

# Pigeons simultaneously attend to static and dynamic features of complex displays

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## ABSTRACT

The simultaneous processing and attention to temporally dynamic and static features remains an open and important question in theories of avian visual cognition. Here, four pigeons (*Columba livia*) learned to discriminate complex displays involving concurrently available static and dynamic features. These displays consisted of 20 elements built from combinations of two, binary-valued, static visual dimensions: red vs. green element color, large vs. small element size; and two binary-valued dynamic dimensions; fast vs slow element motion, right vs up motion direction. One combination of these four features was reinforced on a VI schedule. The remaining 15 combinations of element color, size, speed and direction were never reinforced. During acquisition, all four dimensions were simultaneously discriminated. Varying the number of elements revealed that a single element was sufficient to support discrimination of all four dimensions. The pigeons agreed on the relative discriminability of stimuli within and across the different dimensions, with the difference in motion direction being the hardest for all birds. Redundant facilitation suggested rapid, perhaps parallel, processing of both dynamic and static features. No attentional trade-offs between dynamic or static dimensions were observed. These results agree with theories of avian vision employing the notion of multiple independent channels for different types of information.

## 1. Introduction

Visual objects, possessing both static and dynamic features, regularly form the basis for our interactions with the world. The same appears true for birds. For example, birds might need to recognize the size, coloration and actions of other birds during mating displays or in flight. Such dynamic and static features seem to be processed by different neural and cognitive pathways within the brain. Across mammals and birds, separate dynamic and static processing mechanisms have been identified in distinct neural regions (e.g., Cook et al., 2013; Livingstone and Hubel, 1988; Nguyen et al., 2004; Ungerleider and Mishkin, 1982). Further, the results of various visual grouping experiments have similarly suggested that birds separately process different aspects of the visual world via independent feature-specific channels before they are integrated into a functional representation (Cook and Haggmann, 2012).

Prior research using visual discrimination tasks has established that birds can process such static and motion features from various displays. In both of these domains, the contributions of Marcia Spetch and her colleagues over the years have been deeply insightful in helping us to better understand visual cognition in both birds and mammals (Kelly

et al., 2001; Nankoo et al., 2017; Nguyen et al., 2004; Reid and Spetch, 1998; Spetch and Friedman, 2003, 2006a, 2006b; Spetch et al., 2005). The evidence that pigeons can process a wide variety of static visual features (e.g., color, line orientation, size, etc.) is large, substantial, and long-standing. The evidence that pigeons can identify the dynamic features of complex displays is of more recent origin with the increasing availability of computer-driven displays (Asen and Cook, 2012; Cook and Roberts, 2007; Dittrich et al., 2010; Dittrich and Lea, 2001; Goto and Lea, 2003; Goto et al., 2002; Nankoo et al., 2014; Qadri et al., 2014a,b). For static features, rigorous testing has highlighted how this processing evolves in seemingly separate channels or spatially-coded maps that are later integrated together (for a brief review, see Cook and Haggmann, 2012), and dynamic features like motion have been suggested through neural investigations to function in similar ways (Frost et al., 1988; Frost and DiFranco, 1976; Frost et al., 1990).

Despite these different lines of research, one understudied aspect of avian visual cognition is what happens when features from the domains of temporally static and temporally dynamic dimensions come together to concurrently control behavior. For human vision, rapid attentional capture and visual search studies find evidence of “pre-attentive” channels of information that allow for rapid attentional capture or

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search for particular individual features (Treisman and Gelade, 1980). Under certain task demands, such as during the search for specific feature conjunctions, these separate channels are integrated or conjoined together (i.e., “binding”) in a slow and possibly resource-intensive process. Studies on motion perception and color perception and their binding, reveal largely separate basic visual pathways that eventually integrate in a complex fashion (Baylis et al., 1992; Livingstone and Hubel, 1988; PapaThomas et al., 1991; Seymour et al., 2009; Zhang et al., 2014).

While there is a long history in animals of looking at stimulus compounding with combinations of static features from different dimensions, very few studies have required pigeons to discriminate simultaneously both motion and static features from the same display, though there is evidence of similar specialized channels for motion and color in pigeons (Wang et al., 1993). One recent study showed that pigeons are able to discriminate the combination of static and dynamic aspects of a display using fully-featured complex videos of animated figures exhibiting different actions (Qadri and Cook, 2016). The cognitive mechanisms underlying this cross-domain processing is unclear. Conceivably, both dynamic and static cues could be processed simultaneously from the information in a single visual “scan” (i.e., restricted local processing; cf. Qadri and Cook, 2015). Alternatively, multiple scans could be needed, with each scan’s attention extracting different features in a type of sequential integration. These processing strategies would result in different response dynamics. If processing a particular feature requires a feature-specific visual scan, then displays with multiple relevant features would have longer processing times than displays with only a single relevant feature, for example. If all features are instead simultaneously available in parallel with every scan, then the processing times would be similar with both single-feature and multiple-feature displays.

In the present experiment, we sought to advance our limited understanding of how dynamic and static features come to control visual discrimination behavior at the same time in pigeons. To do so, we employed a multidimensional discrimination recently described as the *multiple necessary cues* procedure (MNC; see Vyazovska et al., 2014). This procedure is well suited to measuring and tracking the processing and attention to compound stimuli having multiple features (cf. Reynolds, 1961). In an MNC task, one multidimensional compound stimulus is designated as positive (S+; stimulus to which responding is reinforced), and all the remaining multidimensional stimuli of different organizations are designated negative (S-; stimuli to which responding is not reinforced). As a result, the negative stimuli can differ from the positive stimulus in one, two, or more feature dimensions. Any contrasting reactions to these different organizations tracks and reveals how processing to each of the dimensions was allocated and how they interacted with one another. For example, the MNC procedure can reveal redundant facilitation by comparing performance on displays with a single negative feature to those with multiple negative feature values. Redundant facilitation would be evident if the displays with multiple negative features supported better peck suppression compared to displays with a single feature. If multiple negative features did not support better suppression, there would be no evidence for redundant facilitation.

In the present case, we tested compound stimuli defined along four binary-valued dimensions. Two were temporally static dimensions, requiring visual processing over a spatial region to identify a feature (element size; element color). Two were temporally dynamic dimensions that required visual processing over both time and space (rate of element motion and direction of element motion). The compound stimuli appeared as “flow fields” consisting of an array of squares of a given color (red or green) and size (small or large), that all moved in a given direction (up or right) and at a given rate (fast or slow). These flow fields could then be generated to independently test every combination of the four dimensions (see Supplemental Methods for example displays).

Using the MNC procedure, we examined how four pigeons processed the dynamic and static features of a moving compound visual display. We first examined how they learned about the different domains and dimensions involved in this complex multidimensional task. Following acquisition, we further evaluated how varying the number of elements in the display affected the pigeons’ discrimination. During each phase, we were keenly interested in the pigeons’ differential capacity to suppress responding to the different negative stimuli to discern how attention and visual control by the different static or dynamic features developed and was maintained.

## 2. Methods

### 2.1. Animals

Four experienced male White Carneaux pigeons (*Columba livia*) were tested (#1R, #2B, #3B, #4N). They were maintained at 80–85% of their free feeding weights and housed individually with free access to grit and water in a colony (12/12 LD cycle). They had previous experience with a variety of both unrelated static and dynamic stimuli (dynamic and static 3D geons, perspective motion, color discriminations, edge alignment, image memorization, and biological motion discriminations, some unpublished; Cook et al., 2011; Cook and Roberts, 2007; Murphy et al., 2015). Tufts University’s Institutional Animal Care and Use Committee (IACUC) approved the procedures used in this experiment (protocol M2013-124).

### 2.2. Apparatus

Testing was conducted in a computer-controlled operant chamber. Stimuli were presented on a 30.5 × 23.2 cm LCD monitor (NEC Accusync LCD 1525X, 1024 × 768, 75 Hz) visible behind a 30.5 × 22.9 cm infrared touchscreen (EZScreen; Houston, TX). The monitor was recessed 8 cm behind the touchscreen. A centrally located houselight was illuminated at all times except during timeouts. A food hopper (Coulbourn Instruments; Whitehall, PA) filled with mixed grain was located under the touchscreen and delivered reinforcement for correct responses. Stimuli were generated in Matlab (Mathworks, Natick, MA). Experimental events were controlled using Visual Basic 6 (Microsoft; Redmond, WA).

### 2.3. Compound visual stimuli

The discriminative stimuli in these experiments were presented as digital videos. Each video display consisted of a set of 20 randomly-placed square elements on a black background. These elements could vary along a combination of four binary-valued dimensions: element color (red vs. green; RGB 255, 0, 0 or RGB 0,255,0), element size (small vs. large; 10 pixels or 18 pixels; approximately 0.3 mm/pixel), motion speed (slow vs. fast; 3 pixels per frame or 9 pixels per frame; about 2.7 cm/s vs 8.1 cm/s), and motion direction (up vs. right). When an element moved off of the central display area, it “re-appeared” on the opposite end of the display as if had “wrapped” around the display. All pigeons were trained with the red-small-slow-up elements used as the positive stimulus (S+). Relative to the S+ stimulus, the elements of the S- stimuli differed from the S+ in either one, two, three or four dimensions. Displays containing one, two, three, and four feature differences will be referred to as “1FD,” “2FD,” “3FD,” and “4FD,” respectively. For example, the 1FD condition contained four types of displays that had elements differed in either just color, shape, speed, or direction. Before the start of discrimination training, the pigeons were trained to peck at the stimuli of all of these conditions. Once discriminative training started, pecks to this S+ stimulus were consistently reinforced on a VI schedule. During training, the remaining 15 compound stimuli were never reinforced, and instead they were followed by a variable-duration dark timeout, 250 ms per peck (S-).

For each of the 16 possible combinations of these four dimensions (e.g., red-small-slow-up, or green-large-fast-right; see supplemental videos), ten different video files were generated for a total of 160 unique video files. Each of these video files was ten times longer than needed for a single complete stimulus presentation, and video playback started from a random frame within this longer video on each trial. The video files were encoded using the Lossless CamStudio Screen Codec (CSCD; camstudio.org) at a playback rate of 30 frames per second and scaled to a 400 × 400 pixel resolution.

## 2.4. Procedure

Each trial started with a peck to a centrally positioned, 2.5 cm white ready signal. Immediately following, the pigeons were presented with an 8-s video in the center of the screen. During this presentation, pecks to the S+ stimulus were reinforced on a VI 4-s schedule (2.9-s access to food). Pecks to any of the 15 S- stimuli increased the length of a subsequent dark timeout by 250-ms per peck. Following a 3-s inter-trial interval (ITI), the ready signal for the next trial was presented.

### 2.4.1. Acquisition

Daily training sessions consisted of three 70-trial blocks (24 S+ /46 S-; 210 total trials). Each block was constructed to test all combinations of the discriminative features. The 46 S- trials in each randomly-organized block consisted of two tests of the 4FD stimulus (2 in total), two tests of each combination of 3FD (8 total) and 2FD (12 total) stimuli, and six tests of each 1FD stimulus (6 repetitions × 4 features = 24 total). The remaining 24 trials in each block were S+ trials. Four of these S+ trials were randomly selected to be non-reinforced probes to provide a measure of continuous pecking, free from interruptions required to obtain food on the VI schedule. Pigeons #N3 and #R4 received 8 sessions of this training, while pigeons #B1 and #B2 received 13. For the purposes of analysis, only the first twenty 70-trial blocks from the first seven completed sessions were examined.

### 2.4.2. Variation in the number of display elements

To better understand how the pigeons were processing the displays, we varied the number of elements in the display. Because of the number of trials involved, for this test, we dropped the 2FD and 3FD conditions to focus on testing on the 1FD and 4FD conditions. These conditions were tested with 1, 2, 4, 8, 16, and 32 elements in each displays. Again, ten different videos were generated for count of elements, each using different start positions for the elements. To equivalently test displays with the different numbers of elements, we constructed two 108-trial blocks (48 S+ /60 S-; 216 total trials) in which two of each 1FD trial (2 repetitions × 4 features × 6 element counts = 48 total trials), two 4FD trials (repetitions 2 × 6 element counts = 12 total trials), and eight positive trials (8 repetitions × 6 element counts = 48 total trials) were tested with each element number. Two of these eight positive trials at each number of elements were randomly selected to be non-reinforced probe trials. Five sessions were tested with each pigeon, except for #4 N who only received three sessions of testing.

## 3. Results

### 3.1. Acquisition

All four pigeons rapidly and easily learned the multidimensional discrimination. The rate of learning varied as a function of the number of feature differences between S+ and S- displays. Fig. 1 shows the learning curves for each type of S- displays with the response metric of discrimination ratio (DR; for each condition: S+ pecks / [S+ pecks + S- condition pecks]) as a function of trial block. The figure shows that learning occurred more rapidly as more features distinguished the S- displays from the S+ display (four differences > three > two > one). A repeated measures ANOVA (Condition × 70-trial Block) using

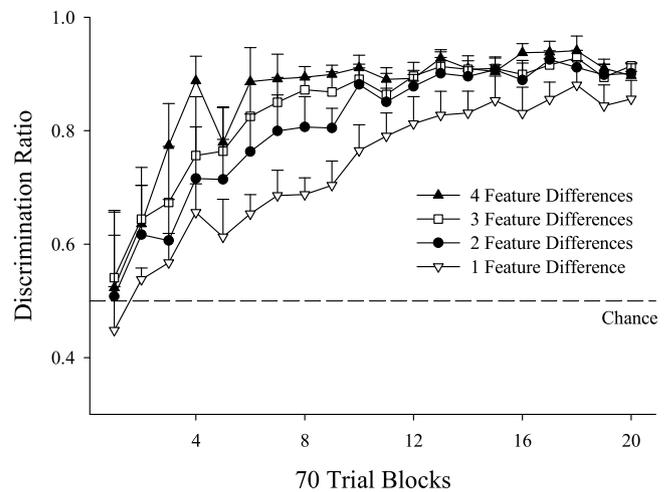


Fig. 1. Acquisition as a function of 70-trial blocks. Discrimination ratio was calculated by using the ratio of all S+ pecks and each condition's S- pecks. Error bars are SEM across birds. The dashed line denotes chance performance.

discrimination ratio confirmed the presence of a significant Condition × Block interaction,  $F(57,171) = 2.58$ ,  $p < .001$ ,  $\eta_p^2 = .462$ . Across all four pigeons, there was significant discrimination of the 4FD condition in comparison to chance by the third block of training (single-mean t-tests across birds;  $t(3) = 3.7$ ,  $p = .034$ ,  $d = 1.8$ ), for the 3FD condition by the fifth block ( $t(3) = 3.4$ ,  $p = 0.043$ ,  $d = 1.7$ ), and the 2FD and 1FD conditions by the sixth block ( $t(3) > 3.9$ ,  $ps < .029$ ,  $ds > 2.0$ ).

This successful acquisition of the four 1FD conditions indicates that the pigeons were capable of processing the speed, direction, color or size of the elements as the only distinguishing feature of the S- displays. Fig. 2 shows the acquisition rate for each individual pigeon with the 4FD maximally redundant condition and the four 1FD conditions (speed, direction, color, size). Multiple one-sample t-tests evaluating the last five 70-trial blocks confirmed that each pigeon significantly discriminated each featural difference from chance performance: color ( $ts(4) > 14.8$ ,  $ps < .001$ ,  $ds > 6.6$ ), size ( $ts(4) > 9.2$ ,  $ps < .001$ ,  $ds > 4.1$ ), rate ( $ts(4) > 12.3$ ,  $ps < .001$ ,  $ds > 5.5$ ), and direction ( $ts(4) > 4.8$ ,  $ps < .009$ ,  $ds > 2.1$ ). Although the pigeons could discriminate each featural difference, the rate of learning that each supported clearly differed. A repeated measures ANOVA (Feature × 70-trial Block) using discrimination ratio indicated this via a significant interaction  $F(57, 171) = 2.2$ ,  $p < .001$ ,  $\eta_p^2 = .425$  (its main effects were also significant; feature  $F(3, 9) = 8.8$ ,  $p = .005$ ,  $\eta_p^2 = .745$ ; block  $F(19, 57) = 21.8$ ,  $p < .001$ ,  $\eta_p^2 = .879$ ). Across the pigeons, learning the discriminations of element color and element speed was significantly faster than the discriminations of element size or direction of motion. The latter dimension was clearly the most difficult for the pigeons to acquire, with motion direction being the most challenging for all four birds.

### 3.2. Variation in the number of display elements

This manipulation revealed that the discrimination depends in part on the number of elements in the presentation. Fig. 3 shows the average DR for each of the five tested conditions as a function of the number of elements in the display. This function looked highly similar across the five conditions. All pigeons performed most poorly when only a single element defined the display. Importantly, however, each of the 1FD conditions could still be discriminated at above chance levels with this single moving element (one sample t-test across birds; color  $t(3) = 5.0$ ,  $p = .015$ ,  $d = 2.5$ ; size  $t(3) = 5.7$ ,  $p = .010$ ,  $d = 2.9$ ; rate  $t(3) = 5.7$ ,  $p = .011$ ,  $d = 2.8$ ; direction  $t(3) = 3.4$ ,  $p = .043$ ,  $d = 1.7$ ). The pigeons' discrimination within each dimension then improved with additional

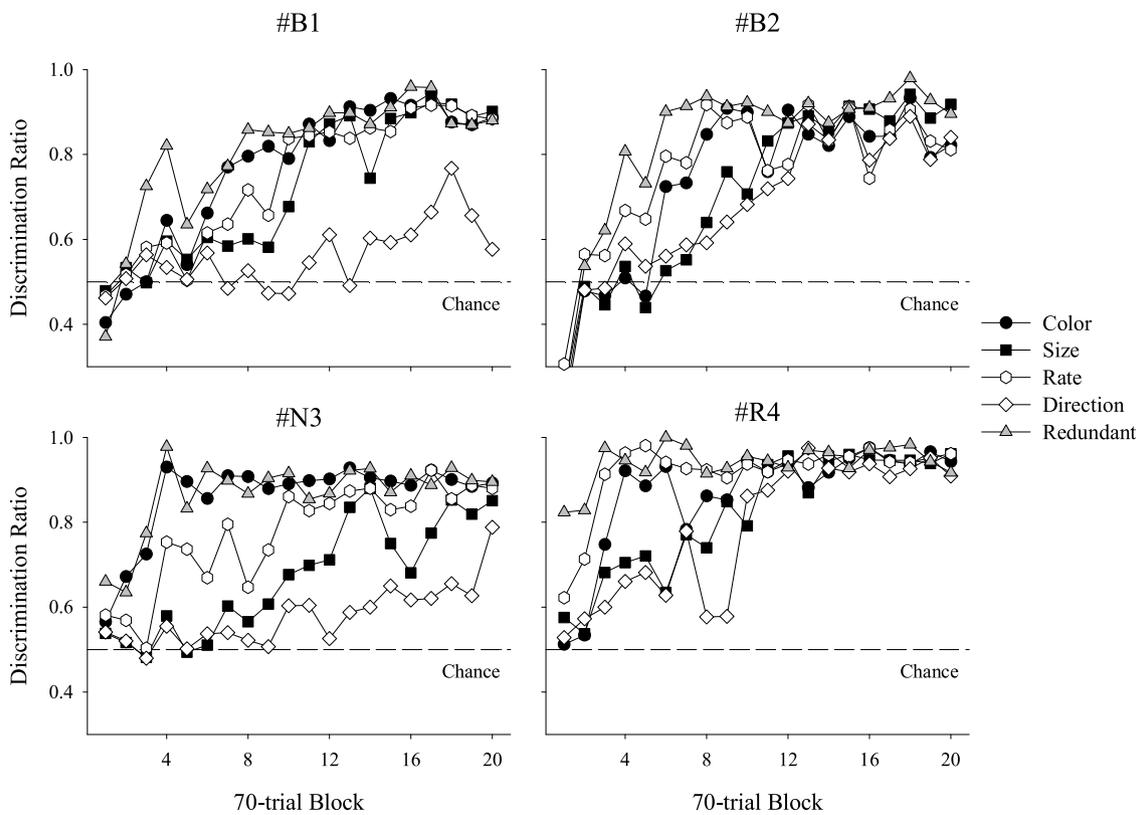


Fig. 2. Acquisition of each of the one Feature Difference (1FD) stimuli and the four Feature Difference (4FD) stimuli. Filled symbols are the static features, and open symbols are the dynamic features. Each panel depicts a separate pigeon's behavior. The dashed line denotes chance performance.

elements. This improvement continued until the display contained 8–16 elements, after which adding further elements did not seem to improve the pigeons' discrimination of the dimensional features. Overall, the 4FD redundant condition supported the best discrimination across all values, with this advantage seemingly slightly enhanced when fewer elements were present. A Condition  $\times$  Element Number  $5 \times 6$  repeated measures ANOVA confirmed a significant Condition  $\times$  Element Number interaction ( $F(20, 60) = 2.53, p = .003, \eta_p^2 = .457$ ). On the single element displays, the location on the display that the pigeons pecked was related to the position of the single element on the screen, but no relationship was observed between overall responding and peck locations.

Within this task, redundant facilitation could exert two forms of influence: better overall discriminability and better discrimination with fewer elements. Each panel of Fig. 3 also shows separate fits for each feature, using a hyperbola ( $y = a * x / [x - b + 1]$ ) defined by an asymptote ( $a$ ) and a horizontal shift ( $b$ ). For our purposes, the asymptote represents the asymptotic discrimination ratio for the stimulus set, and the horizontal shift reflects how close to the asymptote the curve starts. In this context, higher values of  $a$  indicate better overall discriminability, and higher values of  $b$ , closer to 1, indicate better discrimination with fewer elements. Though the differences are small, the redundant displays ( $a = 0.910, b = 0.847$ ) supported better overall discriminability and better discrimination with fewer elements than any single-feature display (color –  $a = 0.894, b = 0.680$ ; size –  $a = 0.902, b = 0.559$ ; rate –  $a = 0.888, b = 0.761$ ; direction –  $a = 0.846, b = 0.653$ ). This ranking was consistent for each bird individually, except for pigeon #R4. For this pigeon, overall discriminability of redundant displays was not estimated to be better than the discriminability for the 1FD displays, though the 4FD display clearly supported better discrimination than the 1FD displays with fewer elements for this bird.

Besides the overall discrimination behavior, we were also interested

in examining the temporal dynamics of how quickly stimulus control developed within a trial. Previous go/no-go investigations accomplished this by examining how quickly peck rates reduced upon S-stimulus presentation relative to S+ presentations (e.g., Qadri and Cook, 2016). We examined within-trial peck suppression for the 4FD and 1FD conditions by putting pecks into successive 250-ms bins relative to stimulus onset. To avoid ceiling effects, we only evaluated the stimulus conditions with four or fewer elements. Fig. 4 shows the results of this analysis for each individual pigeon. Negative S- condition peck rates are shown for each feature as a percentage of the positive S+ peck rate over the same time period. The first 4 s of the trial are displayed to portray the rate at which stimulus control developed. Overall, three of the four birds exhibited excellent stimulus control within 1 s after the onset of the displays. Pigeon #B1 was the slowest with clear stimulus control not developing until after 2 s of stimulus presentation.

A repeated measures ANOVA of the S- conditions peck rates (Condition  $\times$  Time as 16 250-ms bins; using peck rates for the whole trial does not change these conclusions) revealed main effects for both time ( $F(15, 45) = 57.4, p < .001, \eta_p^2 = .950$ ) and Condition ( $F(4, 12) = 8.7, p = .002, \eta_p^2 = .743$ ). There was also a significant interaction between these two factors ( $F(60, 180) = 2.1, p < .001, \eta_p^2 = .409$ ). Overall, pecking in the 4FD condition suppressed significantly more quickly than in any of the 1FD conditions. This condition reached 90% of its eventual asymptotic rate (based over the last 4 s of display time) within 1.5 s after onset of the display. Element color was next in reaching 90% of its asymptote in 1.8 s, followed by speed (2.0 s) and size (2.3 s), with direction being the slowest at 3.3 s. The redundant facilitation in 4FD trials ahead of the peck rate suppression in 1FD trials suggests the pigeons may be simultaneously attending to the multiple features within these complex displays upon their onset. Finally, we also note that the order of the features' abilities to support peck suppression within a trial corresponds with the order of features supporting discrimination acquisition, with element color and speed of motion

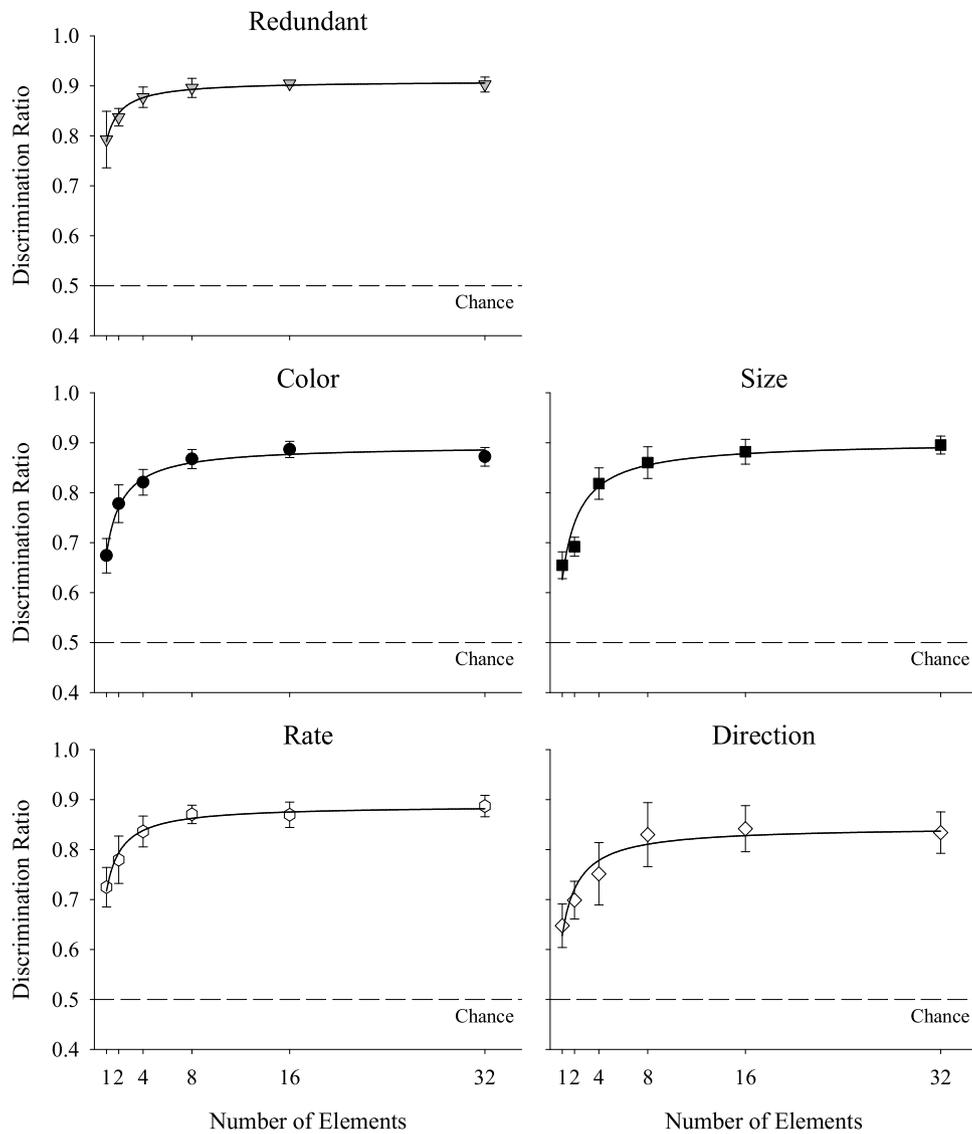


Fig. 3. Discrimination ratio with different numbers of elements in each video during Experiment 2. The solid line drawn through the point shows the best fit hyperbolic function ( $y = a * x / [x - b + 1]$ ). The dashed line represents chance performance. Error bars depict SEM.

supporting the quickest discrimination and direction of motion being the slowest.

#### 4. General discussion

These experiments examined how pigeons attend to both static and dynamic features when simultaneously demanded by a four-dimensional MNC task. Overall, the pigeons easily mastered this complex discrimination. This was true for both the dynamic and static aspects of these multifaceted displays. The pigeons learned to discriminate the features along each of the four dimensions within a mere handful of sessions. Furthermore, the values of these dimensional features were rapidly extracted from the displays, regularly exerting control over behavior within a second or so of stimulus onset. During both presentation time within a trial and during acquisition across sessions, we observed small, but consistent, redundant dimensional facilitation. This result is indicative of the concurrent processing of the four dimensions in the displays. Relatedly, increasing the number of featural differences between the S+ and S- displays always improved the discrimination. Consistently, element color and speed features supported better and faster stimulus control than did either element size or direction features. Although all four pigeons could attend to the four dimensions

when the display contained only one single moving element, adding more elements to the display generally improved their discrimination.

These observations are one of the few to indicate that pigeons can extract, process, and attend to both the dynamic and static aspects of elements within the same compound display. The vast majority of prior experiments examining the processing of multiple compounded dimensions have typically used visual dimensions involving static features (e.g., color and line orientation). The current experiments suggest within this MNC setting that motion features function similarly to static features. They support discrimination and additively contribute to such compound discriminations. Perhaps most interestingly, there was no evidence that the motion and static features competed for any limited processing capacity. During the acquisition of the task, for example, whenever control by motion features was greatest, there was no corresponding lack of control by static features. Instead, motion and static processing were largely positively correlated during acquisition for all of the birds. The absence of attentional trade-offs between dynamic or static dimensions agrees with theories of avian vision that utilize multiple independent channels for different visual features.

The pigeons were strikingly consistent in their discriminative ranking of control by the dimensional features. Among the static dimensions, control by element color was clearly superior to control by

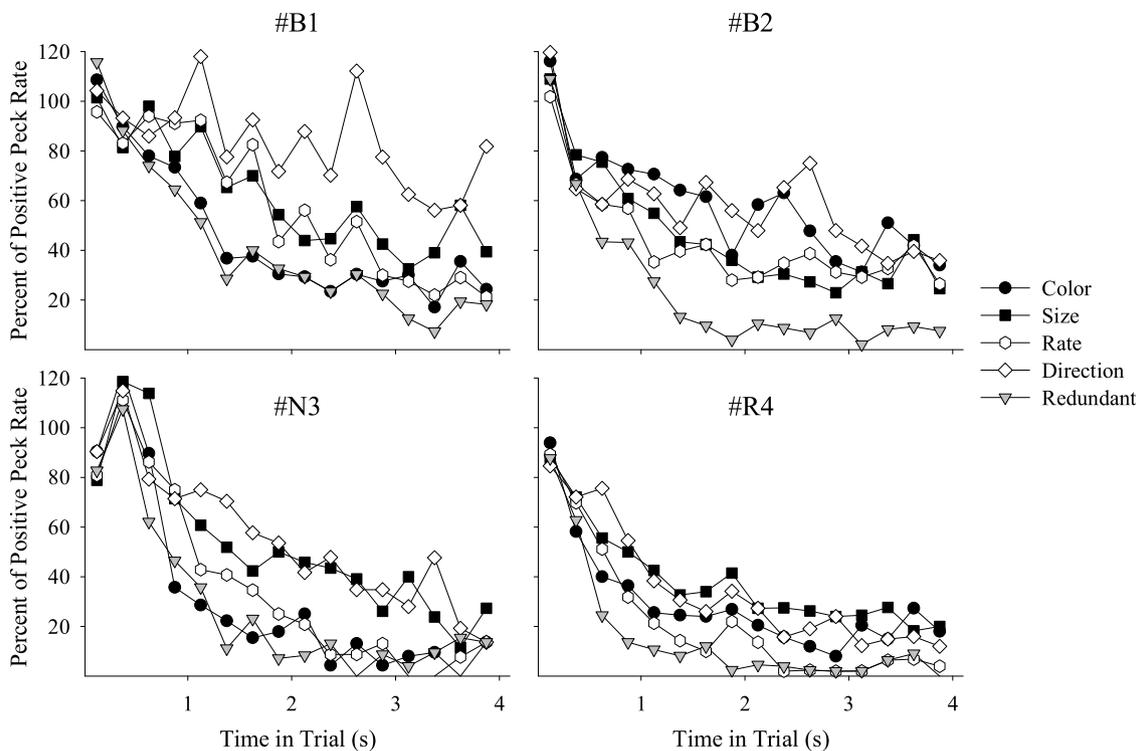


Fig. 4. Suppression of pecking with reduced information displays for the first half of the trial as grouped into 250 ms bins. Each panel depicts a separate pigeon's behavior.

element size, while for the dynamic dimensions, control by motion speed was superior to control by motion direction. Values from these superior dimensions were the most quickly detected features within a trial, and they also consistently supported the fastest rates of learning during acquisition. The dimension of motion direction unequivocally exerted the least control over the pigeons' behavior. Whether this correlation of between-session acquisition and within-trial presentation time results from a causal relationship remains an open question. Were the birds faster to attend to a particular feature most quickly across time because it was the most rapidly noticeable feature within a trial? Or, on the other hand, did the birds come to notice these features quickly within trials because they had learned about those features more quickly during acquisition, effectively accumulating more training with some features than others? Any resolution will await future research.

There is no *a priori* reason for these apparent processing differences among these four different dimensions and their values. In fact, prior to the experiment, a concern was that the speed discrimination would be too difficult, given the psychophysical evidence that pigeons have higher motion detection thresholds than might be expected from a flying bird (Lazareva and Share, 2017; Nankoo et al., 2014). Instead, this feature discrimination was easily learned and its value quickly detected. Some of the detection or processing differences are likely tied to the specific binary values we used. Perhaps different values might have resulted in an altered ranking of the dimensions (although there is no obvious way to make motion direction more discriminable). With that caveat, these results possibly suggest new insights into the relative priority of different static and dynamic features within the pigeon visual system (Frost and DiFranco, 1976; Frost and Sun, 1997; Frost et al., 1990; Wang et al., 1993). Color has always tended to be an easy and dominant feature in pigeons' visual discriminations, for example. Rate of motion may function similarly, at least in comparison to direction. As we learn more about how pigeons process motion, we may learn that the rate of object motion or speed of an actor's behavior is of particular priority relative to other types of motion features.

The pattern of these results are somewhat at odds with the results of

previous MNC experiments. Wasserman and colleagues have used the MNC design to attempt to evaluate competing attentional shifts to different static dimensions across training (e.g., Vyazovska et al., 2014). For example, their birds might start by easily discriminating one dimensional feature, such as color, while poorly discriminating a second feature like stimulus size. Later those same birds might be found, however, to be more controlled by changes in size than to changes in color. As mentioned, this type of attentional shifting was absent in the current experiments. We did not see marked competition for attentional resources across sessions. In this way, these results conform more to the results of Teng et al. (2015), who documented less attentional shifting across their dimensions when using a choice task. Procedural differences could explain why we did not find discriminative tradeoffs. Vyazovska et al. (2014) reinforced their pigeons on an FI schedule and trained to a performance criterion. Our pigeons were reinforced on a VI schedule and trained on a fixed number of sessions. Using Vyazovska et al. (2014)'s strict criterion, two of our pigeons (#B1 and #N3) would have likely gone on to additional training, in which perhaps attentional tradeoffs might have been found. Alternatively, our moving multi-element displays might not support attentional tradeoffs in the same way as the static-only compound displays in the previous MNC tasks, perhaps as a result of how static and dynamic information is processed in the avian visual system.

The current displays contained a different type of motion in comparison to other recent experiments involving the motion of singular figures or objects (Cook et al., 2011; Cook and Katz, 1999; Cook and Roberts, 2007; Qadri et al., 2014a,b; Qadri and Cook, 2016). The use of a flow field-like display fashioned from multiple moving elements could have created new emergent, larger or configural features that might be absent in figural or object motion. Such motion features created via multiple disjoint elements are most similar to the experiments by Spetch and her colleagues involving dot patterns (Bischof et al., 1999; Nankoo et al., 2012). If such configural field or flow features were present, evidence of their impact was minimal. Any such emergent features should be most present when the displays had a large number

of elements and should be removed as elements are reduced. Eliminating elements in our task did reduce performance, similar to what has been reported when testing dense and sparse static random dot patterns (Cook, 2001) and in a motion same/different discrimination (Jitsumori et al., 2013). If present, there is nothing in our data beyond this to indicate that emergent features contributed anything new to the discrimination. Instead, the additional benefit of more elements is that it seems to have simply improved the chances of discriminable information being detected by reducing the size of the area that the pigeons might have needed to scan the display (although different element counts produced no discernible differences in where pigeons pecked at the displays – one measure of pigeon visual attention).

Finally, these results contain consistent, though small, amounts of redundant facilitation effects as the pigeons processed displays with more element differences faster than the single feature condition. Just as the differences between feature dimensions were mirrored between the acquisition curves and within-trial peck rates, these redundant facilitation effects were present throughout the experiment. The boost that this effect contributes suggests an additive processing benefit for each additional feature or a benefit provided by the addition of configural properties due to their compounding. Given how fast these compounds gained control after stimulus onset, this redundant facilitation highlights pigeons' abilities to rapidly attend to multiple dimensions across the static and dynamic domains. The mechanism of this redundant facilitation also remains an open question. One possibility is that the pigeons are very rapidly shifting attention to different features, yielding the appearance of simultaneity. Another, and we think more likely, possibility is that such results, in combination with the absence of attentional competition, agree with theories of avian vision employing the notion multiple independent channels for different types of information. In this possibility, multiple available cues are processed simultaneously by mechanisms that allow the early grouping of information from different channels.

Key questions remain about how pigeons experience multidimensional dynamic displays. Increasingly, evidence suggests such displays are easily discriminated. These digitally generated, animated displays dramatically increase the kinds of items, objects, and motion that can be studied, but their complexity correspondingly offer greater challenges in understanding the mechanisms controlling responding. The avian visual system, like the human visual system, clearly processes simple static features like color, shape, and motion in distinct neural channels early in processing (Cook et al., 1996; Wang et al., 1993). This early separated processing requires a later cognitive function to combine these features into the object representations that seem to guide behavior (i.e., “binding”; Treisman, 1996). Although pigeons bind static features into unified objects in several contexts (Wasserman et al., 2006; Wright et al., 2010), understanding how this feature binding also extends to temporally dynamic features remains to be resolved in birds.

## Author note

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