Pigeons rank-order responses to temporally sequential stimuli

Neil McMillan · William A. Roberts

Abstract We explored pigeons' ability to learn a particular sequence of stimuli in which the durations of each stimulus varied among trials, where the first response at the end of the sequence was reinforced. In Experiment 1A, we found that pigeons failed to use the whole sequence of three stimuli to predict food reinforcement, and instead responded only to the third, "rewarded" stimulus. When rewarded (1–2–3) and nonrewarded (2–1–3) sequences were used in a go/no-go procedure in Experiment 1B, however, pigeons showed a tendency to rank-order responding, with higher response rates to the second than to the first stimulus, as well as lower response rates to the third stimulus on nonrewarded-sequence trials. In Experiment 2, pigeons showed rudimentary rank-ordering of five stimuli in sequence, with lower responding to the final stimulus on nonrewarded trials, even when the sequence presented differed from the rewarded sequence only in a reversal of the second and third stimuli. Pigeons were capable of using ordinal information in a temporal task, but only when that information was easily discriminable and led to explicit consequences (i.e., rewarded vs. nonrewarded sequences).

Keywords Pigeons · Timing · Ordinal · Interval · Serial learning/memory

In a typical environment over the course of a day, animals are required to produce multiple complex behaviors in response to a complicated array of spatiotemporally graded stimuli. Because animals cannot produce all behaviors at all times, and because stimuli are not available at all times, efficient performance requires organizing behavior in some manner in order to maximize reward. Although the laws of conditioning may explain responses made to single stimuli by animals in lab experiments, those explanations often do not extend to the ability to organize behaviors when more complex organizations of stimuli are encountered in a natural environment. For example, if an array of foraging patches replenish on temporally distinct schedules, how does an animal organize its foraging behavior to maximize its reward while minimizing effort and predation risk?

Sequence discrimination

Animals have previously been shown in a wide variety of tasks to be able both to discriminate and to produce sequences of stimuli in particular orders. Shimp (1976) presented pigeons with a sequence of three white Xs on left- and right-side keys in a random order. After the sequence was presented, the pigeon was presented with one of three hues on the center key to peck, and once it had done so, it was presented with that same hue on both side keys. The subjects were reinforced for pecking the side key on which one white X had been presented in the sequence, according to the positional cue provided by the hue: first in sequence for red, second for blue, and third for white. For example, the initial sequence *left–right–left* would correspond to pecking left on a red test cue, right on a blue test cue, or left on a white test cue. Although pigeons' accuracy in this task was modulated by the retention interval and the duration of the stimulus presentations, Shimp found that birds were sensitive to the ordinal position of the stimuli, which he described as remembering "the temporal structure, or organization, or pattern, of events in its recent past" (p. 55).

Another example of a procedure in which animals' ability to represent the order of events has been examined is the delayed sequence-discrimination (DSD) task. In this procedure, a number of stimuli (e.g., red and yellow) are

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presented in different sequences, each for a fixed duration, followed by a test stimulus. Pecking on the test stimulus is only reinforced after one particular sequence (e.g., red–yellow in a two-event DSD, or red–yellow–red in a three-event DSD). Pigeons showed successful discrimination by pecking more on the test stimulus after the correct sequence than after incorrect sequences on both the two-event (Weisman, Wasserman, Dodd, & Larew, 1980) and three-event (Weisman, Duder, & von Konigslow, 1985) DSD tasks.

The procedures discussed thus far were primarily concerned with whether an animal was capable of remembering a succession of events or responding correctly on a test based on working memory, trial to trial. These experiments may be compared to other procedures wherein an animal is shown an array of stimuli on one screen and required to respond to individual stimuli in the correct order on the basis of reference memory. Using a simultaneous-chaining paradigm, it has been found that pigeons, Capuchin monkeys, and Rhesus macaques can learn to respond to as many as five stimuli (colors or patterns) in a correct (reinforced) order (D'Amato & Colombo, 1988, 1989; Swartz, Chen, & Terrace, 1991; Terrace, 1986, 1987, 1991). Tests that required the ordering of nonadjacent subsets of items from a learned list suggested that monkeys, but not pigeons, formed an overall representation of the list (Terrace & McGonigle, 1994). However, recent research, using a more sensitive test controlling for contextual changes in subset testing, has revealed evidence suggesting that pigeons form an overall representation of four- and five-item lists (Scarf & Colombo, 2010). After training on four- or five-item lists, pigeons in this study were faster to learn pairs of internal stimuli that were presented in the same sequence as in list training rather than in a reversed sequence, showing that they represented the order of the internal pairs and not just the terminal items. In a second experiment, birds trained with four-item lists responded correctly to presentations of the internal pairs above chance, even on initial probe trials, so long as training on the four-item list continued on the remainder of trials.

Recently, Scarf and Colombo (2011) used a procedure similar to that previously used in monkeys (Chen, Swartz, & Terrace, 1997), in which pigeons were trained on three different four-item lists. During testing, pigeons were presented with derived lists composed of the previously trained items, with items placed either in the same ordinal positions as in training or in changed ordinal positions. Subjects performed much better on position-maintained derived lists during testing than on changed lists, including on the first session of testing. The researchers ruled out that pigeons were simply forming item–item associations,

because adjacent items were taken from different lists, and the pattern of errors made in changed lists was different from the pattern in maintained lists. These findings suggest that pigeons are capable of ordinal knowledge of lists of items, even with lists greater than three items long.

Pfuhl and Biegler (2012) studied ordinal representation in jackdaws using a hybrid paradigm of reference and working memory procedures. Subjects were trained to respond in the correct order to 14 different three-item "triplets," with each stimulus always being correct at the same position within each triplet. On working memory tests, birds viewed the triplet presented sequentially, and then were tested with four items presented simultaneously: the three stimuli presented as that trial's triplet, plus a distractor item from another list. Birds were rewarded for pecking the correct sequence at test, and the trial was terminated when a bird made any error. Birds showed many more intrusion-error responses to distractors with the same ordinal position as the correct sequence item. Over a series of experiments, the researchers found that the pattern of intrusion errors could best be explained by assuming that jackdaws had learned the ordinal positions of items. In the final experiment, jackdaws "deduced" the ordinal position of a novel item presented with two familiar items. When three novel items were presented, each belonging to different ordinal positions, the birds chose them in the correct order significantly above chance.

Ordinal timing

Although ordinal representation of stimuli presupposes attending to a temporal succession of events, it is rarely discussed in the context of timing. A number of different timing mechanisms has been described recently (Buhusi & Meck, 2005; Carr & Wilkie, 1997a), including circadian timing (24-h entrainable clock), interval timing (seconds to minutes to hours), and millisecond timing (up to 1 s). Along with these more commonly accepted phase and interval timers, Carr and Wilkie (1997a) suggested that animals possess a discrete "ordinal timing" mechanism, a timer that "counts up" from a particular position p through a series of events with n elements. By forming a representation of its position in a sequence of temporally organized events, such as in the serial pattern learning discussed previously, or following a fixed daily foraging circuit ("traplining": Gill, 1995), Carr and Wilkie (1997a) suggested that animals can then predict the next event in time. By defining *timing* as solving a particular problem in the temporal domain (i.e., predicting when an event will occur), the authors stated that this ability for maintaining ordinal information constituted a timing mechanism.

To study this hypothesis, Carr and Wilkie (1997b) tested rats on a daily time–place task. Their rats were trained to

leverpress at two different locations in an operant chamber, with one being correct during morning sessions and the other correct during afternoon sessions. During testing, select morning or afternoon sessions were omitted, and thus the next session would be out of phase. Whether the morning or afternoon session was omitted, on the next afternoon or morning session (respectively), rats chose the location correct for the morning session, and thus the rats were visiting the "first" daily location in both cases. The researchers interpreted this as evidence that rats were using an ordinal timer that was reset each day.

Recent studies have challenged the suggestion that animals use ordinal timers in daily time–place learning tasks. Pizzo and Crystal (2002) reasoned that an ordinal timer should be insensitive to the relative interval location of each item; to borrow their example, knowing who finished first, second, or third in a race does not provide information about how close their race times were. The researchers trained rats to search four food troughs across three daily sessions, either two in the morning and one in the afternoon (Group AB–C) or one in the morning and two in the afternoon (Group A–BC), with each of sessions A, B, and C being differentially rewarded across spatial locations. On probe sessions, the time of session B was shifted later in the AB–C group and earlier in the A–BC group. Rats in both groups performed at chance on these probes, suggesting they were not using an ordinal timer on this task, but were instead using interval or circadian temporal information (subsequent tests suggested that they were using both interval and circadian timing). Furthermore, Pizzo and Crystal (2004) suggested that rats in a time–place task would use a nontemporal alternation strategy (similar to Carr & Wilkie, 1997b) when nontemporal cues, such as handling before each session, are available. Crystal (2006) noted that animals can simultaneously use circadian and interval timing mechanisms for anticipating food in time–place tasks, but omitted the possibility that animals might also simultaneously process temporally ordered information (i.e., an ordinal timer).

Rationale for the present research

There are several limitations to interpreting the results of previous work in daily time–place conditioning as evidence for or against the existence of ordinal timers in animals. Firstly, Carr and Wilkie (1997b) showed that rats would visit the "first" daily location after an omission of either a morning or an afternoon testing session, while Pizzo and Crystal (2002) varied the temporal location of the "middle" foraging bout of three daily trials in testing. Pigeons (Straub & Terrace, 1981) and bees (Collett, Fry, & Wehner, 1993) have been shown to learn the order of first and last ordinal elements relatively easily, as compared to middle elements,

and if rats have a similar difficulty with learning the middle elements of temporal sequences, then this may account for the difference in the ordinal ability of rats between Carr and Wilkie (1997b) and Pizzo and Crystal (2002). These studies also varied from other work in the sequence-learning literature in a number of key ways, largely due to their presentation outside the operant chamber, including fewer training trials and less discrete ordinal stimuli. Using ordered times of day instead of discrete stimuli (such as the different colors and shapes used in operant procedures) could lead to overshadowing of order by more-salient interval cues.

Conversely, the literature focused on ordinal timing in daily time–place tasks has also highlighted questions left unanswered in typical sequencing research. Since many tasks that have shown successful sequence learning have utilized simultaneous presentation of stimuli, it is difficult to apply a timing concept to the behaviors observed in these studies. Even in research in which pigeons have been found to respond accurately to sequences of stimuli presented over time, such as in the DSD task (e.g., Weisman et al., 1985; Weisman et al., 1980), animals have usually observed the presentation of stimuli passively over a short interval and responded to a separate stimulus if the observed sequence was the "correct" (rewarded) order of stimuli. These gaps make it difficult to ascertain how animals represent stimuli in a temporal sequence. *Ordinal timing* is defined as the ability to "anticipate events that reliably occur in a certain order within a period of time" (Carr & Wilkie, 1997a), yet the studies reviewed here have provided little direct evidence that animals maintain their current position within a temporal sequence to anticipate what will happen next in sequence.

In the present experiments, we examined whether pigeons are capable of tracking the identity of a particular sequentially presented sequence of colors and responding on the basis of their temporal location within each sequence. By using an operant chamber and a procedure more typical of interval-timing studies, we determined whether pigeons were capable of rank-ordering their responses on the basis of a particular order of stimuli in time. In Experiment 1A, pigeons were presented with three-stimulus sequences that varied in length from 30 to 90 s (variable interval: VI) throughout training; on test trials, pigeons were presented with fixed-interval (FI) probes of different presentations of the same three stimuli. We expected that if pigeons track the order of stimuli presented in training, they should respond more to the final stimulus in the sequence on probe trials that are identical to the baseline, and less on probe trials whose presented sequence differs from baseline. A secondary prediction was that pigeons might respond more to the second stimulus in the sequence than to the first, but less than to the third, due to its relative proximity to reward in the sequence. In other words, pigeons were expected to

rank-order their responding on the basis of the positional identity of stimuli within the sequence presented. Experiment 1B was procedurally identical to Experiment 1A, except that a nonreinforced order was presented during training on separate trials from the previously rewarded order. We expected that presenting a "no-go" sequence during baseline would enhance discrimination of an "incorrect" order of stimulus presentations, with concomitant decreases in responding to the third stimulus when it was presented out of order. Finally, in Experiment 2, we presented pigeons with various sequences of five stimuli, with only one particular order being rewarded for the first peck after 30–90 s, to study the ordinality of pigeons' responding on a more complex sequence of stimuli.

Experiment 1A

Method

Subjects Six adult White Carneaux pigeons (*Columba livia*) were used. The pigeons had previous experience with operant procedures and were maintained at approximately 85 % of their free-feeding weight throughout the experiment, with constant access to water and health grit. They were individually housed in cages in a room kept environmentally controlled at 22 °C. Fluorescent lights were turned on at 8:00 a.m. and off at 8:00 p.m. each day. Testing was performed between 9 a.m. and 4 p.m. for 5 days each week.

Apparatus Three enclosed, sound-attenuating operant chambers measuring 31 × 35.5 cm (floor) × 35.3 cm (height) were used. The front wall of each chamber held three pecking keys, 2.5 cm in diameter and level with the pigeon's head, in a row, spaced 8 cm apart. Projectors behind each key projected filtered light, presenting different colors or patterns on the keys. Grain reinforcement was delivered by an electromechanical hopper through a 6 × 6 cm opening in the front wall located near the floor, directly below the center key. Presentation of the stimuli, reinforcement, and recording of responses were carried out by microcomputers in another room, interfaced to the operant chambers.

Procedure Each of the 40 sessions consisted of 34 baseline trials. On each trial, pigeons were presented with three different colors (red, green, and blue) presented sequentially (i.e., "1–2–3") on the center key, in the same order on each trial. Two birds saw a red–green–blue order, two saw a green–blue–red order, and two saw a blue–red–green order. Each color was presented for a 10- to 30-s VI (uniform distribution). After the

contingent interval had elapsed for the third-presented stimulus, the first peck to that stimulus ended the trial and resulted in 3 s of access to hopper grain. A 40- to 80-s darkened intertrial interval (ITI; uniform distribution) followed food access. Pecks to the center key were recorded throughout each trial in 1-s time bins.

Nonreinforced probe trials were interspersed randomly among baseline trials from Sessions 11–40. Two each of five types of probe trials were used, for a total of ten per session. All of the probe trials used FIs rather than VIs. The five probe trial types were:

1. Identical to baseline (i.e., *1–2–3 order*), with the exception that the three stimuli were presented for 20 s each;
2. First ordinal stimulus (i.e., *1-only*) presented for 60 s;
3. First and second stimuli (i.e., *1–2 order*) presented for 30 s each;
4. Third stimulus (i.e., *3-only*) presented for 60 s; and
5. Reordered stimuli (i.e., *2–1–3 order*), with stimuli presented for 20 s each. For example, a pigeon whose baseline rewarded order was "red–green–blue" would see the stimuli presented in the order "green–red–blue" on these trials.

The 1-only and 1–2 order conditions were included as controls for interval timing (i.e., the possibility that responding might increase with increasing interval durations, regardless of stimulus presentation), while the remainder of the probe trials were included to illustrate pecking to the typically rewarded third stimulus in a variety of sequences. All probe trials were followed by a 40- to 80-s darkened ITI (uniform distribution). Pecks to the center key were recorded throughout each probe trial in 1-s time bins.

Results and discussion

Probe trial data from the final ten sessions were analyzed in order to eliminate training effects. Figure 1 illustrates the data from each of the five probe-trial types from this period. In all analyses, the stimulus number (1, 2, or 3) represents the order in which the stimuli appeared on baseline trials, and not necessarily the order in which they were presented on a particular probe trial.

We analyzed average data from the last 20 s of three probe-trial types to verify that changes in responding were due to the presentation of the different stimuli, and not simply to interval timing from the beginning of the trial. A one-way repeated measures analysis of variance (ANOVA) comparing the average response rates on the three conditions (identical-to-baseline, Stimulus 1, and Stimulus 1–2) in the last 20 s of the probe trial (i.e., the last 20 s of the first stimulus on condition Stimulus 1,
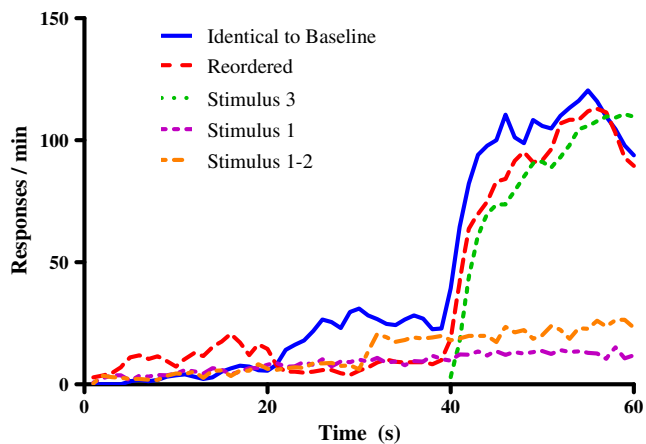
Fig. 1 Experiment 1A: Mean responses per minute across 60-s probe trials. Each stimulus was presented for 20 s, except in the Stimulus 1 and Stimulus 3 conditions (presented for 60 s) and the Stimulus 1–2 condition (each presented for 30 s)

of the second stimulus on Stimulus 1–2, and of the third stimulus on identical-to-baseline) showed a significant effect, $F(2, 10) = 34.50$, $p < .001$. A Bonferroni-corrected post-hoc test showed a significant difference between responding to the third stimulus in the last 20 s, as compared to the second stimulus [$t(5) = 9.72$, $p = .001$] and the first stimulus [$t(5) = 6.54$, $p = .004$]. We found no significant difference in responding between the first and second stimuli in the final 20 s of the trial [$t(5) = 0.74$, $p = 1.000$]. Birds pecked significantly more to the third, typically rewarded stimulus than to either of the other stimuli in the last 20 s of probe sessions, indicating that differences between probe-trial conditions could not be explained by pigeons simply increasing responding using an interval timer from the onset of the first stimulus throughout the 60-s intervals.

A 3 (stimulus: 1, 2, 3) × 2 (condition: identical to baseline, reordered) repeated measures ANOVA examining average response rates showed a nonsignificant interaction, $F(2, 10) = 3.79$, $p = .060$. The main effect of stimulus was significant, $F(2, 10) = 56.139$, $p < .001$, but the main effect of condition was not, $F(1, 10) = 3.265$, $p = .131$. A planned-comparison 2 (stimulus: 1, 2) × 2 (condition: identical to baseline, reordered) ANOVA again showed a nonsignificant interaction, $F(1, 5) = 5.704$, $p = .063$. In this comparison, neither main effect was significant, $Fs \leq 1.48$, $ps \geq .278$. Pigeons did not peck significantly less in the reordered condition than in the identical-to-baseline condition. Also, the lack of a significant main effect for stimulus when comparing just the first two stimuli suggests that pigeons did not, on average, respond differently to the first and second stimuli, regardless of the order in which they were presented.

In a one-way repeated measures ANOVA comparing average response rates to just the third stimulus, no significant difference in responding emerged on baseline, reordered, and third-stimulus-only probe trials, $F(2, 10) = 1.41$, $p = .289$. Pigeons did not appear to alter their responding to the third stimulus on the basis of which stimuli preceded it, even on trials in which the third stimulus was presented without any prior stimuli.

Experiment 1B

In Experiment 1A, pigeons did not appear to rank-order stimuli in a sequence ending in food reward, but instead their behavior appeared to be strongly controlled by the mere presence of the third stimulus. Because the third stimulus was the only one to which responding was directly rewarded, and was thus most proximal to reward, it is not surprising that pecking was largely controlled by the ultimate cue. We hypothesized that birds needed a greater basis for comparison among the stimuli in order to attend to cues preceding the highly salient third cue. In Experiment 1B, we trained the same birds from Experiment 1A on a similar procedure, with half of the baseline trials being presented identically to those in Experiment 1A. However, on the other half of the baseline trials, pigeons viewed the "reordered" trial type, with the first two stimuli being reordered in sequence and no reinforcement available for pecking the third stimulus. We reasoned that with only 50 % reward available for attending to the third stimulus alone, pigeons might attend to the order in which stimuli were presented.

Method

Subjects and apparatus The subjects that we used, and all aspects of animal husbandry and experimental apparatus, were the same as in Experiment 1A.

Procedure Each session consisted of 17 baseline *go* trials and 17 baseline *no-go* trials. Go trials were identical to the baseline trials in Experiment 1A, with each of the stimuli red, green, and blue being presented for 10–30 s, and each bird was maintained on the same order of stimuli used in Experiment 1A. On no-go trials, the order of the first two stimuli was reversed in sequence relative to the go trials (e.g., a bird whose go condition was red–green–blue would have a reordered no-go condition with the sequence green–red–blue). A 40- to 80-s darkened ITI followed food access, on go trials, or termination of the third stimulus, on no-go trials. Pecks to the center key were recorded throughout each trial in 1-s time bins.

All probe trials were identical to those used in Experiment 1A and were presented randomly among baseline trials starting from the first session; probe trials consisting of the first stimulus alone (1-only) and of the first and second stimuli in order (1–2 order) were included only to keep testing consistent with Experiment 1A, and they were not analyzed as part of the present results. The pigeons were run for 33 sessions.

Results and discussion

Only data from the final ten sessions were used, in order to eliminate training effects. Probe-trial data from this period are presented in Fig. 2. In all analyses, the stimulus number (1, 2, or 3) represents the order in which stimuli appeared on go trials, and not necessarily the order in which they were presented on a particular probe trial.

A 3 (stimulus: 1, 2, 3) × 2 (condition: go, no-go) repeated measures ANOVA examining average response rates showed a significant interaction, $F(2, 10) = 33.178$, $p < .001$. The main effect of stimulus was significant, $F(2, 10) = 18.66$, $p < .001$, and the main effect of condition was nonsignificant, $F(1, 10) = 3.28$, $p = .130$. A planned-comparison 2 (stimulus: 1, 2) × 2 (condition: go, no-go) ANOVA again showed a significant interaction, $F(1, 5) = 18.67$, $p = .008$. Neither the main effect of stimulus nor that of condition reached significance. The planned comparisons revealed a significant decrease in responding to Stimulus 2 out of sequence [$t(5) = 3.02$, $p = .029$], but no significant difference in responding to Stimulus 1, regardless of when it was located in the sequence [$t(5) = 0.62$, $p = .56$]. Pigeons appeared to rank-order stimuli, responding more to the second stimulus than to the first, especially when the second stimulus was presented second in sequence. Given the low responding to Stimulus 1, it is
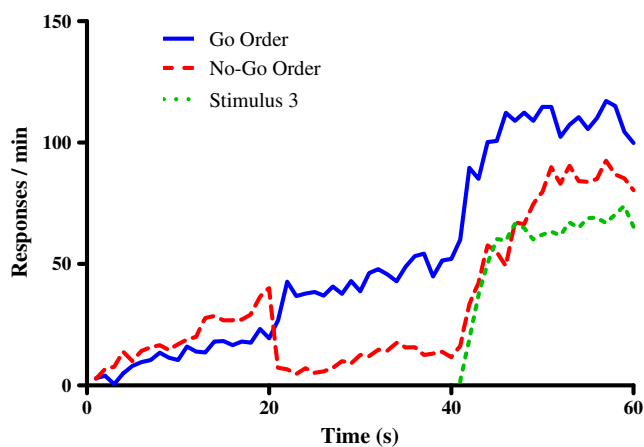

Fig. 2 Experiment 1B: Mean responses per minute across 60-s probe trials, for stimuli presented in sequences contingent with reward in the baseline (go) or not contingent with reward in the baseline (no-go). Data from the first 20 s of the 3-only probe trials are included for comparison

possible that a floor effect could account for the lack of a difference in responding.

In a one-way repeated measures ANOVA comparing the average response rates to just the third stimulus, we found a significant difference in responding among the go, no-go, and third-stimulus-only probe trials, $F(2, 10) = 10.61$, $p = .003$. Planned comparisons showed that responding to the third stimulus on the go probe was significantly different from responding to both the no-go [$t(5) = 2.98$, $p = .031$] and third-stimulus-only [$t(5) = 3.65$, $p = .015$] probes: Pigeons responded more when the third stimulus appeared in the go sequence than when it appeared out of that sequence, suggesting that pigeons were attending to the order of the first two stimuli, even though responding to them was never directly reinforced; however, it is possible that pigeons were not directly attending to the first stimulus, and only to whether the second stimulus preceded the third.

Experiment 2

Experiment 1B showed that pigeons respond less to a typically reinforced stimulus if it is presented at the end of a nonreinforced sequence. However, some results suggested that pigeons might have ignored whether the first stimulus had been presented, and instead attended only to whether the second stimulus preceded the third. Pigeons might simply have been conditioned to the second stimulus in the go condition as a higher-order reinforcer on the basis of its proximity to the third stimulus on reinforced go trials. This would explain high pecking rates to the third stimulus and lower (but still high) rates of pecking to the second stimulus. It could thus be argued that pigeons did not establish a cognitive ordinal "map" of the ranks of each of the three stimuli, but rather based their response rates to the third stimulus on their current rate of pecking when the third stimulus came on. This possibility would explain lower response rates to the third stimulus in both the 2–1–3 condition and the 3-only probe condition, in which the third stimulus appeared when the pigeon was not pecking at a high rate, as compared to the 1–2–3 probe condition, in which the pigeon was already pecking at a high rate when the third stimulus came on.

In Experiment 2, pigeons saw longer, five-stimulus sequences, with one particular sequence being reinforced and the remainder nonreinforced. All sequences started and ended with the same stimuli, because beginning and end elements have been argued to have distinct features, in addition to ordinality (Terrace, Chen, & Jaswal, 1996), but the ordinal position of the second, third, and fourth stimuli varied on nonreinforced trials. By varying the three "middle" stimuli but not the first or

last, we explored the degree to which each stimulus influenced responding on reinforced versus nonreinforced trials in which neither the last stimulus nor the stimulus immediately preceding it perfectly predicted reward. We also used geometric VI distributions for the stimulus and ITI durations, instead of the uniform distributions used in previous experiments, because geometric distributions have been suggested to eliminate subjects' ability to rely on interval timing for rewarded or nonrewarded ITIs (Fleshler & Hoffman, 1962). By using five-stimulus instead of three-stimulus sequences, we sought to examine whether pigeons could learn more about a sequence than simply the order of the last two stimuli.

Method

Subjects and apparatus Six new pigeons were used in Experiment 2, and all aspects of animal husbandry and experimental apparatus were the same as in Experiment 1.

Procedure Each of the 60 sessions consisted of 40 trials. Twenty of the trials were *go* trials, composed of yellow, red, green, blue, and white triangle (1, 2, 3, 4, and 5, respectively) stimuli presented in sequence on the center key. Each stimulus was presented for 8–22 s (geometric distribution), meaning that presentation of the entire sequence occurred with a 40- to 110-s VI. The first peck to the white triangle stimulus after the contingent interval had elapsed was reinforced with 6 s of access to hopper grain, followed by a 32- to 94-s darkened ITI (geometric distribution). To maintain high rates of responding, a limited hold was used, such that failure to obtain reinforcement before 150 s had elapsed since the beginning of the trial led directly to the ITI. Pecks on the center key were recorded throughout each session as total pecks per stimulus.

The other 20 trials on each session consisted of five trials of each of four *no-go* types. On each of these trials, yellow (1) was the first-presented stimulus, and a white triangle (5) the last-presented stimulus, as in the go condition. However, the ordinal locations of the three intervening stimuli (2, 3, 4) were varied from the go condition, with sequences of green–blue–red (3–4–2), green–red–blue (3–2–4), blue–red–green (4–2–3), and blue–green–red (4–3–2) represented. Each of the five stimuli was presented for 8–22 s (geometric distribution), as in the go condition, but after the contingent interval had elapsed for the white triangle, the stimulus turned off and led directly to the 32- to 94-s (geometric distribution) ITI. Pecks on the center key were recorded throughout each session as total pecks per stimulus, and all data were separated such that each of the stimuli on each of the four no-go trial types could be analyzed separately.

Results and discussion

Only data from the final 30 sessions were used, in order to eliminate training effects. Trial response averages for go trials and for each of the four no-go trial types, as well as an average of all four no-go trial types, are presented in Fig. 3.

A one-way ANOVA comparing average response rates to each of the five stimuli on go trials alone showed a significant difference, $F_{(4, 20)} = 18.10$, $p < .001$. This effect was characterized by a significant linear trend [$F_{(1, 5)} = 40.66$, $p = .001$] and a quadratic trend [$F_{(1, 5)} = 9.57$, $p = .027$]. This effect suggests that on average, pigeons responded more to each stimulus in order, but much more to the final stimulus, as was expected on the basis of the previous experiments presented here. Planned comparisons showed no significant differences between the response rates to Stimuli 1 and 2 or to Stimuli 2 and 3, $ts ≤ 1.24$, $ps ≥ .268$. We did find a marginally significant difference between responding to Stimulus 3 and Stimulus 4, $t_{(5)} = –2.55$, $p = .051$, and a significant difference between responding to Stimulus 4 and Stimulus 5, $t_{(5)} = –3.26$, $p = .023$.

A 3 (stimulus: 2, 3, 4) × 2 (condition: go, no-go averages) planned-comparison repeated measures ANOVA showed a marginally significant interaction, $F_{(2, 10)} = 4.07$, $p = .051$. The main effect of stimulus was significant, $F_{(2, 10)} = 6.88$, $p = .013$, but no main effect of condition emerged, $F_{(1, 10)} = 2.19$, $p = .199$.

In a one-way repeated measures ANOVA comparing the average response rates to just the fifth stimulus across each of the five trial types, we found a significant main effect in responding even after performing Greenhouse–Geisser
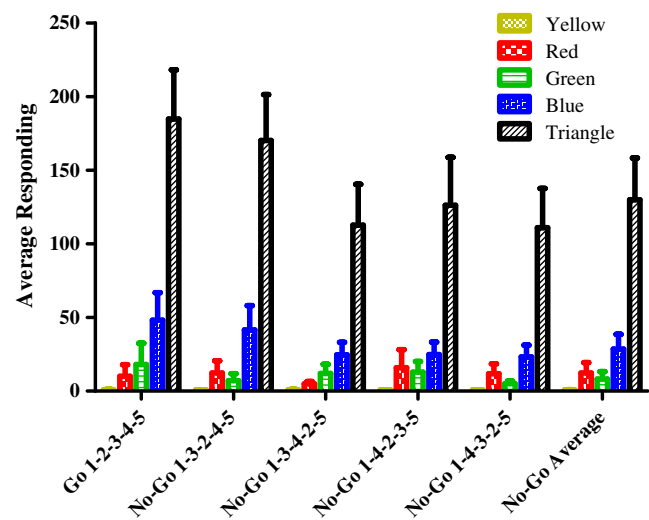

Fig. 3 Experiment 2: Mean responses to each of five colored stimuli presented in sequence in Sessions 31–60, either rewarded (go) or not rewarded (no-go). The numbers (1, 2, 3, 4, 5) are color numbers (*yellow, red, green, blue,* and *white triangle,* respectively) in the go condition

correction of the degrees of freedom, $F(1, 6) = 9.44$, $p = .021$. A simple contrast of responding to the fifth stimulus on go trials relative to the averaged responding to the fifth stimulus across all no-go trials showed a significant difference, $t(5) = 3.55$, $p = .016$. A further planned comparison between responding to the fifth stimulus on go trials and responding to the same stimulus only on 1–3–2–4–5 no-go trials (i.e., between go and no-go trials in which the fifth stimulus was immediately preceded by the fourth) also showed a significant difference, $t(5) = 5.55$, $p = .003$. Although examination of Fig. 3 suggests that responding to the fourth stimulus was very similar between the 1–2–3–4–5 and the 1–3–2–4–5 conditions (with a relatively high degree of between-subjects variability), in fact, all six pigeons showed decreased pecking to the fifth stimulus in the no-go condition, with relatively low within-subjects variability. Finally, a planned contrast showed a significant difference between responding on the fifth stimulus of the 1–3–2–4–5 condition, as compared with the average of the three other no-go trials, $t(5) = 2.80$, $p = .038$. Overall, pigeons responded more when the fifth stimulus appeared in the go sequence than when it appeared in a no-go sequence, including when it was preceded by the same stimulus as in the go condition. This result suggests that pigeons were attending to the order of the stimuli, even though stimuli other than the white triangle were never directly reinforced. Moreover, it suggests that pigeons responded to the final stimulus on the basis of more information than the mere presence of blue as the penultimate stimulus; however, pigeons still responded more to the fifth stimulus on trials with blue (as compared to other stimuli) as the penultimate stimulus.

General discussion

Birds showed behavior suggesting that they were sensitive to the temporal order of a number of stimuli, though they did so only when nonrewarded sequence alternatives were also presented on separate trials. In Experiment 1B, birds showed decreased responding to the third, often-reinforced stimulus when it was presented in a nonrewarded sequence, despite previous experience in Experiment 1A, in which they had ignored the sequence and pecked only the third stimulus. The only difference between the two procedures was the presence of baseline "no-go" sequence trials. With presentation of sequences of five stimuli in Experiment 2, pigeons pecked significantly more to the fifth stimulus when it was in the reinforced rather than in a nonreinforced sequence, even relative to a very similar arrangement of stimuli. This suggests that pigeons were not simply chaining behaviors, by responding to the fifth stimulus only when it followed the usually correct fourth, but rather were tracking

the positional identity of stimuli within the full sequence, or at least of a greater subsection of it than just the final two stimuli.

One important caveat to claiming that the present experiments showed ordinal timing is that, although our results showed significant differences in response rates between rewarded and nonrewarded sequences, the differences were not large. Birds responded at high rates to the final stimulus even at the end of nonreinforced sequences, which is likely a result of the associative strength of the final stimulus, coupled with poor inhibitory control. Also, it is true that without a nonreinforced "no-go" baseline for comparison, birds did not organize their responding sequentially. In simple terms, although birds were capable of ordinal timing in the present experiments, they did not appear to be very good at it. Finally, though birds pecked the final stimulus more on go than on no-go trials with the same penultimate stimulus (sequence 1–3–2–4–5), they also pecked the final stimulus more on those no-go trials than on other no-go trials. These results suggest that although birds have some capacity for temporally ordering their behavior on the basis of sequentially presented stimuli, the mechanism by which they accomplished this does not appear to have automatic control over behavior, as has been suggested of the internal interval timer (McMillan & Roberts, 2010; Roberts, Coughlin, & Roberts, 2000). Perhaps the mechanism underlying this temporal sequencing ability may not be "wired" specifically for ordinal timing, in the sense that we might describe interval timing as directly resulting from an automatic and obligatory endogenous timing mechanism, such as a pacemaker–accumulator or oscillator. Instead, temporally sequenced behavior may result from co-opting a number of other mechanisms available to the animal, in response to a highly complex and dynamic environment.

Ordinal timing is based on the ordinal level of measurement, in contrast to phase and interval timing, which are based on the interval and ratio levels of measurement, respectively (Carr & Wilkie, 1997a). An important feature of Stevens's (1946, 1951) levels of measurement is that ordinal information is relatively impoverished with respect to interval information, and ratio information (interval information with a true zero point) is least impoverished. Ratio information, such as that derived from timing intervals, has a large number of valid operations ($=, <, >, +, -, *, /$), while the number of valid operations for ordinal information is comparably small ($=, <, >$). For example, in Experiment 1A reported here, the wait time from the onset of the first stimulus to food reward was (on average) three times the duration (a mean of 60 s), as compared to the wait to food reward from the onset of the third stimulus (a mean of 20 s); however, it is not meaningful to measure the first stimulus as three times "earlier" or three times "worse" than the third stimulus. Ordinal information may be derived from

ratio information, however, because of the nested nature of operations: The first stimulus is earlier than the third stimulus (thus predicting increased levels of responding to later stimuli). In the present experiments, the pigeons may have been ordinally representing each stimulus in long-term memory on the basis of its average interval delay to food reward (as was shown in Olthof & Santi, 2007), and separately organizing their behavior on a current trial on the basis of how closely the present order of the stimuli matched the overall order of previously rewarded sequences (as had been shown in previous serial pattern-learning studies). By leveraging both of these two previously evidenced mechanisms, pigeons would be expected to produce roughly the results found here, with high rates of responding to temporally proximal stimuli, even on nonreinforced-sequence trials, yet lower rates than on trials in which the "correct" sequence was shown.

If what Carr and Wilkie (1997a, b) described as ordinal timing were in fact an amalgamation of several underlying processes, it would not pose a great threat to its existence as a "timing system" per se. All timing mechanisms, by definition, allow organisms to predict when an event will occur. The breadth of this problem-based definition allows it to encompass multiple processes, so long as it still allows the organism to accomplish a temporally based task. It makes sense that ordinal timing might be a high-level cognitive representation relying on multiple low-level processes, if only because it is required to track a theoretically infinite number of stimuli over a large continuum of time scales.

The concept of ordinal timing presents an interesting contrast with traditional models of timing, such as those described by Buhusi and Meck (2005). Ordinal timing does not map on to any one time scale, as in the case of circadian, interval, and millisecond timers. Instead, an ordinal timer might approximate time on any number of scales by cognitively organizing the stimuli and/or behaviors within that scale. It is already well known that many species array their foraging behaviors into particular, ordered patterns throughout each 24-h cycle, such as in the traplining of bees (Janzen, 1970) and birds (Gill, 1995). Ordinally organized behavior has also been used as an explanation for interval timing; for example, the behavioral theory of timing (Killeen & Fetterman, 1988) suggests that a pacemaker initiated at the beginning of an FI advances an animal through successive adjunctive behavioral states and that the behavioral state present at the moment of reinforcement will be conditioned so as to elicit responding. Finally, though it would be difficult for organisms to track sequences of stimuli in the under-a-second range typical of millisecond timing, many complex behaviors are the result of temporally organized behavior on the millisecond scale. In humans, playing a guitar or piano requires not only coordinating one's fingers from one note or chord to the next, but also smoothly transitioning between a number of notes (sometimes very rapidly) within the constraints of an oscillating time scale (rhythm). Where millisecond, interval, and circadian timers are low-level processes that automatically entrain oscillators based on relatively nonoverlapping time scales (Buhusi & Meck, 2005), an ordinal timer might be called upon to organize behavior on the basis of representations from any of (or across) the three scales. It may be that temporally sequenced behaviors result from an integration of information from more conventional cognitive systems of categorization and timing mechanisms.

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