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Temporal Properties of Visual Search in Pigeon Target Localization

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To examine the mechanisms and time course of visual search behavior, we rewarded 6 experienced pigeons for locating and pecking at an odd target region randomly embedded in a larger rectangular array of contrasting distractor elements. On two-target test trials, a flanking secondary target region was briefly presented (100, 250, or 500 ms) after display onset with stimulus onset asynchrony values of 0, 50, 100, 175, 250, 375, 500, 1000, 2000, and 3000 ms. Two types of interference effects were possibly identified with target localization accuracy. One type occurred early in processing, where the secondary target appeared to interfere with search behavior, perhaps involving mechanisms similar to inhibition of return. A second type of interference was isolated that appeared to be time locked to responding and might occur at a postsearch stage of processing. Several possible connections of these effects to established mechanisms in human visual search and attention are suggested.

Keywords: pigeons, flanker task, visual search, attentional capture, inhibition of return

In humans, flanker tasks have been very useful in examining the nature of different stages in information processing systems (Eriksen & Eriksen, 1974). These tasks consist of presenting a target element with flanking information of varying similarity that can interfere with the processing of the target. Different manipulations of the primary target and flankers, such as the time interval between the stimuli (stimulus onset asynchrony, or SOA) have been shown to affect separate stages of processing of the visual input. Thus such approaches have been useful in informing us about how different parts or components of the human cognitive system senses, detects, identifies, categorizes, decides, and responds to the numerous ongoing moment-to-moment changes in the visual environment. Birds, like humans, also live in a dynamic visual world with many of the same visual and attentional challenges. This article presents new evidence regarding these mechanisms and their time course in pigeons as tested in a target visual search task involving the manipulation of flanking interfering information.

This research stems from Cook, Cavoto, Katz, and Cavoto's (1997) experiments examining the processing of rapidly changing

texture stimuli. In their experiments, pigeons were reinforced for locating and pecking at an odd visual target that differed in color or shape from the surrounding background region of distractor elements (see also Cook, 1992a). Using this target search and localization task, Cook et al. found that rapidly changing the color of the target within a trial facilitated its localization within the display in comparison with trials in which the target remained constant. They also found that rapid changes in the color of the surrounding distractors correspondingly interfered with target localization. This pattern of facilitation and interference with target search behavior suggested that transient color changes in the displays may automatically capture or attract the pigeons' attention to their location in a manner similar to that reported for humans (e.g., Jonides, 1981; Yantis, 1993).

In the current experiment, we investigated more precisely the nature and time course of these attentional search processes using a flanker task. Because Cook et al. (1997) used continuously changing texture displays that made determining the time course of processing more difficult, we introduced and tested a modified two-target procedure that allowed us to accurately control and measure the effects of an additional specific change in the display during search. In this procedure, a "second" target-like flanking region briefly appeared at different times during an otherwise typical target localization trial. The pigeons' task was to identify the primary target present for the entire trial and ignore this secondary short-duration flanking "target." By varying the duration (100, 250, or 500 ms) and onset times (SOA ranging from 0 to 3000 ms) of the secondary target, we could then dissect the timing and processes involved at different points in the identification and location of the initially presented primary target. The novel application of this contemporary procedure to pigeons suggested that their visual search behavior may compose different sequential components.

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Method

Animals

Six highly experienced male White Carneaux pigeons (*Columba livia*) maintained at 80% of their free-feeding weights were tested. No preliminary training was needed, because each pigeon had over 6 years of experience with the target localization task.

Apparatus

Testing was conducted in a flat-black Plexiglas chamber (38 cm wide \times 36 cm deep \times 38 cm high). All stimuli were presented by computer on a color monitor (NEC MultiSync 2A; Wooddale, IL) visible through a 26 \times 18 cm viewing window in the middle of the front panel of the chamber. The viewing window's bottom edge was 20 cm above the chamber floor. A thin piece of glass mounted in this window protected the monitor. Pecks to the monitor screen were detected by an infrared touch screen (EMS Systems, Champaign, IL; resolution of 80 \times 48) mounted behind a 40-mm-wide Plexiglas ledge that went around the inside edge of the viewing window. A 28-V houselight was located in the ceiling and was illuminated at all times, except when an incorrect choice was made. A food hopper was located in the middle of the front panel, its access hole flush to the floor. A video card (VGA Wonder; ATI Technologies, Scarborough, Ontario, Canada) controlled the color monitor (800 \times 600 pixels) for stimulus presentation.

Procedure

Target localization procedure. All texture displays were 20 \times 13 cm in size and consisted of 468 small colored shape elements arranged in a 26 \times 18 rectangular matrix (for examples, see Cook, Cavoto, & Cavoto, 1996). All elements of the texture displays were created from pairwise combinations of 24 colors and 47 shapes (3–6 mm in size). These values resulted in over 27,000 possible color displays and 52,000 possible shape displays available for testing (target values \times distractor value \times irrelevant dimensional value – uniform displays). The target region consisted of a 7 \times 7 block of elements randomly located (240 possible locations) on each trial within the larger matrix of surrounding distractor elements. As determined by control displays with no visible targets, chance performance was 30%.

Each trial began with a peck to a randomly located 2-cm circular white ready signal placed in the upper two thirds of the display area. This darkened the screen for 0.1 s, followed by the presentation of a baseline or two-target test display. For both types of trials, if a pigeon first accumulated five pecks within the target region (including the immediately surrounding row and column of distractor elements), an accurate localization response was judged to have occurred and the food hopper raised for 2 s. If instead they first accumulated five pecks to the distractor region or the location of the secondary target, the display was turned off and the overhead houselight extinguished for 10 s. Trials were separated by an illuminated 5-s intertrial interval.

Two-target test conditions. After the pigeon pecked the ready signal, an entire texture display appeared that included the primary color or shape target. After a specified SOA, a secondary 7 \times 7 target would briefly appear within the display. Secondary

targets differed in color from the surrounding distractors, and their duration was chosen to be too brief (\leq 500 ms) for the pigeons to successfully direct a peck at it while visible. The pigeon's task was to locate and peck at the primary target and ignore the brief secondary target. In order to prevent any overlap between them, the locations of the primary and secondary targets were randomly placed within the upper and lower portions of the display area.

Eight different SOAs (0, 50, 100, 175, 250, 375, 500, and 1000) were tested for the first 13 sessions of testing, and nine different SOAs (0, 50, 100, 175, 250, 500, 1000, 2000, and 3000) were tested over the last 17 sessions. The secondary target's duration was 100, 250, or 500 ms duration. See the top panel of Figure 1 for an example trial. Within a session, each SOA was tested four times each (two color/two shape trials) at the three secondary target durations. Thus, at the end of testing, we completed a 10 SOA \times 3 duration \times 2 dimension design. The remaining trials of each 180-trial session consisted of randomly determined one-target color and shape baseline displays. No two-target test trials occurred before the 20th trial of a session. The first 10 trials of each session were warm-up trials during which the pigeons pecked the display until the target was correctly located. These trials were excluded from the analysis.

Results

The analyses concentrated on first-peck target localization accuracy, as it best isolates the localization phase of the pigeon's search behavior. Prior research had determined that the vast majority, if not the entirety, of visual processing of the display was completed prior to the first peck (Cook, 1992a, 1992b). Consistent with this, we found that first-peck accuracy (74.4%) and trial accuracy (77.4%) on combined color and shape baseline trials differed little. Moreover, first-peck RTs (mean reaction time [RT] = 1213 ms; color = 1152 ms; shape = 1275 ms; infrequent RTs >5000 ms excluded) were considerably longer than the average interresponse interval (IRT) of the remaining pecks to the displays (mean IRT = 441 ms; color = 434 ms; shape = 449 ms). The greater speed of the latter pecks in comparison with the first peck and the absence of any difference between color and shape displays suggest that they were simply filling out the response requirement upon completing their target search prior to the first peck.

Displayed at the bottom of Figure 1 is the mean color and shape first-peck localization accuracy for the two-target test displays. Across all SOAs, increasing the duration of the secondary target produced the greatest interference with localization. Moreover, regardless of duration, the greatest degree of interference was produced at the earliest SOAs. Those SOAs longer than the typical search RT resulted in little interference in relation to the single-target baseline displays (74.4%—upper reference line). A three-way repeated-measures analysis of variance (ANOVA) with Dimension (color/shape), SOA (0 to 3000 ms), and Secondary Target Duration (100, 250, & 500 ms) as factors using first-peck accuracy confirmed these effects. This analysis revealed a main effect of dimension, $F(1, 5) = 83.8$, $p < .001$, indicating that the pigeons remained more accurate on color trials (68.2%) than on shape trials (54.4%). However, the interaction of Dimension with either SOA or duration was not significant, indicating that there was no differential effect across the different dimensions. As a result, these

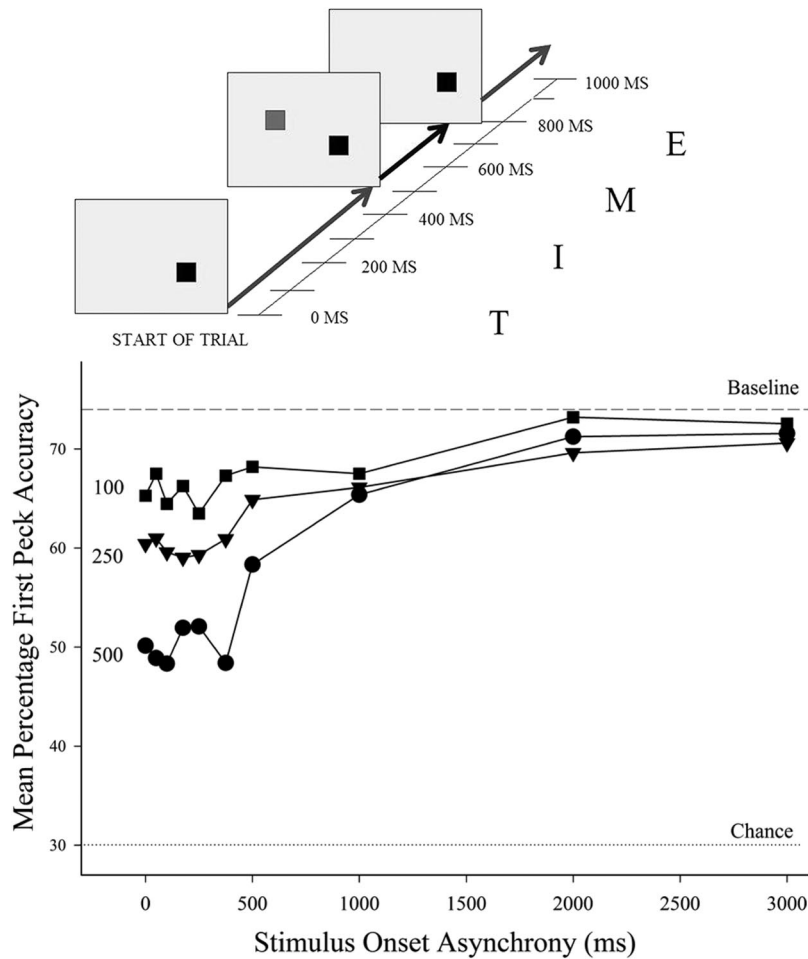


Figure 1. The top panel shows an example of a color baseline texture display used in the experiment; the small individual elements are not shown (see Cook et al., 1996, for similar examples). The location of the odd target region was randomly varied across trials, and comparable shape displays were also tested. The identity of the target and distractor regions' elements randomly varied across trials. The bottom panel shows the mean percentage of first-peck target localization accuracy for the two-target test conditions at the 100, 250, and 500 secondary target duration. The upper dashed reference line shows baseline performance on single-target displays during the experiment. The bottom dotted line shows chance performance.

trials are combined in subsequent analyses. The main effects of duration, $F(2, 10) = 100.2$, $p < .001$, and of SOA, $F(9, 45) = 15.9$, $p < .001$, were significant. But as indicated by the nonparallel curves in Figure 1, in which longer secondary targets produced a greater effect at shorter SOAs than at longer ones, a significant SOA \times Duration interaction, $F(18, 90) = 4.4$, $p < .001$, was also present. Thus, the pigeons were most vulnerable to the interfering effects of these momentary secondary targets early in the processing. Because it takes a pigeon approximately 400–500 ms to execute a peck response (the average IRT), and the birds typically responded within about 1200 ms, target search behavior must have been typically completed within 800–1000 ms after display onset, just as when secondary target SOAs stopped having their greatest effect. Thus, once responding had started, the secondary targets no longer produced much interference. This suggests that their presence was not generally producing, disrupting, or disinhibiting discriminative pecking behavior directly, but in-

stead interfering with active target search behavior during the early portion of a trial.

As planned, the secondary target's durations were too brief for the pigeons to peck at them while they were present ($< .02\%$ of the trials). The former location of the now absent secondary targets did attract pecking on a portion of trials. The proportion of trials in which responses were directed to the secondary target's location were moderate (19.7%) in comparison with the more frequent case in which the secondary target's location was not pecked at all (80.3%). Even fewer trials resulted in all five pecks being directed there ($< 4\%$). Trials with such postpresentation pecks frequently produced incorrect responses (92% of the time) in comparison with those that were correct, $F(1, 5) = 43.5$, $p < .001$. The existence of these trials indicate that "target" identification can occur within 100 ms, because during their very brief existence, some secondary targets appear to have been confused for a real target.

Even when no overt localization behavior occurred to the secondary target or its prior location, they still affected performance. Table 1 displays mean RT for those trials in which no secondary target pecks of any type were recorded. Here their primary effect was to slow responding, because RT showed a significantly linear decrease as a function of later SOA, $F(1, 5) = 8.6$. The duration of the secondary targets also affected RT, with intermediate durations being most disruptive, $F(2, 10) = 4.8$. No interaction between SOA and duration was found. Thus, early SOA presentations noticeably slowed the pigeons in how quickly they started to peck the target, suggesting that the secondary targets had disrupted search behavior. Again, late presentations at long SOAs are hardly noticed once responding has started.

Besides interfering with the search process over the first 1000 ms or so, we also found a source of interference that appeared to be time locked to the pigeons' response to the target. This effect can be seen in Figure 2, where pigeons' first-peck RTs are grouped into five 250-ms bins (RTs of <500 ms or >1750 ms were excluded because of their small N). The striped area in each panel shows the range of RTs included in each panel's curve. The pigeons' contributed on average 1058, 1560, 778, 490, and 317 responses to each RT grouping, respectively. Note that baseline accuracy across the panels decreases as mean RTs increase (the dashed reference line in each panel). This reflects an increasing degree of display difficulty being primarily responsible for the distribution of RTs, as less discriminable displays caused the pigeons to respond both more slowly and less accurately.

Over this spread of RTs, we found that approximately 600–700 ms prior to the first peck, the appearance of the secondary target was most disruptive. The reference arrow in each panel points to a temporal location 650 ms forward of the mean RT of each bin. Although secondary targets certainly produced interference at all SOAs prior to the response, they were clearly most disruptive when they occurred at this particular point in processing. This interference effect seemed time locked to the response as it progressively travels across the increasingly slower RTs among the panels. A two-way repeated-measures ANOVA (SOA \times RT Bin) on first peck accuracy confirmed this significant interaction of SOA and RT bin, $F(32, 180) = 3.4$, $p < .001$. There was also a main effect of SOA, $F(9, 40) = 13.7$, $p < .001$. The shifting nature

of this time-locked effect was further confirmed by a series of polynomial comparisons within each RT bin that revealed significant linear effects of SOA for RTs under 1000 ms, $F_s(1, 5) > 42.7$, and significant quadratic trends for RTs > 1000, $F_s(1, 5) > 6.3$. Further comparisons confirmed that the early interfering effects of SOA remained in these latter U-shaped functions, despite the longer RTs. Comparisons of first-peck accuracy with SOAs ≤ 250 for each curve found that it was significantly lower than overall baseline performance for these curves, $F_s(1, 5) > 6.6$, and significantly lower than baseline performance adjusted for each specific RT bin (1000 ms: $F(1, 5) = 40.1$; 1250 ms: $F(1, 5) = 14.8$; 1500 ms: $F(1, 5) = 5.4$, $p = .068$).

Discussion

By varying the temporal properties of the brief flanking secondary target, the present study reveals important new temporal details about the visual search behavior of pigeons. Secondary target SOAs of less than 1000 ms consistently produced the greatest interference effects with primary target localization, with longer secondary targets producing the most interference. This interference was manifested as both (a) postpresentation pecking behavior to the secondary prior target location on a portion of trials and (b) slowing down search behavior and responding on the remaining trials. Moreover, an additional time-locked interference effect was isolated that appeared to be independent of these early temporal effects of SOA. This interference effect consistently occurred about 650 ms prior to the birds' response. Overall, once search was completed and localization responding initiated, these interfering effects of the secondary target were markedly reduced and essentially disappeared at late SOAs.

We consider next the implications of these results given our current understanding of pigeon visual search behavior. Following display onset, it appears that variably sized portions of the display are serially examined for the presence of the experimentally defined target. The size of the area visually searched at each moment depends on the visual angle of the display and the degree to which its spatial characteristics, perceptual organization, and dimensional structure lend themselves to parallel processing by early vision (D. S. Blough, 1991; P. M. Blough, 1984; Cook, 1992b; Treisman & Gelade, 1980; Wolfe, 1992). This target search continues, presumably at a constant rate, until the current contents of the display match the animal's top-down representation of an acceptable target. By *top-down*, we mean a nonintentional, memory-based control of target or object recognition and identification by an abstracted pattern (D. S. Blough, 2002; Cook, Goto, & Brooks, 2005), and not any human-like conscious or intentional control of attention. These representations are determined by the reinforcement history of the target and can vary from being item specific (Cook, Levison, Gillett, & Blaisdell, 2005; Fagot & Cook, 2006) to generalized and abstract (Cook, Goto, et al., 2005; Cook & Wasserman, 2007; Katz & Cook, 2000). Once a match is determined and the threshold to respond is exceeded, the pigeon begins the biomechanics of making a localized pecking response to the selected area of the display.

In pigeons, the motor and biomechanical processes of the pecking response are relatively fixed (Zeigler, Levitt, & Levine, 1980; Zweers, 1982). In agreement with these prior findings, the fastest our pigeons could peck at the display averaged ~ 400 ms, as

Table 1
Mean Reaction Times (in Milliseconds) for Two-Target Trials
With no Secondary Target Pecks

SOA	Secondary target duration		
	100	250	500
0	1333	1429	1385
50	1331	1297	1443
100	1341	1306	1305
175	1327	1323	1257
250	1397	1379	1257
375	1285	1468	1234
500	1253	1253	1268
1000	1337	1206	1293
2000	1234	1253	1272
3000	1238	1407	1188

Note. SOA = stimulus onset asynchrony.

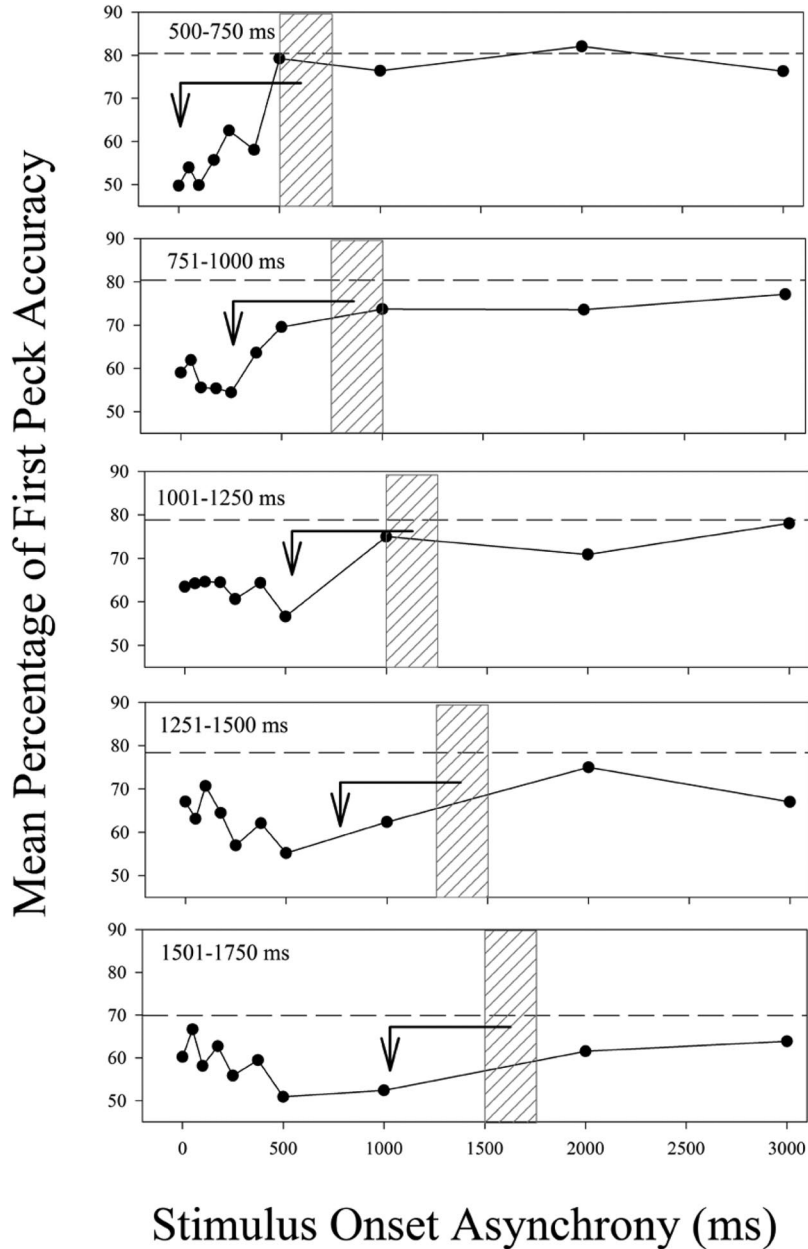


Figure 2. Mean percentage of first-peck target localization accuracy for the two-target test conditions, as a function of first-peck reaction time (RT). Each panel shows first peck RTs as grouped into five 250-ms bins. The striped area in each panel shows the range of RTs included in that panel’s curve. Arrows denote the point in time 650 ms prior to the average first peck for each bin. The upper dashed reference line shows baseline performance on single-target displays with these RTs.

derived from the postlocalization IRT results. Given that only the approach phase of the peck is actually included in first-peck RTs, we can estimate that the motor components of the “peck” contribute roughly 250 ms to this first localization response. That the first-peck RTs to our displays were on average consistently longer (~1200 ms) than these IRTs reflects the temporal costs of the searching and cognitive processing required by the target localization and identification steps outlined above.

During this 1 s or so of processing, a substantial proportion of that time is likely spent searching the display for a suitable target. The odd-item search required of the current task, especially given the very large number of possible targets, would certainly add some time in comparison with a situation in which a small number of known or primed targets are involved (D. S. Blough, 2002; Pietrewicz & Kamil, 1979). Furthermore, the speed of the search is likely dependent upon the discriminability of the elements in the

dimensional structure of the display (Allan & Blough, 1989; D. S. Blough, 1979; Cook, 1992b). For instance, our fastest searches were also the most accurate (e.g., Figure 2), surely reflecting the fact that the regions of these displays were made from highly discriminable elements.

In the present experiment, we establish for the first time that even a very brief presentation of a secondary target for as little as 100 ms during this search phase is problematic. These briefly presented flanking “targets” clearly disrupted the pigeon’s search for the primary target in a display similar to classic flanker effects in humans. These flankers surely attracted attention to their location. Part of this was expressed as localization reflected in their belated pecking to this spot. One implication of this is that it suggests target “identification” proceeds very quickly (~100 ms), because the birds confused the flanker with the real target. It is possible that the sudden onset of the secondary target additionally attracted processing in a manner similar to the idea of attentional capture in humans (Yantis, 1993). Even when direct responses to the flanker’s location are controlled for, the secondary targets also served to slow down responding to the primary target. In the present case, the brief secondary targets may have attracted attentional processing, but not responding (cf. Brown, Cook, Lamb, & Riley, 1984), resulting in the birds having more difficulty in reengaging their search or returning to the location occupied by the primary target (for a contrasting result, see Gibson, Juricevic, Shettleworth, Pratt, & Klein, 2005). This description shares similarities with the human phenomenon of “inhibition of return” (Posner & Cohen, 1984). This effect occurs when attention has been redeployed to a new object or location and the processing of formerly actively attended items or locations is suppressed. It is hypothesized that this occurs to encourage the active search for new information by not perseverating on previously processed information (Klein, 2000).

Besides the early effects of the secondary target, an interference effect that was time locked to the response was also uncovered here. This suggests that its source reflects a potentially different part of the processing stream from the early effects of the flankers. One possible explanation for this time-locked interference is that it is tied to a simple delay in the initiation of normal search. The idea here is that the temporal shifts across the panels in Figure 2 reflect increasing amounts of display inattention before engaging in the start of search. Such a variable phase of initial inattention would predict that the search phase would be initiated later on some trials than others, producing later response times. Thus, the interference effect in this case travels in a time-locked fashion with the response simply because the “same” search phase itself is being pushed increasingly further into the trial because of this initial delay. As a result, this interference effect occurs at the same relative point in processing. Although possible, it seems implausible that highly experienced birds would not pay attention for seconds at a time to a reward-producing stimulus. Such an inattention mechanism would be incompatible with the objective of attaining food reward as quickly as possible in the task. The birds certainly remained motivated throughout a session. An examination of RTs across the trials within a session revealed that though RTs were generally slower (~300 ms longer) over the first 20 trials of a session, the birds quickly “warmed up” to the task, and RTs never changed or, if anything, decreased over a session. This suggests that the pigeons were highly motivated to respond quickly

during testing. Second, the increases in response time across panels appear far more likely to represent increases in display difficulty. It is well established that more similar items result in slower search times and reduced accuracy in pigeons (D. S. Blough, 1979, 1988, 1993; Cook, 1992b). Consistent with these findings, mean accuracy on the baseline trials in Figure 2 consistently decreases as a function of response time across the different panels. If it were solely a delay in starting the same process, one should not find any differences in accuracy. This suggests that the longer response times across Figure 2 are due to the pigeons engaging in a greater amount of search behavior with difficult displays.

Another possibility is that the time-locked effect may be attached to the other end of the processing stream, and somehow related to the execution of the response itself. If so, this is the first time such an interference effect has been isolated. Perhaps the sudden onset of the secondary target at the critical decision/response initialization interrupts responding like a form of startle response. Whatever its source, its effects are limited to the processing portion of the trial. There is little evidence from late SOAs that any similar distraction or startle effect occurred once the pigeons had begun responding to the display. Accuracy on trials during which the secondary target appeared after the pigeon had already committed to pecking a location was essentially equivalent to baseline performance. Thus, once they have entered the response stage, they were immune to sudden onsets in the visual field.

Although it is difficult to determine the exact source of this latter effect, the pattern suggests that the final stages of target identification and response initialization are likely about 650 ms in duration. Subtracting out the ~250 ms or so of motor time to approach the display, there remains ~400 ms just prior to emitting a peck that is unaccounted for. Presumably the variable search phase for a target (primary or “confused” secondary target) has been completed. One possibility is that it reflects target identification and confirmation that can occur in durations as short as 100 ms, because some briefly presented secondary targets are treated as primary ones at this duration. However, this is a best case, and it may be slightly longer, because 500-ms flankers were more effective than were 100-ms ones.

Regardless, the current results suggest that even simple visual search in birds is a complex concatenation of separate steps, which involve for the current task target search/localization, target identification, and response completion. D. S. Blough (2000) has also suggested that pigeon visual search comprises separable stages. Using a different approach, he models the distribution of visual-search RTs using a convolution of two different component distributions (exponential and log-normal). He presents evidence that variables, such as the validity of a priming stimulus or context, affects a variable-duration search component captured by changes in the exponential component of the RT distribution. This stage is analogous to the visual search phases outlined above. He also found that variables, such as changes in reinforcement frequency, affect a separate postsearch process that was captured by changes in the log-normal component of the RT distribution. Although speculative, this postsearch processing may somehow be involved with the time-locked effects observed here. Experimental dissociation of the two possible interference effects that we may have isolated here is clearly an avenue for future research.

Thus, there appear to be a number of similarities between avian and human processing, at least with regard to the early segregation and search of visual information. For instance, the human theoretical concepts of attentional capture and inhibition of return seem potentially quite useful in understanding the current results looking at the chronometry of avian visual search and processing. The disruption of visual search and attention by similar mechanisms are frequently proposed to account for such antipredator actions as flocking or the presence of “eye spots” (Powell, 1974; Siegfried & Underhill, 1975; Stevens, 2005). Future research should bring together the kind of precise measurement of these processes possible in the laboratory with the natural behavior of birds exhibited in the wild. Visual search is fundamentally critical to birds in their day-to-day foraging and survival. Small differences in how successful and quickly birds can find food would have substantial fitness consequences (Bond & Kamil, 2002; Dukas & Kamil, 2000). Although the stimuli here are artificially constructed, the processes and time scale engaged by them must be highly similar to those involved with the search and identification of prey items and predators in the natural world. Barring convergent evolution, the present data would suggest that the origin of some of the control mechanisms for directing visual processing, search, and selection likely predate the ancestral separation of birds and mammals more than 250 million years ago.

References

- Allan, S. E., & Blough, D. S. (1989). Feature-based search asymmetries in pigeons and humans. *Perception & Psychophysics*, *46*, 456–464. doi:10.3758/BF03210860
- Blough, D. S. (1979). Effects of the number and form of stimuli on visual search in the pigeon. *Journal of Experimental Psychology: Animal Behavior Processes*, *5*, 211–223. doi:10.1037/0097-7403.5.3.211
- Blough, D. S. (1988). Quantitative relations between visual search speed and target-distractor similarity. *Perception & Psychophysics*, *43*, 57–71. doi:10.3758/BF03208974
- Blough, D. S. (1991). Perceptual analysis in pigeon visual search. In G. R. Lockhead & J. R. Pomerantz (Eds.), *The perception of structure: Essays in honor of Wendell R. Garner* (pp. 213–225). Washington, DC: American Psychological Association. doi:10.1037/10101-013
- Blough, D. S. (1993). Reaction time drifts identify objects of attention in pigeon visual search. *Journal of Experimental Psychology: Animal Behavior Processes*, *19*, 107–120. doi:10.1037/0097-7403.19.2.107
- Blough, D. S. (2000). Effects of priming, discriminability, and reinforcement on reaction-time components of pigeon visual search. *Journal of Experimental Psychology: Animal Behavior Processes*, *26*, 50–63. doi:10.1037/0097-7403.26.1.50
- Blough, D. S. (2002). Measuring the search image: Expectation, detection, and recognition in pigeon visual search. *Journal of Experimental Psychology: Animal Behavior Processes*, *28*, 397–405. doi:10.1037/0097-7403.28.4.397
- Blough, P. M. (1984). Visual search in pigeons: Effects of memory set size and display variables. *Perception & Psychophysics*, *35*, 344–352. doi:10.3758/BF03206338
- Bond, A. B., & Kamil, A. C. (2002). Visual predators select for crypticity and polymorphism in virtual prey. *Nature*, *415*, 609–613. doi:10.1038/415609a
- Brown, M. F., Cook, R. G., Lamb, M. R., & Riley, D. A. (1984). The relation between response and attentional shifts in pigeon compound matching-to-sample performance. *Animal Learning & Behavior*, *12*, 41–49. doi:10.3758/BF03199811
- Cook, R. G. (1992a). Acquisition and transfer of visual texture discriminations by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 341–353. doi:10.1037/0097-7403.18.4.341
- Cook, R. G. (1992b). Dimensional organization and texture discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *18*, 351–363. doi:10.1037/0097-7403.18.4.354
- Cook, R. G., Cavoto, B. R., Katz, J. S., & Cavoto, K. K. (1997). Pigeon perception and discrimination of rapidly changing texture stimuli. *Journal of Experimental Psychology: Animal Behavior Processes*, *23*, 390–400. doi:10.1037/0097-7403.23.4.390
- Cook, R. G., Cavoto, K. K., & Cavoto, B. R. (1996). Mechanisms of multidimensional grouping, fusion, and search in avian texture discrimination. *Animal Learning & Behavior*, *24*, 150–167. doi:10.3758/BF03198963
- Cook, R. G., Goto, K., & Brooks, D. I. (2005). Avian detection and identification of perceptual organization in random noise. *Behavioral Processes*, *69*, 79–95. doi:10.1016/j.beproc.2005.01.006
- Cook, R. G., Levison, D. G., Gillett, S. R., & Blaisdell, A. P. (2005). Capacity and limits of associative memory in pigeons. *Psychonomic Bulletin & Review*, *12*, 350–358. doi:10.3758/BF03196384
- Cook, R. G., & Wasserman, E. A. (2007). Learning and transfer of relational matching-to-sample by pigeons. *Psychonomic Bulletin & Review*, *14*, 1107–1114. doi:10.3758/BF03193099
- Dukas, R., & Kamil, A. (2000). The cost of limited attention in blue jays. *Behavioral Ecology*, *11*, 502–506. doi:10.1093/beheco/11.5.502
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Attention, Perception, & Psychophysics*, *16*, 143–149.
- Fagot, J., & Cook, R. G. (2006). Evidence for large long-term memory capacities in baboons and pigeons and its implication for learning and the evolution of cognition. *Proceedings of the National Academy of Science*, *103*, 17,564–17,567. doi:10.1073/pnas.0605184103
- Gibson, B. M., Juricevic, I., Shettleworth, S. J., Pratt, J., & Klein, R. M. (2005). Looking for inhibition of return in pigeons. *Learning & Behavior*, *33*, 296–308. doi:10.3758/BF03192859
- Jonides, J. (1981). Voluntary versus automatic control over the mind’s eye’s movement. *Attention and Performance*, *9*, 187–203.
- Katz, J. S., & Cook, R. G. (2000). Stimulus repetition effects on texture-based visual search by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *26*, 220–236. doi:10.1037/0097-7403.26.2.220
- Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, *4*, 138–147. doi:10.1016/S1364-6613(00)01452-2
- Pietrewicz, A. T., & Kamil, A. C. (1979). Search image formation in the blue jay (*Cyanocitta cristata*). *Science*, *204*, 1332–1333. doi:10.1126/science.204.4399.1332
- Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. *Attention and Performance X: Control of Language Processes*, *32*, 531–556.
- Powell, G. V. N. (1974). Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour*, *22*, 501–505. doi:10.1016/S0003-3472(74)80049-7
- Siegfried, W. R., & Underhill, L. (1975). Flocking as an anti-predator strategy in doves. *Animal Behaviour*, *23*, 504–508. doi:10.1016/0003-3472(75)90126-8
- Stevens, M. (2005). The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. *Biological Reviews*, *80*, 573–588. doi:10.1017/S1464793105006810
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*, 97–136. doi:10.1016/0010-0285(80)90005-5
- Wolfe, J. M. (1992). “Effortless” texture segmentation and “parallel” visual search are not the same thing. *Vision Research*, *32*, 757–763. doi:10.1016/0042-6989(92)90190-T

- Yantis, S. (1993). Stimulus-driven attentional capture. *Current Directions in Psychological Science*, 2, 156–161. doi:10.1111/1467-8721.ep10768973
- Zeigler, H. P., Levitt, P., & Levine, R. R. (1980). Eating in the pigeon (*Columba livia*): Movement patterns, stereotypy and stimulus control. *Journal of Comparative Physiological Psychology*, 94, 783–794. doi:10.1037/h0077818
- Zweers, G. A. (1982). Pecking of the pigeon (*Columba livia*). *Behaviour*, 81, 173–230. doi:10.1163/156853982X00148

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