Trade-offs in stimulus control in a temporal discrimination task

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A B S T R A C T

To study how multiple stimuli may control discriminative behavior, we exposed fifteen pigeons to a symbolic matching-to-sample task with three samples that differed only in duration (2, 6, and 18s) and two keylight colors as comparisons. The pigeons learned to choose one comparison after the shortest sample, and the other comparison after the intermediate and longest samples. A 30-s intertrial interval (ITI), illuminated with the houselight, separated the trials. Previous data has suggested that, in this arrangement, both sample keylight and the ITI houselight influence choice. To assess this joint stimulus control, we introduced two tests. In the no-sample test, the keylight was not illuminated and the comparisons followed the ITI immediately; in the dark-ITI test, the houselight was not illuminated. Results confirmed that both stimuli influenced choice, with an apparent trade-off between them: The more a pigeon relied on one stimulus, the less it seemed to rely on the other. We discuss potential models of joint stimulus in temporal discrimination tasks.

1. Introduction

To adapt to complex and dynamic environments, an animal must attend to cues that signal relevant events (e.g., Kamin, 1968; Leith & Maki, 1975; Mackintosh, 1965; Sutherland & Mackintosh, 1971; Wagner et al., 1968). When two or more cues signal the event, that is, when they are redundant, the animal may attend to one of them at the expense of the others (e.g., overshadowing; Mazur, 2016; Pavlov, 1927; Spetch, 1995), or it may attend to multiple cues and use them flexibly according to the environmental demands. To illustrate, Roberts and Mitchell (1994) taught pigeons to discriminate between sequences of two or eight light flashes. Each flash was presented at the rate of one per second, so that the 2-flash sequences lasted 2s, and the 8-flash sequences lasted 8s. Stimulus number correlated perfectly with stimulus duration, and for that reason the discrimination could have been learned by attending to only one of the two cues. Tests in which one of the cues remained fixed while the other varied (i.e., a 4-s sequence comprising from 2 to 8 flashes, or a 4-flash sequence lasting from 2 to 8s) revealed that the pigeons based their choices on both time and number. Similar results were found when number and duration of tones (Meck & Church, 1983) or location and duration (Cheng, Spetch, & Miceli, 1996) were confounded. Two durations may also share stimulus control: For instance, when a 30-s stimulus ended with food and, during its last 10s, another stimulus was also present, McMillan and Roberts (2010) found control by both stimuli when each was presented separately.

Joint stimulus control may involve an attentional trade-off such that the more one cue is attended to, the less other cues are attended to, in a sort of conservation of attending principle (*inverse hypothesis*, Thomas, 1970; see also Broadbent, 1957). Thus, Kirkpatrick-Steger and Wasserman (1996) combined two stimuli, a cube and another shape (wedge, cylinder, handle, or cone), placed

in one of four locations (left, right, above, below), to yield 16 images, but only one, the S+ , was reinforced when pecked at. Pigeons discriminated the S+ by attending to both shape and location and showed a negative correlation in the degree of stimulus control exerted by each feature. The stronger the influence of shape, the weaker the influence of location, and conversely, the weaker the influence of shape, the stronger the influence of location. A similar procedure, but employing stimuli differing along more dimensions (size, shape, orientation and brightness), also found evidence of trade-offs between stimulus dimensions (Gottselig et al., 2001; Vyazovska et al., 2014; see also, e.g., Blough, 1969; Miles & Jenkins, 1973; Yokoyama et al., 2006). Frequency of reinforcement has also been found to affect the relative degree of stimulus control (Davison, 2018; Davison & Elliffe, 2010; Gomes-Ng et al., 2019; 2020; Shahan & Podlesnik, 2006; 2007).

Pinto and Machado (2015; 2017) found joint stimulus control in a symbolic matching-to-sample task with three samples (a white hue on the center key lasting 2, 6, or 18s) and two comparisons (one side key illuminated with a red hue and the other with a green hue). One comparison was correct following the 2-s sample, while the other comparison was correct following both the 6- and 18-s samples). This task was originally designed to study learning flexibility, given that the asymmetric mapping of 3 samples to 2 comparisons allowed different learning strategies (e.g., creating one response rule per sample vs. creating a specific rule for 2-s samples and a general rule for the other samples; see also Clement & Zentall, 2000; Singer et al., 2006). During the 30-s inter-trial interval (ITI), a houselight illuminated the experimental chamber. Given that the end of the ITI, signaled by the offset of the houselight, coincided with the beginning of a new trial (signaled by the onset of the center keylight, the sample), both events, the houselight offset and the keylight onset, were equally-valid cues to learn the task. That is, "short" and "long" trials could be discriminated either by attending to the houselight or the sample keylight. Even though the sample was arguably the most likely candidate to exert control over responding (it was the stimulus event closest to choice), our results suggested that the houselight and the sample keylight influenced choice; the pigeons attended to both stimuli. The long duration and salience of the ITI houselight may have competed with sample recency such that both controlled choice.

Despite its original goal of studying coding flexibility, this many-to-one matching task proved useful to study joint stimulus control. Reasoning that, when a stimulus is attended to, its removal (or variation) leads to changes in behavior (Reynolds, 1961), Pinto et al. (2017) trained pigeons with the task and then ran two tests, each removing one of the focal stimuli. In dark-ITI tests, the houselight was not illuminated during the ITI, but the sample stimulus occurred normally. In no-sample tests, the houselight was illuminated normally during the ITI, but no sample followed it; instead, the comparisons occurred immediately after the ITI. Each test assessed how much each stimulus influenced responding. Moreover, by comparing the two test results the authors estimated the relative degree of each stimulus influence. The results confirmed the pigeons' reliance on both stimuli, with a trade-off between them.

However, the two tests could have confounded stimulus control with reinforcement effects: Whereas the no-sample tests were conducted in extinction – in the absence of the sample, no choice was correct and hence reinforced –, the dark-ITI tests were reinforced whenever the choices accorded with the sample. The difference in the reinforcement contingencies during the tests could have confounded the stimulus control acquired during the original training. Hence, in the present study we reproduced the experiment but ran both tests with non-differential reinforcement. Equal conditions during testing should afford more valid measures of stimulus control.

Additionally, as an animal is exposed to a task, its reliance on different cues may change. To prevent such changes from contaminating the measures of stimulus control, Pinto et al. (2017) included both no-sample and dark-ITI tests in each daily session. But each session was divided in blocks, and each block included only one test. Therefore, the two tests were still separated in time. In the present study, the two types of test trials were randomly interspersed throughout the whole session. Given that our goal was to clarify the nature of stimulus control established in this task, we kept all other procedural details unchanged during training (such as the duration of the ITI, or the samples and comparisons used). Although the asymmetric mapping may be unnecessary to the establishment of joint stimulus control, given our goal of clarifying the nature of control established in the task and compare results across studies, we maintained the many-to-one matching arrangement.

Finally, informed by our previous results, we also propose two models of joint stimulus control, an attentional model that conceives of the animal as using probabilistically one or the other cue to guide its choices, and a stimulus-competition model that shares some features with the Rescorla and Wagner (1972) model. We contrast the models with the test trial results, and discuss their strengths and limitations. The exploration of the theoretical space may help us identify the strengths and limitations of each model and thereby improve our understanding of joint stimulus control.

2. Method

2.1. Subjects

Fifteen pigeons (*Columba livia*) were maintained at approximately 85 % of their free-feeding body weight. They were housed in individual home cages, where water and grit were freely available. The pigeon room was under a 13-h:11-h light/dark cycle (with lights on at 08:00) and temperature between 20 and 22 °C. The experiment was conducted once a day, at approximately the same time for each pigeon, 6 days a week. Seven pigeons were experimentally naïve, and the eight remaining pigeons all had experience with symbolic matching-to-sample tasks.

2.2. Apparatus

Three similar LVE (Lehigh Valley Electronics) operant chambers, measuring 34 cm (height) × 35 cm (length) × 31 cm (width), were

used. On the response panel, three circular response keys, 2.5-cm in diameter and 9 cm apart, center-to-center, were horizontally arranged. The bottom of each key was 22.5 cm above the wire mesh floor. Each key was equipped with a 12-stimulus IEE (Industrial Electronics Engineers) projector. Each stimulus in the projector was illuminated through a 28-V, 0.1-A lamp. In the present study, the side keys presented only red or green hues, and the center key presented only a white hue. Food (mixed grain) was accessible through a 6-cm wide × 5-cm high opening, centered horizontally on the response panel, 8.5 cm above the floor. When the LVE hopper was activated, a 28-V, 0.04-A lamp illuminated its opening. On the wall opposite the response panel, 30 cm above the floor, a 28-V, 0.1-A houselight provided general illumination. The operant chamber was equipped with an exhaust fan that circulated air through the chamber and also helped to mask outside noises. Personal computers running the ABET II software (Lafayette Instrument Company) controlled the experimental events and recorded the data.

2.3. Procedure

2.3.1. Training I

The pigeons learned a symbolic matching-to-sample task. After a 30-s inter-trial interval (ITI) during which only the houselight was on, the houselight was turned off and the center key was illuminated with a white hue for 2s, 6s or 18s (sample stimulus). When the sample duration elapsed, the white center key was turned off and the two side keys were illuminated, one with a red hue and the other with a green hue (comparisons). One comparison was correct following the 2-s sample and the other comparison was correct following both 6-s and 18-s samples. The correct comparison following each sample was counterbalanced across animals. After a single peck to either comparison, both comparison keylights were turned off. If the correct comparison was chosen, reinforcement was delivered and then the ITI followed; if the incorrect comparison was chosen, no reinforcement was delivered, and the ITI started immediately. A correction procedure was in effect: following an incorrect choice, the trial was repeated; after three consecutive incorrect choices, only the correct comparison was presented. The birds began each session at approximately 85 % of their free-feeding weight. To minimize feeding outside the experimental session, reinforcement duration was adjusted individually from 2s to 4s (average = 2.8s).

Each session comprised 64 trials (excluding correction trials), and trial presentation was divided into two 32-trial blocks (refer to Table 1 for a summary of the session structure). Each block contained 16 2-s sample trials, 8 6-s sample trials, and 8 18-s sample trials, presented in random order. After all trials in the first block were presented, the second block ensued. The trial proportions ensured that each comparison was correct the same number of times in each session. The left-right location of the comparisons varied pseudo-randomly across trials with the constraint that each comparison was presented the same number of times on each side key. Training I lasted a minimum of 15 and a maximum of 20 sessions, and within that range it ended when the pigeon met a criterion of at least 80 % correct responses to each sample (excluding correction trials) for three consecutive sessions.

2.3.2. Training II

This phase was similar to Training I, but the overall probability of reinforcement decreased to adapt the pigeons to the upcoming tests in which not all trials would end with reinforcement. When the correct comparison was chosen, reinforcement was delivered on a maximum of 75 % of the trials. The trials baited for reinforcement (24 of the 32 2-s sample trials, 12 of the 16 6-s sample trials, and 12 of the 16 18-s sample trials) were selected randomly before the beginning of each session. On baited trials reinforcement was delivered when the correct choice was made, on non-baited trials reinforcement was never delivered. During Training II, there was no correction procedure. Reinforcement durations were readjusted and varied across birds from 2s to 4s (average = 3.1s). The phase lasted 10 sessions.

2.3.3. Testing

In each session, there were three types of trials: regular training trials, no-sample test trials, and no-houselight (or dark-ITI) test trials. The regular training trials were the same as in Training I (reinforcement always followed a correct choice). On no-sample trials, the center key was not illuminated and the comparisons were presented immediately after the ITI. A dark-ITI trial was the same as a regular training trial except that the houselight was not turned on during the ITI that preceded the trial.

Each session comprised 64 trials (rightmost column of Table 1). Of these, 40 were regular training trials – 20 2-s sample trials, 10 6-s sample trials, and 10 18-s sample trials. The remaining 24 trials were test trials, 8 no-sample trials and 16 dark-ITI trials. Of the 8 no-

Table 1
Number of trials in Training I, Training II and Test sessions.

Trial type		Training I	Training II	Test
Training trials	2s	32 (32)	32 (24)	20 (20)
	6s	16 (16)	16 (12)	10 (10)
	18s	16 (16)	16 (12)	10 (10)
No sample		0	0	8 (4)
Dark ITI	2s	0	0	8 (4)
	6s	0	0	4 (2)
	18s	0	0	4 (2)
Total		64 (64)	64 (48)	64 (52)

Note. Baited trials are presented in parentheses. On baited training trials, reinforcement was delivered only following a correct choice. On baited test trials, reinforcement was always delivered.

sample trials, 4 randomly chosen were reinforced regardless of the pigeon's choice; the other 4 were not reinforced. Of the 16 dark-ITI trials, 8 were 2-s sample trials, 4 were 6-s sample trials, and 4 were 18-s sample trials. For each sample duration, half of the trials, randomly chosen, ended in reinforcement regardless of the pigeon's choice; the other half were not reinforced. Overall, then, a pigeon could be rewarded on at most 81.25 % of the trials. Test sessions were not divided in blocks and all trials occurred in random order. Reinforcement durations varied from 2s to 4s (average = 3.1s) across birds. Testing lasted 10 sessions.

2.4. Data analysis

Statistical tests were conducted using IBM SPSS Statistics for Windows (Version 28) with Type-1 error rate set at 0.05. We analyzed the proportion of "short" choices, on both types of test trials, on tests with the houselight but no-sample, and on tests with no houselight but with a sample. To determine whether the pigeons were indifferent between the comparisons when no sample was presented, we constructed 95 % Confidence Intervals and checked whether they included 0.5. To determine whether choices on no-sample trials were a function of the last-seen sample, and whether choice varied with lit versus unlit ITI trials, we used two-tailed, paired-samples t-test, and computed effect sizes (and the correspondent 95 % confidence intervals) with Cohen's d_z (the standardized mean difference; see, e. g., Cohen, 1988, p. 48; Lakens, 2013). To compare performance on both types of test trials, we used Pearson's correlation.

3. Results

3.1. Training

The pigeons took an average of 17.9 sessions (range: 15–20) to complete Training I. During the last three sessions of this phase, matching accuracy averaged 90 % on 2-s trials (range: 76–97 %), 87 % on 6-s trials (range: 69–98 %), and 95 % on 18-s trials (range: 83–100 %). Performance improved slightly during Training II: By the last three sessions of this phase, matching accuracy averaged 94 % on 2-s trials (range: 85–100 %), 95 % on 6-s trials (range: 88–100 %), and 98 % on 18-s trials (range: 90–100 %).

3.2. Test

During the ten sessions of testing, matching performance on the regular training trials remained accurate: Proportion correct averaged 92 % on 2-s trials (range: 82–99 %), 89 % on 6-s trials (range: 73–99 %), and 96 % on 18-s trials (range: 90–100 %).

On no-sample test trials, there was an overall preference for the comparison associated with the short sample: On average, the "short" comparison was chosen 61.6 % of the trials (range: 21.3–88.8 %). This preference was significantly different from 50 %, 95 % Confidence Interval (CI) = [58.8–64.3 %]. At the individual level, out of the 15 birds, eight chose "short" significantly above chance, and two showed the opposite preference, choosing "long" significantly above chance. The remaining five pigeons did not differ significantly from chance.

Choice on no-sample trials did not appear to be determined by the sample last seen on a previous trial: when the last-presented sample was 2-s long, the pigeons chose "short" on 60.2 % of the no-sample test trials, and when it was 6- or 18-s long, they chose "short" on 63.5 % of the trials, a difference not statistically significant, $t(14) = 1.30$, $p = .214$, $d_z = 0.34$, 95 % CI [− 0.19, 0.85].

On the dark-ITI test trials, performance varied with sample duration – see Fig. 1. Whereas accuracy remained high following 6-s samples (89 % vs 90 %) and 18-s samples (96 % vs 97 %), it decreased markedly following 2-s samples (92 % vs 43 %). Paired-samples t-tests confirmed that the decrease in accuracy for 2-s samples was statistically significant, $t(14) = 8.91$, $p < .001$, $d_z = 2.30$, 95 % CI [1.31, 3.27], and that performance was not significantly different between training and dark-ITI trials for 6-s samples, $t(14) = -0.30$, $p = .772$, $d_z = 0.08$, 95 % CI [− 0.58, 0.43], and 18-s samples, $t(14) = -1.22$, $p = .241$, $d_z = 0.32$, 95 % CI [− 0.83, 0.21].

Fig. 2 combines two metrics, one from each test, which will allow us to estimate the relative influences of houselight and keylight
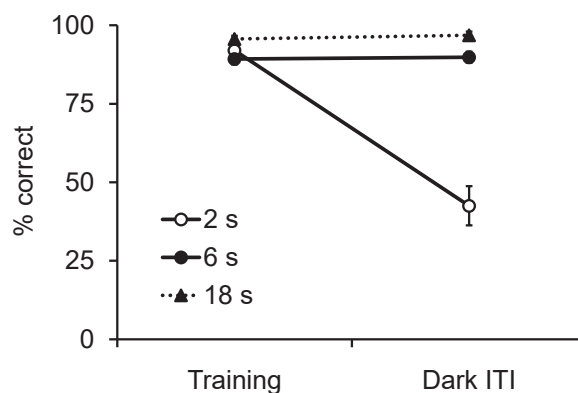

Fig. 1. Mean (with SEM) percent correct following each sample duration during testing, in training trials (left side) and in dark-ITI test trials (right side).

on choice: the proportion of "short" choices on no-sample trials (X axis) and the proportion of correct choices of the "short" comparison following a dark ITI (Y axis). The data seem to form two separate clusters, one with 9 (filled) and the other with 6 (empty) data points. We refer to them as Group 1 and Group 2, respectively. Group 2 has lower average values in both metrics, but both reveal a linear trend (Pearson correlation coefficients were statistically significant, Group 1: $r(7) = -.85$, $p = .004$, Group 2: $r(4) = -.97$, $p = .001$). The clustering in two groups was not a function of experimental history: Group 1 contained 4 naïve (and 5 experienced) pigeons, and Group 2 contained 3 naïve (and 3 experienced) pigeons.

4. Discussion

To explore how two stimuli may jointly control responding on a discrimination task, we trained pigeons in a symbolic matching-to-sample task that seemingly induces joint stimulus control (see Pinto et al., 2017; Pinto & Machado, 2015; 2017). The two stimuli of interest were the houselight that illuminated the inter-trial interval (ITI) and the keylight that signaled the samples. We assessed their control over choice with two tests, each consisting in the removal of one of the stimuli: a dark-ITI (with no houselight during the ITI) and a no-sample test (with no sample keylight following the ITI).

Regarding the no-sample test, there was moderate group preference for the "short" comparison (61.6%), a result consistent with previous studies, not only in the direction but also in the degree of the preference: P("short") on no-sample tests has been found to fall somewhere within the 60–80 % range (Church, 1980; Pinto et al., 2017; Pinto & Machado, 2015; 2017; Pinto & Sousa, 2021; Spetch & Wilkie, 1983). The results on the dark-ITI test trials depended on the samples: Whereas choice accuracy following the 6-s and 18-s samples remained high, the accuracy following the 2-s samples decreased markedly (Fig. 1).

Changing trial conditions, such as turning off the ITI houselight, could lead to a general decrease in accuracy (generalization decrement). However, given that only 2-s samples were affected by this manipulation, the results do not seem to be due to an overall generalization decrement. Alternatively, we could consider that the pigeons attended solely to the sample stimulus, and that the change in ITI illumination affected the samples differently. Although the "start" time marker for all samples is contiguous with the houselight offset, the "stop" time marker for longer samples is further away from the houselight offset than the "stop" time marker for the short sample. If we assume that, the closer the sample events are to the houselight offset, the greater the disruption caused by changes in the ITI, accuracy following short samples should be more impacted than following longer samples. Although matching accuracy following 2-s samples did show the greatest decrease, 6-s samples should show an intermediate degree of disruption – not as pronounced as in 2-s samples, but greater disruption than the 18-s samples – which was not the case.

Another possibility is that the pigeons could have been timing the interval since the last houselight presentation (which had happened at least one trial ago), leading to the estimation of long intervals (the ITI duration would be added to the sample duration) and thus to a strong preference for the "long" comparison. In other words, matching accuracy following 2-s samples would be expected to be very low (close to 0 %). That was not the case, so this possibility also does not seem to account for the results of the dark-ITI test.

The finding that removing the ITI illumination affected 2-s sample matching accuracy is consistent with the ITI houselight exerting some stimulus control. One aspect to consider is that ITI houselight and sample keylight may differ in how they control choice. Whereas the sample stimulus is present during the trial and until the moment of choice, the houselight is absent from the period that immediately precedes choice. So, on the one hand, we expect temporal control by the keylight because not only the reinforcement
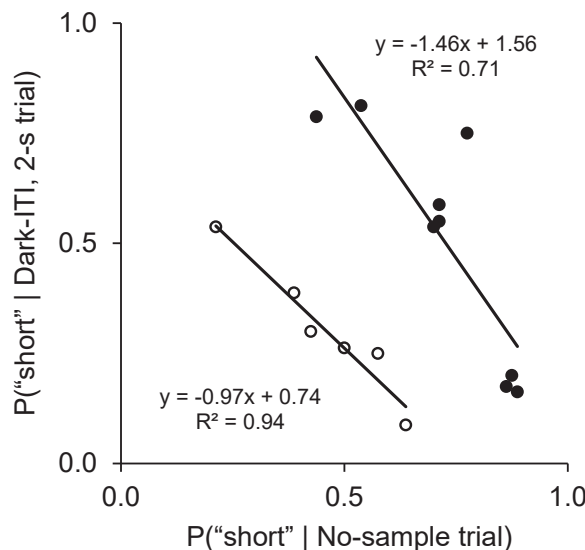

Fig. 2. Proportion of choices to the "short" comparison in no-sample test trials (X axis) plotted against proportion of correct responses following 2-s samples in dark-ITI test trials (Y axis). Each data point refers to the performance of one pigeon. Filled (Group 1) and empty (Group 2) data points identify the two clusters of data. Regression lines are presented for each cluster.

contingencies depend on its duration, but also because the keylight onset and offset are the stimulus events closest to the comparisons. On the other hand, the memory trace of the houselight at the moment of choice may also become differentially associated with the two comparisons. If the trace is significantly stronger after 2s than 6 or 18s, the trace will become associated mainly with the 'short' comparison, and a weaker trace or the absence of the trace will become associated mainly with the 'long' comparison. In other words, the pigeons would not base their choices on the estimation of the interval since houselight offset, but on the strength of the memory trace for the houselight relative to a threshold – it could be seen as akin to a presence-versus-absence discrimination (see also temporal vs. situational control, Staddon, 1972).

If this trace hypothesis is correct, then during training the pigeons will learn to select the "short" key when under the control of the houselight, and the "long" key when not. This would lead, on the dark-ITI test, to a decrease in accuracy only for 2-s samples (the houselight would not be exerting control) and, on the no-sample test, to a preference for the "short" comparison (the houselight would be exerting strong control). We found both results. However, these tendencies were not as strong as expected if only control by the houselight determined choices, which suggests that both ITI houselight and sample keylight controlled responding. Next, we explore two models of how this joint stimulus control may take place.

Model I. Similar to other selective-attention models (e.g., Lovejoy, 1968; Mackintosh, 1965; Sutherland & Mackintosh, 1971; Trabasso & Bower, 1968; Zeaman & House, 1963), the first model assumes there is a competition between the ITI houselight and sample keylight, and that on a given trial the pigeon relies on only one of the two. Specifically, consider a pigeon that on each trial attends to the houselight (HL) with probability p, and to the sample keylight (KL) with probability 1-p. These two possibilities combine with the two test types to yield the four cases displayed in Table 2.

On a <u>no-sample trial</u>, if the pigeon attends to the houselight, given that it was presented immediately before choice, its memory trace will be at its strongest level, and therefore the "short" comparison should be chosen frequently. Hence, P("short") = $\alpha_{HL} \approx 1$. On the other hand, if the pigeon attends to the sample keylight then, given its absence, it should choose the two comparisons randomly: P("short") = $\beta_{KL} \approx .5$. Alternatively, if the pigeon remembers the last sample presented one or more trials before, choice also would be close to indifference because the proportion of times each sample preceded no-sample trials was approximately equal. Therefore, the probability of choosing the "short" comparison on a no-sample trial (Table 2, average of the left cells) is given by

$$P(\text{"short" | No-sample trial}) = p\cdot\alpha_{HL} + (1-p)\beta_{KL} = (\alpha_{HL} - \beta_{KL})p + \beta_{KL} \tag{1}$$

Given that $\alpha_{HL} > \beta_{KL}$, the percentage of choices of the "short" comparison on a no-sample trial correlates positively with the influence of the houselight, p.

On a <u>dark-ITI trial</u>, choice on 2-s sample trials should depend on the stimulus attended to: If the pigeon attends to the houselight, it should prefer the "long" comparison because the last time the houselight was present occurred one or more trials before and therefore its memory trace will be weak: P("short") = $\beta_{HL} \approx 0$. However, if the pigeon attends to the sample then, given that the sample is presented as on a regular training trial, its performance should not be disrupted and the bird will choose the "short" comparison with the same probability as on a training trial, α_{KL} (in the present experiment, that probability averaged .92). Thus, the probability of choosing the "short" comparison on a 2-s sample trial preceded by a dark-ITI (Table 2, average of right cells) is given by

$$P(\text{"short" | Dark-ITI, 2-s trial}) = p\cdot\beta_{HL} + (1-p)\alpha_{KL} = (\alpha_{KL} - \beta_{HL})(1-p) + \beta_{HL} \tag{2}$$

Given that $\alpha_{KL} > \beta_{HL}$, the percentage of correct choices following 2-s samples on a dark-ITI trial correlates positively with the influence of the sample, 1-p.

Solving Eqs. 1 and 2 for p and combining them – with X = P("short" | No-sample trial), and Y = P("short" | Dark-ITI, 2-s trial) – yields

$$Y = \frac{\beta_{HL} - \alpha_{KL}}{\alpha_{HL} - \beta_{KL}}X + \frac{\alpha_{HL} \quad \alpha_{KL} - \beta_{HL} \quad \beta_{KL}}{\alpha_{HL} - \beta_{KL}} \tag{3}$$

That is, the probability of choosing the "short" comparison correctly given a dark-ITI trial – a measure of sample influence – is a linear function of the probability of choosing the "short" comparison given a no-sample trial, – a measure of houselight influence. Because $\alpha_{KL} > \beta_{HL}$ and $\alpha_{HL} > \beta_{KL}$, the slope will be negative, which expresses the tradeoff in stimulus control between houselight and keylight.

Table 3 shows the estimated parameters when Eq. 3 is adjusted to the two trendlines in Fig. 2. The parameters of the fitted function for Group 1 are close to the predicted values (from Table 2), but that is not the case for Group 2. Alternatively, the model adjustment can be assessed via its predictions of baseline performance: On a regular training trial, when the houselight and the sample keylight are

Table 2
Probability of choosing the "short" comparison according to stimulus controlling responding and test type.

Control by	Test	
	No sample	Dark ITI, 2-s sample
ITI Houselight (p)	P("short") = $\alpha_{HL} \approx 1$	P("short") = $\beta_{HL} \approx 0$
Sample keylight (1-p)	P("short") = $\beta_{KL} \approx .5$	P("short") = $\alpha_{KL} \approx .92$

Note. p is the probability of attending to the houselight. α refers to the cases where the to-be-attended stimulus is presented and β to the cases where it is not.

both presented, proportion of correct choices following a 2-s sample is given by $p.\alpha_{HL} + (1–\alpha p)\alpha_{KL}$, a value always between α_{HL} and α_{KL}. Therefore, the predicted value is always between .91 and 1.00 for Group 1, a range consistent with the .93 observed value, and between .75 and .77 for Group 2, a range considerably lower than the .90 observed value.

For Group 2, test performance underestimates baseline performance, possibly because for this subset of pigeons testing disrupted the discrimination severely, making comparisons between phases more difficult. Nonetheless, even under this potential generalization decrement, the animals still behaved in a manner consistent with a trade-off between the two cues.

Earlier, we considered the possibility that the animals could have learned the task by attending only to the sample, with the decrease in accuracy following 2-s samples on the dark-ITI test stemming from generalization decrement. Given that performance on that test ranged considerably (.09 –.81), the result could mean that the pigeons were differentially resistant to generalization decrement effects. Greater resistance would lead, on dark ITI tests, to higher matching accuracy following 2-s samples, and on no-sample tests, to a preference for the "short" option (a 0-s sample is closer to the short than to the long samples). Conversely, a pigeon more vulnerable to generalization decrement would show indifference in both tests, and thus a steeper decline in accuracy following 2-s samples on dark-ITI tests, and a lower proportion of "short" choices on no-sample tests. In other words, the two metrics contrasted in Fig. 2 would show a positive correlation. Given that the opposite pattern was found, it seems unlikely that the birds learned the task by attending only to the sample.

Model II. The second model is also a stimulus-competition model, but it stresses less fluctuations of attending across trials and more the differential associations of the stimuli with the comparisons. It assumes that the houselight (HL) and the keylight (KL) become associated with the comparisons during training: A strong houselight trace and a relatively weak keylight trace would be associated with the "short" comparison, whereas a weak (or absent) houselight trace and a stronger keylight trace would be associated with the "long" comparison.

If we call the associative strength between the houselight trace and the "short" comparison S_{HL}, the associative strength between a 2-s keylight trace and the "short" comparison S_{KL}, and the combined associative strength of all stimulus traces with the "long" comparison L, and assume that probability of choosing "short" equals the ratio of associative strengths, then P("short") during the regular 2-s training trials is given by

$$P(\text{"short"} \mid \text{HL} + \text{KL}) = \frac{S_{HL} + S_{KL}}{S_{HL} + S_{KL} + L} = \frac{S_{HL}/L + S_{KL}/L}{S_{HL}/L + S_{KL}/L + 1} = \frac{R_{HL} + R_{KL}}{R_{HL} + R_{KL} + 1} \tag{4}$$

The prediction depends only on two ratios, $R_{HL} = \frac{S_{HL}}{L}$ and $R_{KL} = \frac{S_{KL}}{L}$, which can be estimated from the no-sample and dark-ITI tests, respectively. The probability of choosing the "short" comparison on no-sample trials (that is, when only the houselight is presented) equals

$$P(\text{"short"} \mid \text{HL}) = \frac{S_{HL}}{S_{HL} + L} = \frac{R_{HL}}{R_{HL} + 1} \tag{5}$$

And the probability of choosing the "short" comparison on a 2-s sample trial preceded by a dark-ITI (that is, when only the keylight is presented) equals

$$P(\text{"short"} \mid \text{KL}) = \frac{S_{KL}}{S_{KL} + L} = \frac{R_{KL}}{R_{KL} + 1} \tag{6}$$

The estimated values of R_{HL} and R_{KL} allow us to compare the relative influences of the houselight and the keylight stimuli.

Fig. 3 shows, on the left panel, how well the ratios estimated from test trials predict baseline performance. The data from Group 1 fall close to the equality line, but the data from Group 2 show significant discrepancies, with the model predicting worse accuracy than observed, nearing chance levels. Other ratio values could reduce the discrepancy but only at the expense of worsening the fit between the model and the two types of test trials. The right panel of Fig. 3 plots one ratio against the other. The separation between the two groups of pigeons reappears, and each group still reveals a trade-off between houselight and keylight (the higher one ratio, the lower the other), a tradeoff reasonably well described by power functions.

In conclusion, with its procedural improvements, the present study confirmed that pigeons solve this many-to-one temporal discrimination task by attending to two cues, the ITI houselight and sample keylight, with an apparent tradeoff between them. As such, this task can be a valuable tool to study joint stimulus control. However, it is not clear yet which of the task features are necessary for joint stimulus control to emerge (e.g., the asymmetric sample-comparison mapping, the number of samples and their durations, or the relative salience of the stimuli). Therefore, further inquiries into these variables may reveal boundary conditions for different learning strategies.

Table 3
Predicted and observed parameters of the attentional model.

Parameter	Prediction	Observed	
		Group 1	Group 2
α_{HL}	≈ 1	1	.77
α_{KL}	$\approx .92$	.91	.75
β_{HL}	≈ 0	.1	0
β_{KL}	$\approx .5$	.45	0
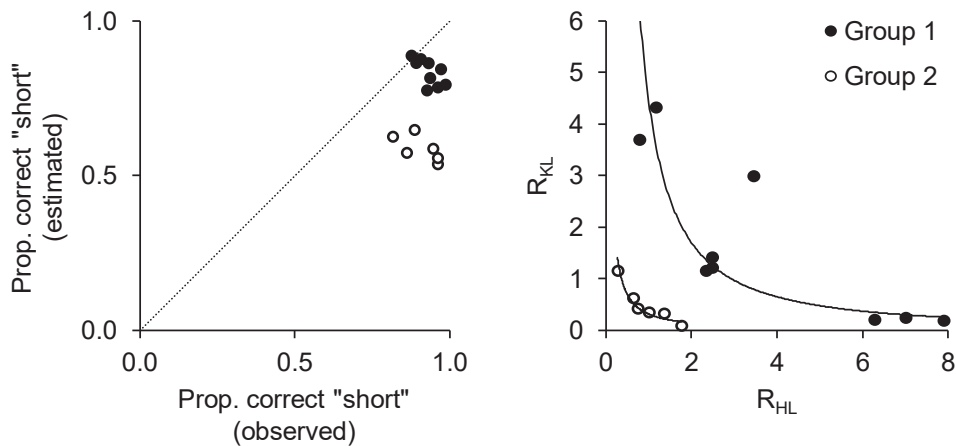
Fig. 3. Left: Proportion of correct choices following short samples plotted against estimations of the stimulus-competition model. Right: The two ratios of the stimulus-competition model, R_{HL} and R_{KL}, plotted against each other. Filled (Group 1) and empty (Group 2) data points identify the two clusters of data.

We also advanced two models of how a tradeoff in stimulus control could take place, both assuming stimulus-competition but one more attentional and the other more associative (for similar approaches in the domain of timing see, e.g., McMillan et al., 2017; Santos et al., 2021). Performance on test trials fell into two groups, and while both models accounted well for Group 1, they were less successful for Group 2. Although the pigeons clustered in two groups, both were consistent with a tradeoff between houselight and keylight. This finding stresses how identifying the stimuli attended to does not tell us the whole story; in particular it does not tell us what is being learned. Therefore, it is important to identify not only which stimuli an animal may use to learn a task, but how the stimuli are used. The models presented here, though unable to explain the full set of results, may provide a framework to assess shared reliance on multiple cues, as well as clarify the empirical challenges ahead.

Compliance with ethical standards

The research was carried out in agreement with the European (Directive 2010/63/EU) and Portuguese law (Ordinance 1005/92 of October 23), being approved by the Directorate-General for Food and Veterinary, the Portuguese national authority for animal health (Authorization #024946).

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CRediT authorship contribution statement

Carlos Pinto: Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization. **Armando Machado**: Conceptualization, Methodology, Formal analysis, Writing - Review & Editing, Visualization.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest.

Data availability

The datasets generated and analysed inthe study are available in the DataRepositoriUM repository, https://doi.org/10.34622/datarepositorium/F9SWHO.

Trade-offs in stimulus control in a temporal discrimination task (Original data) (University of Minho Data Repository (datarepositoriUM))

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