $F(1,9) \leq 1.0$, or interaction, $F(1,9) = 1.61$, both $p > 0.2$ (Figure 4B).

Switching

Inhibition resulting from sequential priming was examined by comparing accuracy and log response time before and after the switch trials, where the target type changed over in Primed versus Both treatments. For analysis, we used the five trials before the switch point as controls, comparing them to the two trials including and immediately following the switch. A treatment versus trial type ANOVA of accuracy showed a nonsignificant trend in the main effect of treatment, $F(1, 9) = 4.79$, $p = .057$, and a significant main effect of trial type, $F(1,9) = 8.33$, $p < 0.02$, $d_c = 1.19$, 95% CI = (1.18, 1.19).

Both of these effects probably mirrored the significant treatment by trial type interaction, $F(1,9) = 5.19$, $p < 0.05$, $d_c = 1.29$, 95% CI = (1.27, 1.31): Detection accuracy was lower after a switch than during the preceding control trials, but only in the Primed sessions; the inhibitory effect of switching targets was not apparent in Both sessions, where predictive associative cues were provided (Figure 5A). The effect size was impressive, given how close the birds were to a performance ceiling. In the Primed treatment, only two of the 10 subjects showed a lower accuracy in the trials before a switch than

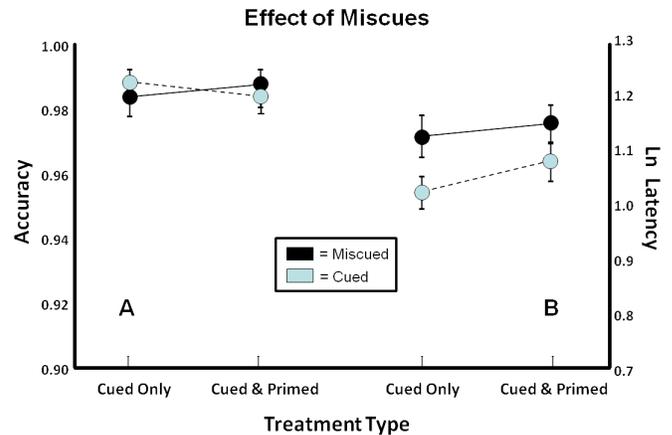


Figure 4. Interference effects on accuracy (A) and log latency (B) from associatively cued trials. Black symbols are means from miscued probes; gray symbols are means from the five correctly cued trials preceding each miscue. Data are separated by session type, separating sessions consisting of only cued trials from those consisting of trials with both cuing and priming. Error bars enclose one SEM, adjusted for between-subjects error variance.

immediately afterward, and the mean decrease in accuracy due to the switch was 3.7 percentage points. In the Both treatment, half of the birds were less accurate before the switch than afterward, and the mean effect was 0.06 percentage points.

Like miscuing, switching yielded slower response times. ANOVA of log latency showed a significant main effect of trial type, $F(1,9) = 5.84$, $p < 0.04$, $d_c = 0.29$, 95% CI = (0.09, 0.49). There was no main effect of treatment, however, $F(1,9) \leq 1.0$, and no significant interaction, $F(1,9) \leq 1.0$, both *ns* (Figure 5B). The difference in mean response time between switch and control trials across both treatments was 332 ms.

Discussion

Visual attention to a focal target can result from two distinctive cognitive processes (Buschman & Miller, 2007): It can be cued by prior stimulus associations (Wolfe, 2007) or primed by the appearance of a recently detected target (Bravo & Farid, 2009; Kristjánsson, 2008). There is, thus, a bright theoretical line between sequential priming and associative cuing (Blough, 1989, 1991). Cuing is produced not by the targets themselves, but by stimuli that are secondarily reinforced by the subsequent choice of a correct target. For example, the shape of a tree's leaves may cue a search for a particular type of prey (Heinrich & Collins, 1983; Real et al., 1984). The predator does not attempt to eat the leaf, but it may remember the leaf's shape after a caterpillar has been found on the leaf and consumed. Priming, in contrast, is the direct consequence of a previous target choice. It seems likely that priming would be stronger for choices that resulted in a food reward. (That is, erroneous responses may have minimal influence on attentional allocation.)

Although these two processes initially derive from divergent sources, they apparently affect focal attention through a

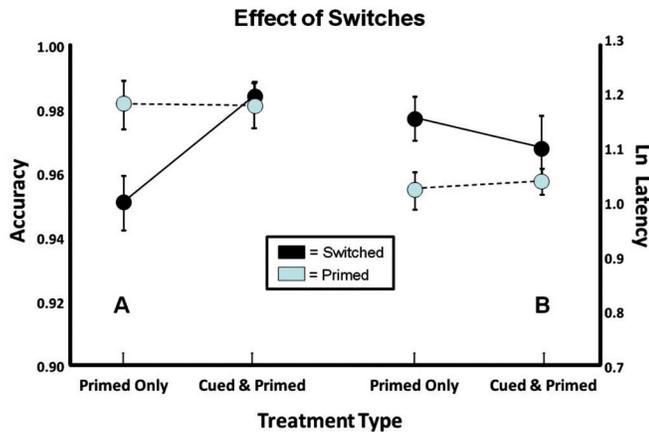


Figure 5. Interference effects on accuracy (A) and log latency (B) from sequentially primed trials. Black symbols are means from the first two trials after a switch to the alternative target; gray symbols are means from the five blocked trials preceding the switch point. Data are separated by session type, separating sessions consisting of only primed trials from those consisting of trials with both cuing and priming. Error bars enclose one SEM, adjusted for between-subjects error variance.

final common path—a representation of the target as a search template in working memory (Bravo & Farid, 2009; Zhang et al., 2011). In associative cuing, the cue stimulus elicits a recall of the associated target representation from long-term memory. In sequential priming, the target representation is often seen as being maintained in working memory as the residue of the previous trial (Kristjánsson, 2008). One must be cautious here, however: the magnitude of the priming effect is cumulative. Birds are more accurate and faster following two or three prior detections of the same target than following just one (Bond & Kamil, 1999). Goto (2013) has recently shown in pigeons that the effects of prior detections continue to increase for homogeneous runs of up to 20 trials. This suggests that with repeated experience, some aspects of a primed representation are also stored in long-term memory, from which they can be retrieved as an expectation at the beginning of the next trial. During acquisition, the birds undoubtedly learn the characteristic features of all four of their target types. Two targets are uniquely associated with particular colored cues; the other two are both associated with the same noncolored cue. At the start of each trial, therefore, the bird probably has available some representation associated with recent prior experiences, as well as another representation associated with the cue stimulus. The issue is how these representations interact in generating the operational search template.

In the current study, we have explored the relationship between cuing and priming using methods that were crafted to address earlier experimental difficulties. Unlike the background cuing approach in Kono et al. (1998), for example, we used maximally distinctive targets with a diverse array of similar distractors (Figure 1), thereby avoiding the need to control for background resemblance. We employed a factorial, within-subjects design with four treatments—cuing, priming, cuing and priming, or neither—but unlike Belik's (2002) procedure,

carry-over effects from prior sessions were avoided. Subjects received alternating sessions with one pair of target types that were predictively cued and another pair with ambiguous cuing. The presence or absence of sequential priming was tested in separate runs of the experiment.

As a consequence of this last feature, we were able to contrast subjects that had learned the discrimination task in sessions primed with contiguous blocks of a single target type (the Blocked First group) with those that were initially trained on the same stimuli in randomly ordered trials (the Random First group). The trials of Blocked First birds were all sequentially primed and either predictively or ambiguously cued. Their acquisition was consistently faster overall than that of the Random First birds (Figure 3). Within the Blocked First group, acquisition in sessions with only priming was faster than in ones with both priming and cuing (Figure 3). The simplest explanation might attribute the inferior performance of cued birds in blocked sessions to the necessity of associative learning. Sequential priming is a built-in predisposition in the visual system (Fecteau & Munoz, 2003; Kristjánsson & Campana, 2010). It does not require secondary reinforcement and is operational from the onset of training. The relationship between the target configuration and the cue stimulus, in contrast, is entirely attributable to secondary reinforcement, which only accrues to the cue when the response to the subsequent target display is correct. This constraint could slow initial acquisition.

The Random First subjects, however, suggest an alternative account. These birds were trained on one set of stimuli with predictive pretrial cues and another with ambiguous ones. They showed no significant differences due to cuing (Figure 3), suggesting that having to learn the relationship between the cue and the target was not the sole consideration. Cuing apparently retards task acquisition only in the presence of priming, implying that the two processes interfere with one another during initial discrimination learning. Several visual search studies on human subjects have found that associative cuing is generally weaker than sequential priming from the outset (Knapp & Abrams, 2012; Wolfe et al., 2003, 2004). Competition from the less effective cuing process may degrade the performance benefits of priming during initial acquisition in the Blocked First group.

Once the subjects had been trained to asymptotic levels, however, the effects of attentional guidance were manifested only in inhibition—the consequences of miscuing and target switching. Apparently because performance was at ceiling during the test sessions, there was no statistically reliable evidence of facilitation. The facilitative effects of attention generally seem more evident in more difficult tasks (Bond, 1983; Bond & Kamil, 1999; Washburn & Putney, 2001). So although priming may have facilitated initial task acquisition, once the task was learned to criterion with a full complement of distractors it became far less demanding no matter what form of guidance was provided. With practice, it is apparently feasible to switch among alternative search templates with minimal delays, with the maximum number of fast-switching alternatives being constrained only by the capacity of working memory (Zhang et al., 2011). Vreven and Blough (1998) found that highly experienced pigeons required a set of at least eight distinctive stimuli to display long-term facilitative effects of attentional guidance. Our blue jays only had to learn four target types.

Cuing and priming produce distinguishable inhibitory effects that are revealed in the birds' performance on miscued trials in associatively cued sessions and on trials following the switch point in primed sessions. Miscues consistently resulted in slower target detections: the difference in response time between miscued and correctly cued trials was more than 300 ms, whether or not the trials were also sequentially primed (Figure 4). This might be thought of as a cost of switching between two well-trained search templates (Dukas & Kamil, 2000). The bird is cued to expect target A1 (Figure 2), but A1 is not immediately evident in the subsequent display. There is a momentary lag to switch to the other associated template (A2). The bird then finds the corresponding target and completes the trial. There was no decrease in response accuracy in miscued trials (Figure 4). When miscued, the birds do not generally select a distractor that is in some way similar to A1. In a sense, they are prepared to respond only to the two predictively cued stimuli.

The observation that miscuing results in a comparable increase in latency irrespective of the presence of sequential priming has interesting implications for the interaction of the two forms of guidance. In the Both treatment sessions, miscues displayed the same target type as the rest of the surrounding block of trials, but were preceded by the opposite (incorrect) cue stimulus. Sequential priming was therefore maintained, but the predictive accuracy of the cue strip was violated. If the sequential prime had an influence in these trials, one would expect that it should have ameliorated the consequences of the miscue, and this did not occur. The consistency of the increased delay suggests that priming played no part in the birds' responses in those trials. One may speculate that because the cue onset is prior to the target display, the elicited transfer of the cue-associated representation into working memory essentially overwrites the previously established sequential prime. In this context, as in the initial task acquisition, cuing and priming appear to interfere with one another.

Inhibitory effects of switching between blocks in primed treatments resulted in a similar increase in response latency (Figure 5B). But the most striking effect of switching was a significant reduction in response accuracy, a result that was only apparent when sequential priming was not accompanied by a predictive pretrial cue (Figure 5A). At least some of the time, birds responded to the switch from one primed target to the next one with a temporary increase in the likelihood of pecking distractors. They did not simply access the current alternative representation from long-term memory, but appear to have given higher weighting to the degree of resemblance of the distractors to the expected, pre-switch target. Because there was no similar decrease in accuracy after a miscue (Figure 4A), this finding could reflect a difference in the specificity of primed and cued representations. In the treatment with both priming and cuing, response accuracy was unaffected by switching (Figure 5A). As in the analysis of miscues, the response to a switch between target blocks appears to be another indication of interference between the two processes. At the switch point in a primed and cued trial, the subject is warned by the pretrial cue of an impending change in the target. The alternative search template is activated, and the existing primed representation in working memory is overwritten, eliminating errors attributable to aggregate similarity between the target and distractors.

So how priming and cuing interact to influence search performance may be an effect of the inherent temporal order of the processes. The representation in sequential priming is derived from the target displayed in the previous trial; the representation in associative cuing is elicited by the nontarget stimulus that immediately precedes the target display. As there is room in working memory for only one operational template, the most recent activation takes priority, and the effects of priming are lost when it is accompanied by a predictive pretrial cue. The presence of a valid pretrial cue also appears to interfere with initial acquisition of a primed discrimination task, though it is not clear that the same mechanism is responsible. Wolfe et al. (2004) noted a similar effect in comparing word cues (essentially associative cues) with picture cues (which are somewhat similar to sequential priming). They remark that although "word cues are never as effective as picture cues ... a valid word cue can be used without interference from an invalid picture cue" (p. 1412).

In spite of these findings, it still seems an open question as to whether priming and cuing can ever simultaneously contribute to a real-world visual search in animals. Cuing works as well as it does in human subjects because the cue is usually verbal or symbolic and does not require a maintained conditioned association. Because animals have to learn the significance of the cue from repeated successful discoveries, however, associative cuing in a natural environment can readily be disrupted by variation in the abundance and appearance of the different target types. It may only work well when the food items are not that difficult to see and are reliably detected when present. It would also help if the target stimuli were distinctive from one another and limited in diversity. And of course, the cues themselves would need to be highly predictive of eventual reward. Coincidentally, these are precisely the conditions in which sequential priming is least useful and least likely to show a significant effect in animals (Bond, 1983, 2007; Bond & Kamil, 1999).

Situations in which both forms of attentional guidance can operate at the same time are, therefore, unlikely to be common in nature. What seems more probable is a sequential interaction in which different forms of guidance operate at successive stages. So cues from the location of a tree or the appearance of its leaves might attract a foraging insectivorous bird and direct its attention to particular branches (Royama, 1970; Heinrich & Collins, 1983). If the prey items are cryptically colored, sequential priming would then become paramount, enhancing the success of subsequent detections (Tinbergen, 1960). Visual predation is an inherently hierarchical activity (Curio, 1976), and there is reason to expect different kinds of attentional guidance to dominate at different points in the process.

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