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ORIGINAL PAPER

Pigeons (*Columba livia*) show change blindness in a color-change detection task

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Abstract Change blindness is a phenomenon whereby changes to a stimulus are more likely go unnoticed under certain circumstances. Pigeons learned a change detection task, in which they observed sequential stimulus displays consisting of individual colors back-projected onto three response keys. The color of one response key changed during each sequence and pecks to the key that displayed the change were reinforced. Pigeons showed a change blindness effect, in that change detection accuracy was worse when there was an inter-stimulus interval interrupting the transition between consecutive stimulus displays. Birds successfully transferred to stimulus displays involving novel colors, indicating that pigeons learned a general change detection rule. Furthermore, analysis of responses to specific color combinations showed that pigeons could detect changes involving both spectral and non-spectral colors and that accuracy was better for changes involving greater differences in wavelength. These results build upon previous investigations of change blindness in both humans and pigeons and suggest that change blindness may be a general consequence of selective visual attention relevant to multiple species and stimulus dimensions.

Keywords Pigeon · Attention · Change detection · Change blindness · Color

Selective attention is highly adaptive. Rather than devoting comparable resources to all sensory inputs, it allows one to prioritize processing of those elements and locations that are likely to be of consequence and/or suppress processing of those that are not. Such selectivity is essential because not all environmental stimuli are equally important. Some may even have critical survival-related implications in either the short or long term (e.g., food sources, conspecifics, or predators). Not surprisingly, comparative research has concluded that many animals are capable of actively directing attention in many of the same ways humans do, by selecting specific features, spatial locations, and/or hierarchical levels for preferential analysis, as the situation might demand (see Herbranson 2017).

As useful as it may be, attention is not flawless. Humans, for example, are subject to failures of attention such as inattentional blindness and change blindness, which presumably reflect some important limitations on attention. Simons and Levin (1998), for example, demonstrated that people failed to notice that their conversation partner had changed during a brief visual interruption: After a confederate had initiated a conversation by asking for directions, workers walked between the participant and the confederate, at which point a worker and the confederate surreptitiously exchanged places. Failure to detect such an important change suggests that our visual representations may contain very few lasting details.

Another example of attentional failure comes from the laboratory-based flicker task (Rensink et al. 1997). In this task, an original image repeatedly alternates with a slightly modified version, in which a single feature is changed. Participants are instructed to identify the change, and most do so very quickly. However, if a brief inter-stimulus interval (ISI) is inserted between the alternating images (creating the flickering image for which the task is named), the change in the alternating displays is much more difficult to identify, leading to longer identification times and lower accuracy rates.

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The flicker task is appealing to experimenters because they can easily isolate and manipulate specific stimulus characteristics such as the size, location, and salience of the change, as well as the timing of stimulus displays and ISIs. It also provides a concise operational definition of change blindness: the difference in accuracy between trials featuring an ISI, and those without. Furthermore, awareness of the change blindness phenomenon and extensive training do not seem to eliminate the effect. All of these characteristics hold extra appeal for comparative investigators, as non-human animals often require extensive training and cannot be directly queried about what they see. Other established procedures (e.g., Simons and Levin 1998) for studying change blindness and/or inattentional blindness can be methodologically quite complex and would not be as easily adapted for use with non-human animals.

While comparative research has repeatedly shown that non-human animals possess many of the useful aspects of human attention (Zentall 2005), such similarities do not necessarily imply that the mechanisms underlying attention are always the same or that they would also mirror the weaknesses of human attention. Thus, just as the methods used to study change blindness have revealed some details about attention in humans, they may hold similar promise for non-humans and in doing so may tell us more about the relationship between human and non-human attentional processes.

Experiment 1

Pigeons ought to be an apt candidate for a comparative study of change blindness. They possess excellent visual acuity and the cognitive abilities required to consistently detect changes in visual stimuli. Indeed, there have been several successful studies of change detection in pigeons, and the results generally parallel those from human studies of change detection. Wright et al. (2010) trained pigeons to detect color change between a sample array consisting of two colored circles and a subsequent test array with the color of one circle altered. Their pigeons successfully learned to choose the circle that changed color, even when successive displays were separated by a time delay of several seconds. Thus, pigeons must have relied on short-term memory, rather than attentional capture, and more importantly, they successfully learned a change detection task identical to those used to test human memory. Hagmann and Cook (2013) utilized a dynamic change detection task, in which pigeons were trained to detect continuous, gradual changes in brightness on a computer display. Pigeons' ability to detect change was controlled by the rate of change and paralleled human change detection in a similar procedure. These two studies demonstrate that pigeons can be trained to search for and detect changes in various contexts and that their change detection abilities are in many ways similar to those of humans.

However, not all change detection tasks show a strong parallel between humans and pigeons. Lazareva and Wasserman (2016) presented pigeons with displays consisting of four elements, each having three attributes (color, location, and orientation). Birds were trained to respond differently when consecutive displays were identical (no change) and when they were different (change). Pigeons readily discriminated between change and no-change trials when all three attributes of the display elements changed. However, when individual features were replaced by novel ones or were swapped between different elements, pigeons responded as though there was no change. Humans, in contrast, reported both as changes. The authors conclude that pigeons failed to detect some kinds of change because they did not bind features into integral objects. Most importantly, the results indicate one way in which pigeons' change detection abilities differ from those of humans.

Given these previous results, it is not immediately obvious if pigeons would be susceptible to change blindness, as humans are. In order to further investigate change detection and see whether pigeons show the equivalent of a change blindness effect, Herbranson et al. (2014) created an analog of the flicker task, comparing change detection accuracy on trials featuring an ISI to accuracy on trials with no ISI. Their methodology used displays consisting of up to 24 distinct line features across three response keys. A single line feature changed between the original and modified visual displays on one of three response keys and pecks to the key that featured the change were reinforced. Pigeons were significantly better at detecting changes if no ISI was present.

Thus, Herbranson et al. showed a basic change blindness effect characteristic of the flicker paradigm. Subsequent research has shown that many of the variables that affect change blindness in humans influence change blindness in pigeons in the same way: Longer ISI durations make change detection more difficult (Herbranson et al. 2014); larger changes are more salient and thus easier to detect overall and less likely to produce change blindness (Herbranson 2015); and longer trials result in better change detection, with the facilitation primarily due to additional search time (Herbranson and Davis 2016). Nevertheless, some conclusions regarding change blindness in pigeons must remain tentative at this point. First, each of these experiments has utilized the same birds, the same kinds of stimuli (line features), and the same kind of change (presence/absence of a feature). Thus, replicability remains in question, as does the generality of change blindness. In order to strengthen the claim that change blindness in pigeons parallels change blindness in humans, the phenomenon must be replicated and demonstrated under a variety of conditions.

The following experiments utilized different birds, having no previous experience in a change detection task. Furthermore, while the general procedure and measure of change blindness was the same, the stimuli and type of change differed. Rather than adding or deleting a line feature, stimuli consisted of patches of uniform color, and changes were changes in color. Recall that Wright et al. (2010) successfully used similar color stimuli in a pigeon change detection task, suggesting that birds should be able to learn to search for and detect these kinds of changes.

Two primary hypotheses parallel prior investigations of change blindness in both pigeons and humans. First, change detection accuracy on trials with an ISI should be worse than on trials without. Second, repetition should enhance change detection accuracy, especially on the more difficult ISI trials.

Methods

Animals

Four White Carneau pigeons (*Columba livia*) were purchased from Double T-Farm in Glenwood, IA. The pigeons were maintained at 85% of their free-feeding weights to approximate the condition of healthy wild birds (Poling et al. 1990). They were housed in individual cages in a colony room with a 14:10-h light/dark cycle and had free access to water and grit.

Apparatus

Four identical operant chambers were used (BRS/LVE, Laurel, MD). Each had three circular response keys (2.5 cm in diameter) located in a horizontal row in the front wall and a food hopper located directly below the center key. A houselight located on the front wall and directly above the center key was illuminated for the duration of each experimental session.

Stimuli

Stimuli consisted of colored key lights, back-projected onto each response key using LED light sources (Martek Industries, Cherry Hill, NJ). Each color uniformly illuminated an entire key. The set of colors used in Experiment 1 consisted of blue (460 nm, FWHM[1] ~ 35 nm), yellow (600 nm, FWHM ~ 20 nm), red (640 nm, FWHM ~ 20 nm), and white (575 nm, FWHM ~ 130 nm). On each trial, the computer randomly generated an original and a modified display, each consisting of one color on each of the three response keys. Colors for each key in the original display were independently selected with $P = .25$ for each of blue, yellow, red, and white (it was possible for multiple keys to display the same color). Thus, each original display was one of $4^3 = 64$ possible combinations of colors. The alternate display was identical to the original with the exception of the color displayed on one of the three keys. The location of the variant key was randomly determined on each trial ($P = .33$ for each of the left, center, and right locations), and the color was pseudorandomly selected with the only constraint that it could not match the color of the corresponding key in the original display.

Each trial consisted of alternating 250-ms presentations of the original and modified displays. The two displays were each presented 2, 4, 8, 16, or 32 times (randomly determined on each trial with $P = .20$ for each). Each presentation of the original display was followed by the modified display, and each presentation of the modified display was followed by either the original display or a trial-terminating display consisting of three white key lights (if and only if it was the final repetition of the trial). On one-half of all trials, the transition from an original to a modified display and vice versa was instantaneous, with no time delay. That is, once stimulus presentation began, there was no time when one of the two displays (base or modified) was not present on the response keys until the end of the trial. On the other half of the trials, there was a 250-ms ISI between each subsequent stimulus display. During the ISI, the keys were completely dark and no colored stimulus lights were visible. Thus, on trials with an ISI, the same number of repetitions took twice as long because each 250-ms stimulus presentation was followed by an ISI of the same duration. The top panel of Fig. 1 summarizes a sample stimulus display with an ISI.

Pretraining

Two birds had previous experience with the experimental apparatus in a probability learning experiment based on the Monty Hall dilemma (Herbranson and Wang 2014) and thus required no pretraining. Other, naïve birds were initially pretrained to respond via handshaping and autoshaping (Brown and Jenkins 1968). Stimuli during autoshaping were key lights illuminated with white, red, yellow, green, or blue light. Following pretraining, birds completed 100 trials in a daily experimental session (gradually increased from ten trials over the first 20 days of the experiment). Early pretraining sessions (115 days) also included geometric shapes, back-projected in white among

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[1] FWHM, full width at half maximum, is a measure of spectral bandwidth. It is the difference between the two most extreme wavelengths at which intensity drops to half the of the peak wavelength.

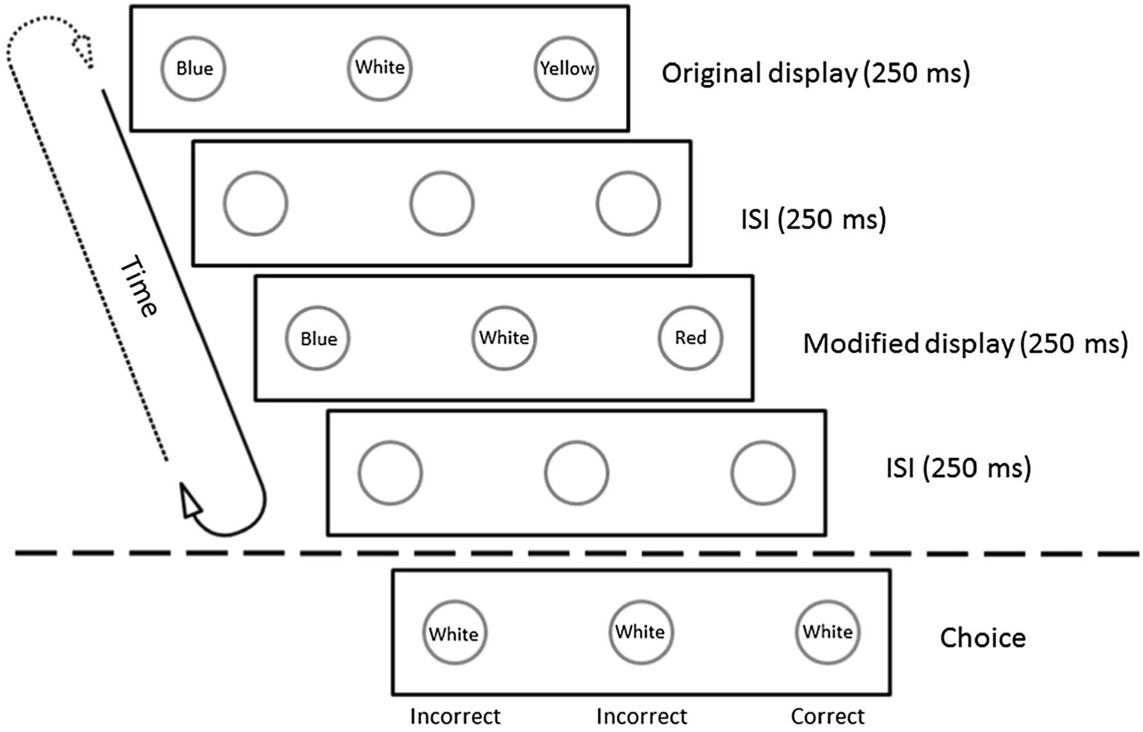

Fig. 1 Structure of a trial with an inter-stimulus interval (ISI). The *top panel* illustrates one repetition of the stimulus presentation portion of a trial. The change is on the right key (yellow–red). The *bottom panel* illustrates the choice portion of a trial. The correct response is the rightmost key, corresponding to the location of the change. A trial with no ISI would omit the blank displays (labeled ISI in the second and fourth positions) during stimulus presentation

the stimulus set, but based on poor performance, these were removed, leaving only the color stimuli described.

Procedure

Each trial consisted of a 5-s inter-trial interval (ITI), a stimulus presentation, a choice response from among the three keys, and reinforcement if the response was correct. The houselight remained on throughout each session. During the ITI, the computer generated an original and a modified display and determined the number of repetitions to be presented as well as whether or not to include an ISI, as described above. During stimulus presentation, keypecks had no programmed consequences and were not recorded. After the display, all three keys were uniformly illuminated with white light, and the first peck on any key was automatically recorded. If that peck corresponded to the location of the color change, a bird was presented with approximately 2.5-s access to mixed grain (access times varied between birds in order to maintain individual running weights). If a bird's response corresponded to either of the other two locations, then it was followed by a 10-s error signal during which the houselight alternated between on and off every 0.5 s. After either reinforcement or the error signal, the experiment continued along to the next trial. Birds completed a total of 30 sessions, at which point accuracy appeared to be stable.

Results

All statistics presented are based on data from the final 10 days of Experiment 1. There were no appreciable differences between naïve birds and those with previous experimental experiences. Thus, all results presented here and in Experiment 2 combine all birds into a single group. The overall percent of correct responses across all birds and trial types was better than chance accuracy of 33.3%, $M = 78.0$, $CI = [64.4, 91.6]$, $d = 2.135$. Thus, birds performed accurately on the task and were reliably capable of detecting changing colors in the stimulus displays. Having confirmed that birds learned the task, planned analyses were conducted to explore the influence of manipulated variables: ISI presence, number of repetitions, and color combinations.

To confirm the presence of previously demonstrated change blindness effects, a 2 (ISI: present, absent) × 5 (repetitions: 2, 4, 8, 16, 32) repeated-measures ANOVA was computed on the percentage of correct responses. The influence of these variables is shown in Fig. 2. There was a significant main effect of ISI indicating that accuracy on

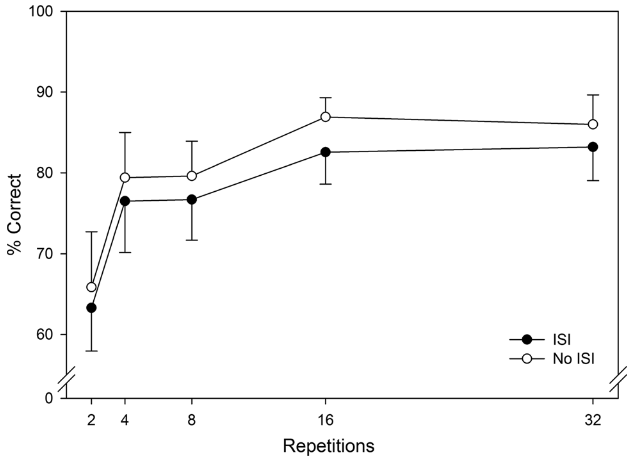

Fig. 2 Accuracy over the final 10 days of Experiment 1 as a function of ISI presence and repetitions. *Error bars* depict ± one standard error

ISI trials ($M = 76.4$) was worse than accuracy on no-ISI trials ($M = 79.6$), $F(1, 3) = 11.338$, $P = .043$, partial $\eta^2 = .791$. There was a main effect of repetitions indicating that accuracy improved as the number of repetitions increased from 2 to 32 (Ms = 64.6, 77.9, 78.1, 84.7, 84.6, respectively), $F(4, 12) = 11.104$, $P = .001$ partial $\eta^2 = .787$. There was no significant interaction between ISI and repetitions, $F(4, 12) = 0.114$, $P = .975$, partial $\eta^2 = .037$. The main effect of ISI is a replication of the basic change blindness effect as seen in previous implementations of the flicker task, whereby the presence of an ISI impairs change detection. The main effect of repetitions is also consistent with a previously identified serial search process in which each repetition constitutes an additional opportunity to consider (or reconsider) a possible change location and consequently better accuracy.

To investigate whether the specific colors involved in a change influenced accuracy, a repeated-measures ANOVA was computed, comparing accuracy on each of the six unique two-color combinations that were presented: white–red, white–yellow, white–blue, red–yellow, red–blue, and yellow–blue. Means for each color combination are shown in Fig. 3. There were no significant differences between color combinations, $F(5, 15) = 2.765$, $P = .058$, partial $\eta^2 = .480$. Nevertheless, accuracy on only five of the six color combinations was significantly better than chance performance of 33.3%, $t(3) \geq 8.228$, $P \leq .004$, $d \geq 4.083$. Only red–yellow was not reliably better than chance, $M = 61.3$, $t(3) = 2.141$, $P = .122$, $d = 2.116$.

Discussion

Experiment 1 constitutes a replication and extension of previous change blindness research using the flicker task with pigeons, showing that the basic findings extend to the detection of changes in color. As was the case in previous research (Herbranson et al. 2014; Herbranson 2015; Herbranson and Davis 2016), pigeons were worse at detecting changes on trials that featured an ISI than on trials with no ISI. This difference in accuracy is the operational definition of change blindness and originates in human implementations of the flicker task (Rensink et al. 1997). In addition, there was an effect of repetition, indicating that accuracy was better when there were more opportunities to detect a change. This has been previously demonstrated in pigeons by Herbranson and Davis (2016), who proposed that pigeons engage in a serial, self-terminating search, as humans do (Rensink 2000). Such a serial search process would seem to be a possibility in the present procedure as well. More importantly, the results demonstrate that change blindness in pigeons is replicable and applies to changes involving a new kind of visual feature (specifically, color). Previous demonstrations of change blindness in pigeons had all used the same individual animals, and changes were always of the same type: the addition/deletion of line features. Thus, these results contribute to the possibility that change blindness could be a general consequence of perception and/or selective attention that applies to a variety of stimulus types and situations.

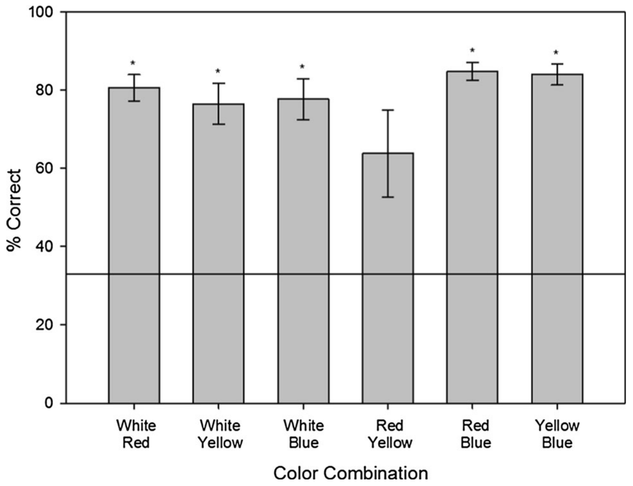

Fig. 3 Accuracy for each unique color combination over the final 10 days of Experiment 1. *Error bars* depict ± one standard error. *Asterisks* indicate values significantly better than chance accuracy of 33%

While Experiment 1 replicated the important main effects pertaining to change blindness (the effects of ISI presence and repetitions), there were some differences between the results of Experiment 1 and previous change blindness experiments in pigeons that deserve consideration. Most notably, overall accuracy in Experiment 1 was higher (78% overall) than in previous experiments using line stimuli (48% from Herbranson et al. 2014 for example). The basis for this difference is unclear at this point. It could be the case that changes in color are easier to detect than the appearance or disappearance of line features. Alternatively, it could be that the size of a change is important, and changes encompassing an entire key (as in the present experiment) are more prominent than changes on a small portion of a key. Regardless of the reason for the higher accuracy, our important conclusions remain the same, as the important measure of performance is not the overall level of accuracy, but the difference in accuracy between ISI and no-ISI trials.

Another important difference between the present experiment and previous investigations was in the number of exemplars presented during training. While there were many possible stimulus displays (576 pairs of original and alternate displays, not counting differences in numbers of repetitions) that could be generated, the number is considerably smaller than in other investigations (over 800 million possibilities in Herbranson et al. 2014). Thus, even though it would have been difficult for pigeons to memorize the entire stimulus set, it remains possible that their performance could have been augmented by memorization of a subset of stimuli. As with many general cognitive processes, a test involving transfer to novel colors would be the ideal assessment of whether pigeons learned a general rule involving change detection that could be applied uniformly.

An interesting unhypothesized result was the non-uniform accuracy on trials displaying various different color changes (see Fig. 3). In particular, trials involving red–yellow color pairs were not better than chance, whereas accuracy on every one of the remaining color pairs was. The reason for this difference remains uncertain, but it is worth noting that the difference between the peak wavelengths of the red (640 nm) and yellow (600 nm) stimuli was relatively small and considerably smaller than the difference between either one and the other tested wavelength, corresponding to blue (460 nm); note that the fourth color stimulus included, white, is not a single wavelength, but many. Thus, it is possible that the small 40 nm change constituted a particularly subtle change and was thus more difficult for pigeons to detect. Also consider that Cumming et al. (1965) trained pigeons on a matching to sample procedure using red-, green-, and blue-colored light bulbs. When they introduced a novel yellow bulb, pigeons produced a pattern of accuracy that was consistent with the possibility that birds coded the yellow sample as red. Wright and Cumming (1971) subsequently attempted to identify color-naming functions for pigeons and concluded that 540 and 595 nm may constitute transitional wavelengths for pigeons. Our red and yellow stimuli were both on the same side of these transition points, creating the possibility that red–yellow might be a particularly difficult discrimination, and more difficult than the other color pairs tested, which spanned both of these transition points. Physiological (Remy and Emmerton 1989; Wortel et al. 1984) and genetic (Kawamura et al. 1999) evidence supports the notion that pigeons do have the necessary visual hardware to discriminate wavelengths within this range, and behavioral evidence indicates that with training, they can learn to do so (Blough 1972; Wright and Cumming 1971). Nevertheless, it appears that not all color changes may be equally easy to detect. Experiment 2 will delve further into possible effects of color and test pigeons' ability to transfer their learning to novel colors and color combinations.

Experiment 2

Comparative investigations often rely on transfer to novel stimuli in order to assess whether animals have learned a general rule, or whether instead they relied on memorization of specific exemplars to support accurate performance during training. Investigations of category learning, for example, often train birds using a set of images until they reach a performance criterion and then test those birds on different images that were not part of the training set (e.g., Herrnstein et al. 1976). Correct categorization of novel images provides evidence that birds have learned a general category and are not relying solely on memorization of exemplars. Using the same logic in the current procedure, transfer to changes involving novel colors and color combinations has the potential to disambiguate the results from Experiment 1, by clarifying whether birds learned to respond to the specific stimuli used during training, or whether they learned a general rule that could be applied to novel color pairs.

The four colors included in Experiment 1 were selected mostly out of technological convenience. However, note that they possess some important characteristics. Three of the four colors (red, yellow, and blue) were approximately "spectral colors" (each consisting of only a very narrow range of wavelengths), and the three peak values spanned a wide range within the pigeon's visible spectrum. The fourth color (white) was non-spectral, as it consists of a broad range of wavelengths. Thus, an additional color could be added to the stimulus set in either of two possible ways: either (a) by presenting a wavelength not already in the set or (b) by presenting a novel combination of wavelengths. The former would yield a novel spectral color. The latter would yield a novel, non-spectral color.

Thus, Experiment 2 introduced a new spectral color (green) and two new non-spectral colors (magenta and cyan). Magenta is a combination of blue and red, and cyan is a combination of green and blue. Note that the former of these novel non-spectral colors consists of two familiar components that were used as stimuli in Experiment 1. The latter consists of one familiar color from Experiment 1, and one novel color introduced in Experiment 2 for the first time.

If birds' performance in Experiment 1 was due to a general rule, three results should be borne out in Experiment 2. First, if birds learned a general change detection rule, then accuracy to detect changes on trials involving novel colors should be better than chance and perhaps even as good as trials involving familiar colors. Second, if pigeons can use their change detection abilities on a range of color types, then accuracy on trials involving non-spectral colors should be as good as accuracy on trials involving spectral colors. Third, novel color combinations involving large changes in wavelength (e.g., green–red) should produce better accuracy than novel color combinations involving small differences in wavelength (e.g., green–blue).

Methods

Animals and apparatus

The same pigeons and operant chambers from Experiment 1 were used in Experiment 2.

Stimuli and procedure

Stimuli were generated as in Experiment 1, with the following exceptions. The set of colors that could be displayed on each key was expanded from 4 (blue, yellow, red, white) to 7, by adding three new colors (green, cyan, and magenta). The green stimulus corresponded to 520 nm, FWHM ~ 30 nm. Cyan and magenta were both created by illuminating the key with two colors simultaneously. Cyan was an equal mix of blue (460 nm) and green (520 nm). Magenta was an equal mix of blue (460 nm) and red (640 nm). The additional colors expanded the number of unique three-key displays to $7^3 = 343$. The remainder of the procedure remained the same. Birds completed ten daily experimental sessions, each consisting of 100 trials.

Results

All statistics presented are based on data from the entire 10 days of Experiment 2. The overall percent of correct responses across all birds and trial types was better than chance accuracy of 33.3%, $M = 61.4$, $CI = [48.7, 74.2]$, $d = 7.027$. Thus, birds performed accurately on the task and were reliably capable of detecting changes in the stimulus displays.

To explore whether the novelty of colors involved in a change influenced performance, a 2 (ISI: present, absent) × 3 (colors: 2 familiar and 0 novel, 1 familiar and 1 novel, 2 novel and 0 familiar) repeated-measures ANOVA was computed on change detection accuracy. The effects of both variables are shown in Fig. 4. The main effect of ISI was significant and indicated that accuracy was worse on ISI trials ($M = 54.9$) than on no-ISI trials ($M = 63.8$), $F(1, 3) = 26.595$, $P = .014$, partial $\eta^2 = .899$. There was also a significant main effect of color novelty, $F(2, 6) = 26.786$, $P = .001$, partial $\eta^2 = .899$. In particular, accuracy decreased with the number of novel colors in a stimulus, though each remained above chance accuracy of 33%: 0 novel colors (2 familiar) $M = 70.3$, $CI = [52.1, 88.5]$, $d = 6.468$; 1 novel color (1 familiar) $M = 60.3$, $CI = [48.6, 72.6]$, $d = 7.312$; 2 novel colors (0 familiar) $M = 47.5$, $CI = [41.1, 53.9]$, $d = 7.013$. Finally, the interaction between ISI and novel colors was not significant, indicating that the change blindness effect (the difference between ISI and no-ISI trials) was comparable for each type of color combination, $F(2, 6) = 0.724$, $P = .523$, partial $\eta^2 = .194$.

To explore birds' performance on specific color combinations (whether those individual colors were novel or familiar), a 2 (ISI: present, absent) × 21 (colors: specific two-color combinations listed in the leftmost column of Table 1) repeated-measures ANOVA was computed on accuracy across the 10 days of Experiment 2. The effect of both variables is shown in Fig. 5. There was a significant main effect of ISI, $F(1, 3) = 18.966$, $P = .022$, partial $\eta^2 = .863$. There was also a significant main effect of colors, $F(20, 60) = 5.668$, $P < .001$, partial $\eta^2 = .654$. There was no interaction between ISI and colors, $F(20, 60) = 1.294$, $P = .219$, partial $\eta^2 = .301$.

Of particular interest are trials involving novel colors, as they would indicate whether birds learned a general change detection rule during Experiment 1 that could be applied when new colors were introduced in Experiment 2. These

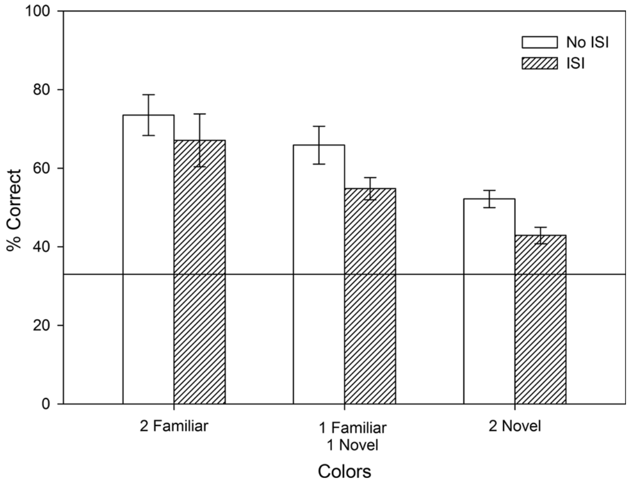

Fig. 4 Accuracy during Experiment 2 as a function of ISI presence and color novelty. *Error bars* depict ± one standard error

Table 1 Accuracy of responses to novel stimuli in Experiment 2

Colors	ISI	All trials		First trial				
		Mean	95% CI	Bird 1	Bird 2	Bird 3	Bird 4	Total
White–Green		74.7	[54.9, 94.6]*					
	No	81.6	[70.8, 92.5]*	C	C	C	C	4/4
	Yes	67.8	[38.0, 97.7]*	I	C	C	C	3/4
White–Cyan		65.4	[47.2, 83.6]*					
	No	69.0	[45.4, 92.5]*	C	C	I	C	3/4
	Yes	61.9	[47.0, 100.0]*	C	I	I	C	2/4
White–Magenta		60.1	[36.0, 84.2]*					
	No	66.3	[40.0, 92.6]*	C	I	C	I	2/4
	Yes	53.9	[25.8, 82.1]	C	C	C	C	4/4
Green–Red		70.1	[53.7, 86.5]*					
	No	70.4	[49.1, 91.8]*	C	I	C	C	3/4
	Yes	69.8	[56.2, 83.4]*	I	C	C	I	2/4
Green–Blue		55.6	[40.5, 70.6]*					
	No	64.7	[49.1, 80.4]*	C	C	C	C	4/4
	Yes	46.4	[28.6, 64.3]	I	I	I	I	0/4
Green–Yellow		67.1	[49.0, 85.2]*					
	No	66.7	[34.1, 99.3]*	I	C	C	C	3/4
	Yes	67.4	[54.5, 80.3]*	C	C	I	C	3/4
Green–Cyan		43.3	[29.3, 57.2]					
	No	41.5	[25.2, 57.8]	C	C	C	I	3/4
	Yes	45.0	[33.0, 57.1]	C	I	I	C	2/4
Green–Magenta		58.8	[43.0, 74.6]*					
	No	63.7	[46.3, 81.1]*	I	I	C	I	1/4
	Yes	53.9	[37.4, 70.3]*	C	I	C	C	3/4
Red–Cyan		61.4	[45.2, 77.6]*					
	No	70.5	[51.8, 89.3]*	I	C	I	C	2/4
	Yes	52.2	[25.2, 79.3]	I	C	I	I	1/4
Red–Magenta		59.8	[35.9, 83.6]*					
	No	65.5	[39.7, 91.4]*	C	C	I	I	2/4
	Yes	54.0	[27.4, 80.5]	I	I	I	I	0/4
Blue–Cyan		33.6	[20.6, 46.7]					
	No	37.1	[12.5, 61.7]	I	C	C	I	2/4
	Yes	30.2	[18.4, 42.0]	I	I	I	I	0/4
Blue–Magenta		42.2	[16.7, 67.7]					
	No	53.5	[7.6, 99.4]	I	I	C	I	1/4
	Yes	31.0	[6.8, 55.1]	I	I	I	I	0/4
Yellow–Cyan		67.2	[57.2, 77.2]*					
	No	69.8	[54.7, 85.0]*	C	C	C	C	4/4
	Yes	64.6	[52.7, 76.5]*	C	C	C	I	3/4
Yellow–Magenta		71.6	[50.4, 92.7]*					
	No	74.9	[56.2, 93.6]*	I	I	C	I	1/4
	Yes	68.3	[42.2, 94.3]*	C	C	C	C	4/4
Cyan–Magenta		39.7	[29.6, 49.9]					
	No	51.2	[40.3, 62.1]*	I	C	I	C	2/4
	Yes	28.3	[18.5, 38.0]	I	I	I	I	0/4

Table 1 continued

Colors	ISI	All trials		First trial				
		Mean	95% CI	Bird 1	Bird 2	Bird 3	Bird 4	Total
Total		58.0	[47.4, 68.7]*	15/30	17/30	17/30	15/30	64/120
	No	63.1	[49.7, 76.5]*	8/15	10/15	11/15	8/15	37/60
	Yes	53.0	[43.9, 62.1]*	7/15	7/15	6/15	7/15	27/60

Note C and I indicate correct and incorrect responses. Trial types in *italics* indicate combinations of two novel colors. An asterisk indicates that the 95% confidence interval does not contain a value of 33%, corresponding to chance performance

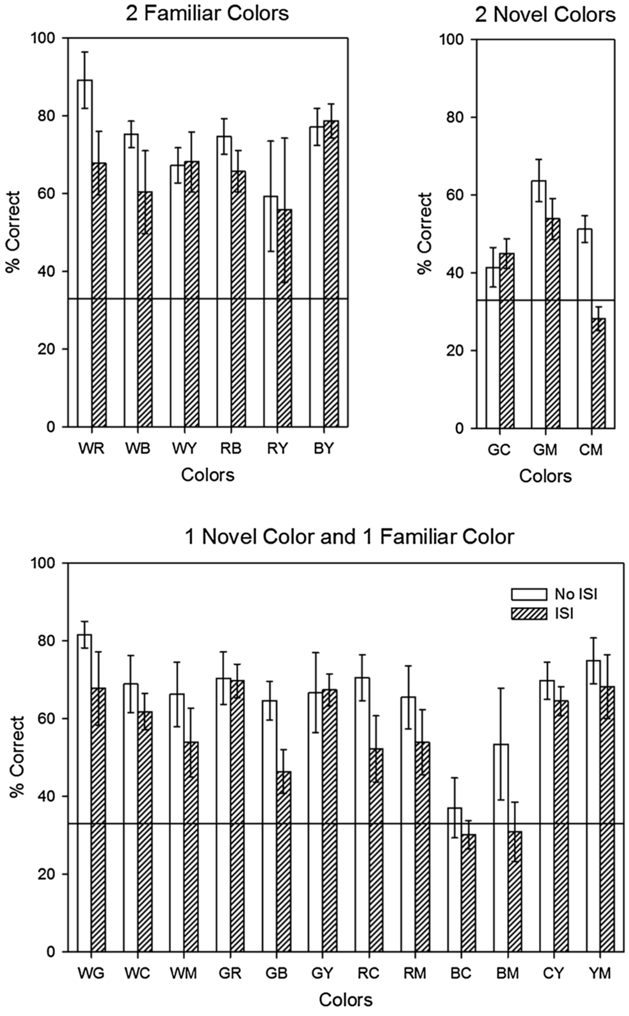

Fig. 5 Accuracy during Experiment 2 as a function of ISI presence and color combinations. Panels group stimuli according to the number of novel and familiar colors. *Error bars* depict ± one standard error. *B* blue, *C* cyan, *G* green, *M* magenta, *R* red, *W* white, *Y* yellow

novel color trials are visible in the bottom (one novel color) and top-right (two novel colors) panels of Fig. 5. In addition, Table 1 provides means and confidence intervals for each novel color combination, as well as the accuracy of each bird's first exposure to each novel color combination. Note that the overall means for both novel ISI and novel no-ISI trials are better than chance and that the confidence interval for most individual color combinations does not include 33% (chance accuracy) as a viable population mean. The exceptions are ISI and no-ISI trials in green–cyan, blue–cyan, and blue–magenta, as well as ISI trials in white–magenta, green–blue, red–cyan, red–magenta, and cyan–magenta. Furthermore, birds were better than chance overall at detecting changes on the first instances of novel stimuli, using a binomial distribution assuming chance accuracy of $P = .33$, for ISI trials only (27/60, $P = .040$), for no-ISI trials only (37/60, $P < .001$), and for all first-exposure trials (64/120, $P < .001$). Thus, it is unlikely that birds could have performed as accurately as they did on these first exposures if they did not learn a general rule that could be deployed upon their first encounter with a novel color combination.

In order to investigate a possible effect of change salience, a difference in wavelength was computed for each combination of the spectral colors red (640 nm), yellow (600 nm), green (520 nm), and blue (460 nm), excluding stimuli that featured white, cyan, or magenta (because a simple difference could not be computed for these non-spectral colors). Figure 6 shows the relationship between the magnitude of this wavelength change and accuracy for both ISI and no-ISI trials. In both cases, there was a

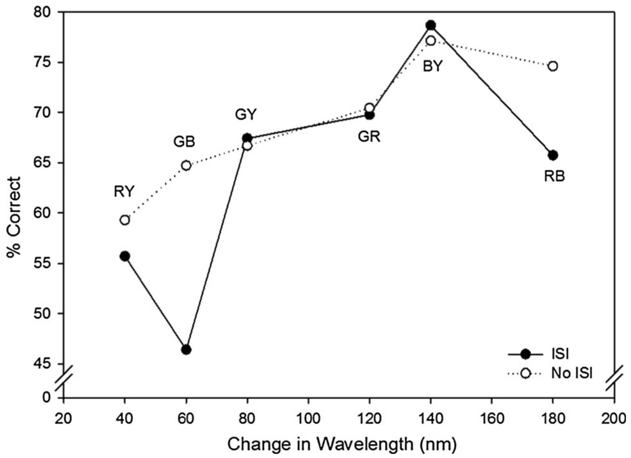

Fig. 6 Accuracy during Experiment 2 as a function of ISI presence and change in wavelength for pairs of spectral colors. Letter pairs identify colors for each change type. *B* blue, *G* green, *R* red, *Y* yellow

positive correlation between change in wavelength and accuracy, though the correlation was only significant for no-ISI trials: $r = .923$, $N = 6$, $P = .009$ for no-ISI trials; $r = .660$, $N = 6$, $P = .153$ for ISI trials.

Discussion

Birds in Experiment 2 were better than chance at detecting changes to both familiar and novel transfer stimuli. The latter indicated that memorization would be an inadequate explanation for the accurate performance of these same pigeons in Experiment 1. While familiarity did improve accuracy (i.e., accuracy increased with the number of familiar colors involved in a change), accuracy remained better than chance for all trial types, including those consisting entirely of novel colors. Furthermore, birds were better than chance on their first exposures to novel stimuli, indicating that the results of novel color combinations cannot be easily accounted for even by a fast learning process.

These results imply that birds learned a general change detection rule that could be applied when facing new stimuli. This basic approach has previously been used in other contexts such as categorization (Herrnstein et al. 1976) and same/different discrimination (Blaisdell and Cook 2005) to show that birds learned a general rule and did not merely memorize specific training stimuli. Thus, it appears that pigeons can generalize the concept of color change to novel instances and can apply the rule to spectral as well as to non-spectral colors. Note, however, that there was some decrement in performance: changes involving novel colors were not detected as accurately as changes involving familiar colors. Considering trials involving novel color combinations as transfer trials, we might say that they did not transfer to a baseline level of accuracy. This may have been a consequence of set size, as pigeons were trained in Experiment 1 on a relatively small set of six unique color pairings. Wright and Katz (2006) showed that when learning a same/different concept, training set size influenced degree of transfer, and only with large training sets (256 items) did pigeons respond to novel transfer stimuli at a baseline level of accuracy. Thus, a larger set of training stimuli might have produced even better change detection accuracy to novel color combinations. If the concept of color change is relevant to pigeons in the wild, then we should expect that the cognitive processes involved in change detection should apply not just to narrow bandwidth, LED-generated colors in the laboratory, but also to the myriad of spectral and non-spectral colors that are part of the natural world.

Results also indicated that the salience of a change is important for change detection. Here we defined change salience as the magnitude of the difference in wavelength between two spectral colors, and more salient changes produced better accuracy than less salient changes. This finding is also consistent with previous manipulations of change salience in a different modality. Herbranson (2015), using stimuli that changed by the addition/deletion of line features, showed that more salient changes (those involving more line features) also resulted in better accuracy.

Despite accuracy that was better than chance overall, performance was not uniformly good, and some color combinations resulted in poorer accuracy. In particular, note in Table 1 that there were five color combination that resulted in worse change detection than the worst color pair in Experiment 1, red–yellow (at 57.5%): blue–cyan (33.6%), cyan–magenta (39.7%), blue–magenta (42.2%), green–cyan (43.3%), and green–blue (55.6%). Of these, green–blue is the only combination of two spectral colors, and it also constitutes the smallest difference in wavelength (60 nm), just greater than (but comparable to) the difference between red and yellow (40 nm). Three of these other color pairs involved one non-spectral color, and those non-spectral colors all shared a component wavelength with the other (spectral) color in the pair. The final color pair was cyan–magenta, a pairing of two non-spectral colors, which share a common component wavelength (blue). While it is more difficult to quantify salience for changes involving non-spectral colors than it is for changes involving only spectral colors, it makes intuitive sense that changes involving color pairs with common wavelength components would be less salient and thus more difficult to detect.

In contrast, more salient changes produced the best accuracy. Note that the best trials that did not involve the color white were blue–yellow (77.9), yellow–magenta (71.6) red–blue (70.2), and green–red (70.1). These include pairs of spectral colors with large inter-wavelength differences (blue–yellow, red–blue, and green–red) and one non-spectral color that was not paired with either one of its component wavelengths (yellow–magenta). It may also be relevant to note that some of these involved opposing color pairs specified by opponent processing theories of color vision (see Hurvich and Jameson 1957). While opponent processing is not specific to any particular animal, it has been verified to be at work in pigeons, as opponent-color units have been found in the pigeon thalamus: Yazulla and Granda (1973) identified single neurons in the nucleus rotundus that are, respectively, excited and inhibited (or inhibited and excited) by short- and long-wavelength (blue and yellow) light and could be a physiological contributor to some of these more easily detected changes.

In addition to the general effect of change salience based on wavelength difference, recall that some specific color combinations may constitute more difficult discriminations. Wright and Cumming (1971) proposed that 540 and 595 nm might be transition points in pigeon color-naming functions. If so, then we might expect that colors falling on the same side of these transition points to be particularly difficult. This was the case for our red (640 nm) and yellow (600 nm) color pairs in Experiment 1 and for the green (520 nm) and blue (460 nm) color pairs in Experiment 2. In Experiment 1, pigeons were not significantly better than chance at detecting red–yellow changes. In Experiment 2, birds were better than chance at detecting green–blue changes, but only when there was no ISI (see Table 1). Furthermore, as noted previously, our birds were no better than chance at detecting blue–cyan and green–cyan changes, stimuli consisting only of wavelengths in the same color-naming region. Thus, these instances might reflect the combined effects of a small wavelength difference and those important transitional wavelengths.

General discussion

These results add to a growing body of research on change detection in pigeons. They also constitute an additional demonstration of change blindness in pigeons, extending the phenomenon into a new modality, color. Given that change blindness has been useful for investigating the mechanisms of attention in humans (see Simons and Ambinder 2005), we think that it holds similar promise for understanding mechanisms of attention in pigeons. Note that we interpret the difference in accuracy between ISI and no-ISI trials in terms of the attention-related phenomenon of change blindness. This is consistent with the human literature, but not by itself a necessary conclusion. Consider that in other tasks, a time delay can similarly impair performance, but presumably does so for different reasons. Matching to sample, for instance, is impaired by the introduction of a delay, and this impairment is normally attributed not to attention but to the decay of memory over the time course of the delay. In the flicker task however, it is commonly assumed that the impairment is not due to the length of the delay, but to the interruption of visual continuity between consecutive displays. Herbranson and Davis (2016) found that longer ISIs made accuracy better, rather than worse, and this finding points toward the current interpretation (change blindness, rather than memory trace decay).

The results described here are consistent with previous change blindness results from human participants. In humans, the presence of an ISI impairs accuracy and also results in slower change detection. Though our procedure did not allow for collection of response times from pigeons, repetitions act as a stand-in that can be analyzed in a more systematic way. Presumably, response times in humans and the effect of repetition in pigeons are both due to the use of a serial search process on trials featuring an ISI. That is, possible change locations must be considered sequentially, a process that takes time (see Herbranson 2015). It might be possible to collect response times from pigeons by eliminating the required number of repetitions and simply recording the first response during stimulus presentation, though we suspect this could result in unacceptably high error rates. Another possibility would be to collect responses throughout stimulus presentation. Wright et al. (2010) showed that in a similar change detection task, pecks during stimulus presentation could reliably predict accuracy. If pigeons are engaging in a serial search, locations of pecks during the ongoing stimulus display might reveal additional details of that search process. We are also optimistic about the possibility of using the same flicker methodology to investigate additional kinds of change, perhaps incorporating more complex stimulus types. For example, shapes having multiple attributes (color, shape, texture, etc.) would allow for comparison of change detection, perhaps revealing which kinds of changes are easier or harder to detect. Implementation of the method using larger displays (perhaps including photographic images on a touch-screen display) would allow for more possible change locations and presumably require a more sophisticated search strategy than the limited number of response-key locations available in a standard operant chamber.

Perhaps the most exciting consequence of a change blindness effect in pigeons is that it has the potential to reveal more details about cognitive processes such as visual short-term memory (VSTM) in non-human animals. It may be the case that change blindness reflects a general limit on the capacity to encode and retain visual information from one moment to the next and that it would apply to any animal with control over selective attention including, but not limited to pigeons and humans. This possibility is supported by findings of change blindness in macaque monkeys (Cavanaugh and Wurtz 2002), though there are many more candidate species that could reasonably be tested. In addition to specifying the capacity limitations of VSTM, change detection tasks may have the potential inform us about its basic structure; there has been renewed debate about whether VSTM consists of a fixed number of discrete slots, or is instead a continuous resource distributed across all items in memory. Both models can account for the limited capacity of VSTM in humans, and color-change detection tasks have provided much of the critical data (see van den Berg et al. 2012). Given the strong parallels between pigeon and human change detection, it may be time to reassess traditional slot-based models of short-term memory as they have been applied to pigeons.

While the demonstration of change blindness in pigeons is exciting, we must also concede that stimuli in laboratory experiments are not always very realistic. For example, the stimuli in the flicker task change suddenly (rather than gradually), whereas objects in the real world do not suddenly change color, or pop into or vanish from existence. Note, however, that such scenarios are just as unnatural for humans as they would be for pigeons, and the flicker task has long been a valuable tool for the study of human attention and perception. Furthermore, the flicker task was originally inspired by the finding that changes presented during an eye saccade were more difficult to detect than those presented between saccades (Bridgeman et al. 1975). If the flicker task indeed works by mimicking the conditions that produce saccade-contingent change blindness in humans, then it would appear to be just as relevant to pigeons, whose eye and head movements are quite prominent. Pigeons' characteristic head-bobbing gait serves to stabilize a visual image on the retina during walking (Necker 2007). By this interpretation, those head movements may actually be a mechanism to combat such movement-based sources of change blindness, or at least constrain them to specific, predictable moments during locomotion. It should also be noted that the flicker task is only one procedure for producing change blindness under laboratory conditions. Simons et al. (2000) demonstrated change blindness for gradual changes, without the visual disruption that is a defining feature of the flicker task. Hagmann and Cook (2013) used a similar approach with pigeons and found that manipulation of the rate of change similarly affected pigeons' change detection without visual disruption. Thus, it appears that change blindness is not limited to the (admittedly unnatural) flicker methodology. We hope that additional change blindness research paradigms will be similarly adapted in the future to further explore the phenomenon in non-human animals.

These results underscore the primary conclusion that attention (in both pigeons and humans) is limited and imperfect, and we must remember that these limitations have real-world implications. Cryptic prey, for example, take advantage of attentional limitations in predators by forcing them to perform more difficult searches that require identification of conjunctions of features rather than individual features (Cook et al. 1996; Reid and Shettleworth 1992). Change blindness could be another example of the limitations of attention exerting themselves, as moment-to-moment changes are frequently critical events (consider, for example, the possibility of missing a sudden change such as the appearance of a predator or an in-flight obstacle). It would not be surprising if some ambush predators adopt stalking strategies (such as motion camouflage; Kane and Zamani 2014) because they take specific advantage of attentional limitations in their prey (such as change blindness), or if prey in turn adopt specific vigilance strategies (such as social foraging; Fernández-Juricic et al. 2004) that compensate for such weaknesses. Future research may serve to illuminate the relevance of attentional limitations such as change blindness, and the ways humans, pigeons, and other animals may attempt to compensate for them.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures were in accordance with the Office of Laboratory Animal Welfare and with US Public Health Service Policy on Humane Care and Use of Laboratory Animals. The experiments reported were approved by Whitman College's Institutional Animal Care and Use Committee.

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