

Joint stimulus control in a temporal discrimination task

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Abstract The ability to identify stimuli that signal important events is fundamental for an organism to adapt to its environment. In the present paper, we investigated how more than one stimulus could be used jointly to learn a temporal discrimination task. Ten pigeons were exposed to a symbolic matching-to-sample procedure with three durations as samples (2, 6, and 18 s of keylight) and two colors as comparisons (red and green hues). A 30-s intertrial interval (ITI), illuminated with a houselight, separated the trials. Both the houselight and the sample keylight could control responding, so two tests were run to assess how these stimuli influenced choice. In the no-sample test, the keylight was not presented; in the dark-ITI test, the houselight was not illuminated. Results suggest that both houselight and keylight controlled choice, and with the exception of one animal, the more a pigeon relied on one of these stimuli, the less it appeared to rely on the other.

Keywords Stimulus control · Discrimination learning · Attentional trade-off · Timing · Many-to-one matching · Key peck · Pigeons

Introduction

Not all stimuli are equally important for understanding how an animal adapts to its environment. Stimuli that correlate with important events (e.g., food, predators, or partners) tend to be attended. Moreover, not all features that define

a stimulus (e.g., size, color, or shape of a visual stimulus; loudness, frequency, or location of an acoustic stimulus; nature and intensity of a smell) may be equally informative in a given situation. Naturally, then, many animals can learn to respond selectively to the critical stimulus features in their surroundings (e.g., Miles and Jenkins 1973; Sutherland and Mackintosh 1971; Wagner et al. 1968).

Researchers have studied attention to stimuli in a variety of ways. In one of them, they have used stimuli with multiple elements, compound stimuli, and attempted to identify the stimulus features an animal attends to. In a classic study, Reynolds (1961) trained two pigeons with a compound stimulus, a key displaying a white triangle on a red background, and then tested them with the elements of the compound separated. He found that whereas one pigeon pecked mostly to the red hue, another pecked mostly to the triangle. The two birds seemed to have attended to different elements of the compound (cf. Wilkie and Masson 1976). Other studies have used compounds with elements from the same modality (e.g., visual stimuli: Leith and Maki 1975; Maki and Leith 1973) or from different modalities (e.g., visual + auditory stimuli: Blough 1969; Kraemer and Roberts 1985; spatial + visual stimuli: Kraemer et al. 1987).

When a task has two redundant cues such that relying on only one of them is sufficient for correct performance, animals may nevertheless attend to both. Roberts and Mitchell (1994) trained pigeons to discriminate between two flashes of light (lasting, in total, 2 s) and eight flashes of light (lasting, in total, 8 s). The pigeons could have learned to respond based on the number of flashes (2 vs. 8) or the cumulative duration of the stimuli (2 vs. 8 s). Subsequently, the authors ran two types of test trials, one in which the number of flashes remained constant at four flashes while cumulative duration varied from 2 to 8 s, and another in which cumulative duration remained constant at 4 s while the number

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of flashes varied between 2 and 8. Results showed that the pigeons attended to both number and duration (see also Meck and Church 1983).

In another study (Cheng et al. 1996), pigeons saw a white rectangle moving horizontally and at constant speed in a touch-sensitive screen. The first peck on the rectangle after 10 s had elapsed granted access to food. Because the rectangle moved at constant speed, its location also signaled reinforcement. Therefore, the pigeons could have learned either to wait 10 s before pecking, or to peck when the rectangle reached a specific screen location. On test trials, the authors varied the speed of the rectangle and found that both time and location influenced responding; the two dimensions shared stimulus control (see also Sutton and Roberts 1998). There is also evidence showing that animals are able to simultaneously time more than one interval, each signaled by a distinctive stimulus (e.g., Kirkpatrick and Church 2000; Leak and Gibbon 1995; Meck and Church 1984; Vieira de Castro and Machado 2010).

Even when tasks are not designed to study joint stimulus control, they may provide redundant sources of information. In interval timing tasks, for example, more than one event may mark the same to-be-timed interval. For instance, we (Pinto and Machado 2015, 2017) trained pigeons in a symbolic matching-to-sample task in which a center key was illuminated with a white hue for 2, 6, or 18 s (sample), and then a choice was given between a green and a red side key (comparisons). The red key was correct if the light was on for 2 s, and the green key was correct if the light was on for 6 or 18 s. During the 30-s intertrial interval (ITI), a houselight illuminated the whole box.

Although we designed the task assuming that the pigeons would learn to time the duration of the sample stimulus, marked by the center white keylight onset, the houselight offset also was a valid time marker. This was because the end of the ITI (signaled by the offset of the houselight) and the start of the sample (signaled by the onset of the white keylight) occurred simultaneously, so the pigeons could have learned the task by either using either the houselight offset or sample onset to initiate timing. For a graphical representation of a typical training trial from the present study (also Pinto and Machado 2015, 2017), refer to the top panel of Fig. 1. A series of test trials with retention intervals, with and without the sample, and with dark ITIs suggested that the pigeons attended to both the white keylight and the houselight. Evidence for joint control in temporal conditional discrimination tasks is particularly important because researchers often assume that their subjects are timing *only* the sample stimulus. If other stimuli control performance in these and similar tasks, it is important to identify them and to understand how two or more sources of stimulus control relate to one another. Without this knowledge, our ability to predict and understand behavior will remain limited.

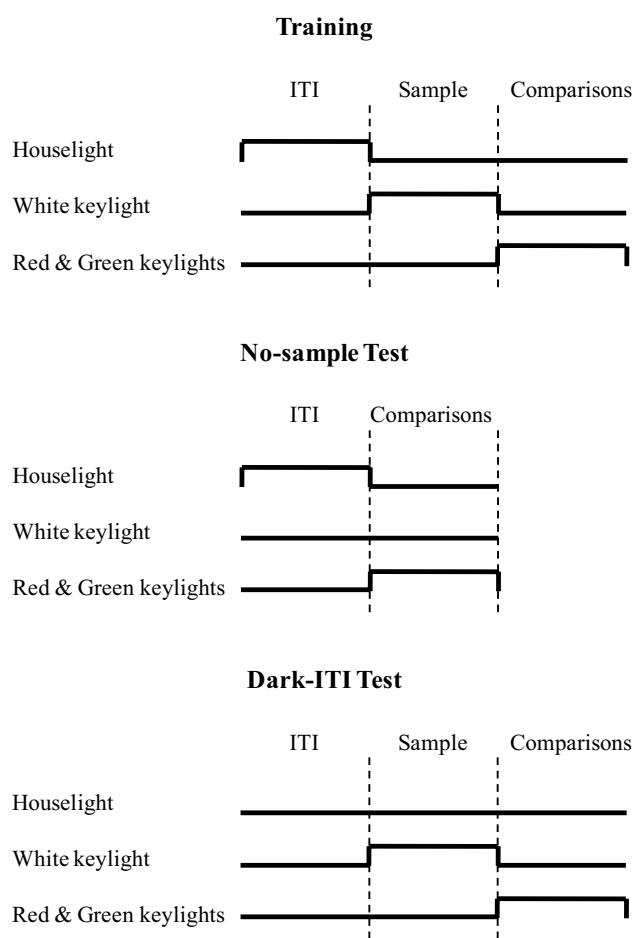


Fig. 1 Schematic of the stimuli presented during a trial in training (top panel), no-sample test (middle panel) and dark-ITI test (bottom panel). Each line is raised whenever its corresponding stimulus was turned on

In the present experiment, we examined the nature of joint stimulus control using a three-sample, two-comparison task. As mentioned before, Pinto and Machado (2015, 2017) found that in this task both sample and houselight controlled responding. Hence, in the present study, we used the same task to examine how the two sources of stimulus control combined. More specifically, we evaluated the possibility that both stimuli affected responding in a competitive way: The more an animal relies on one stimulus, the less it relies on the other (e.g., Blough 1969; Chase and Heine-mann 1972; Kirkpatrick-Steger and Wasserman 1996; Miles and Jenkins 1973; Vyazovska et al. 2014; see also Thomas 1970).

To evaluate the influence of the sample keylight and the houselight, we ran two types of tests after the pigeons had learned the task. On each test, one of the stimuli was removed, while the other remained. On the no-sample test, the choice keys were illuminated immediately after the houselight offset (Fig. 1, middle panel). Depending on the

stimulus-controlling choice, the pigeons could respond in one of two ways. When the houselight controls responding, the pigeons should prefer the comparison associated with the shortest sample (the “short” comparison), because of stimulus generalization—the interval between houselight offset and comparisons onset (0 s) is closest to the short duration (2 s). On the other hand, when it is the sample keylight controlling responding, random choice should be expected, because without the sample there would be no time marker to trigger the timing process. Alternatively, if the pigeon remembered the last sample presented (one or more trials ago), since the proportion of times each comparison was correct was equated, on-average responding would also approach indifference. Table 1 summarizes the predictions (left column). Assuming joint control by sample and houselight, a preference for the “short” comparison would be predicted. The extent of this preference would depend on relative reliance on each stimulus, falling somewhere between .5 (an animal responding exclusively based on the sample) and 1 (an animal responding exclusively based on the houselight). This prediction is consistent with previous studies that found a reliable preference for the “short” comparison in no-sample tests (e.g., Church 1980; Spetch and Wilkie 1983).

On the dark-ITI test, the houselight was never turned on, so the ITI that preceded the trial was spent in darkness (Fig. 1, bottom panel). Once again, the predicted results depend on the stimulus-controlling choice on each trial. When the pigeons base their choices on the estimation of the interval since houselight offset, given that the last time the houselight was presented and turned off was one or more trials ago, the pigeons should prefer the “long” comparison, which means errors following the 2-s but not the 6- or 18-s samples. When the sample controls choice, because the sample is unchanged on dark-ITI tests, performance should remain similar to the training trials (or at least the three samples should not be affected differentially). Table 1 summarizes the predictions (right column).

In preceding experiments (Pinto and Machado 2015, 2017), the no-sample and dark-ITI test trials were combined with retention intervals, a feature that rendered the analysis more challenging. Additionally, the two tests were run in separate phases, so that the pigeons’ intervening experiences may have changed their reliance on the two cues. By removing the

retention intervals and running both types of test trials in each test session, we expected to assess more clearly the effect of each stimulus on choice.

Method

Subjects

Ten pigeons (*Columba livia*) were maintained at approximately 80% of their free-feeding body weight. The animals were kept in individual home cages, where water and grit were freely available. The pigeon room was maintained in a 13:11-h light/dark cycle, with lights on at 08:00, and its temperature was maintained between 20 and 22 °C. The experiment was conducted once a day, at approximately the same time for each pigeon, 7 days a week. Three of the pigeons had previous experience with temporal discriminations (P876, PG18, PG35) and symbolic matching-to-sample tasks; the remaining seven pigeons had no experience with symbolic matching-to-sample tasks: five had experience with an auto-shaping procedure (P022, P234, P301, PG24, PG29) and two were experimentally naïve (P858, P958).

Apparatus

Four identical LVE operant chambers, measuring 34 × 35 × 31 cm (h × l × w), were used. On the response panel, three circular response keys, 2.5 cm in diameter, and 9 cm apart, center to center, were arranged horizontally. 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) in-line projector. The food hopper 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 hopper was raised, a 28-V, .04-A light illuminated its opening. On the wall opposite the response panel, 30 cm above the floor, a 28-V, .1-A houselight provided general illumination. The operant chamber was enclosed in an outer box equipped with an exhaust fan that circulated air through the chamber and masked outside noises.

In this experiment, red or green hues were presented on the side keys, and a white hue was presented on the center key. Personal computers running the ABET II software (Lafayette Instrument Company) controlled the experimental events and recorded the data.

Procedure

Training

The pigeons learned a symbolic matching-to-sample task. A session started with a 30-s ITI during which the houselight

Table 1 Predicted preferences in no-sample and dark-ITI tests, as a function of stimulus controlling responding

Control by	Test	
	No sample	Dark ITI
Houselight offset	“Short” key	“Long” key
Sample onset	Indifference	Baseline performance

was turned on. Afterward, the houselight was turned off, and the center key was turned on with a white hue for 2, 6, or 18 s (sample). At the end of the sample, the center keylight was turned off and the two side keys were illuminated, one with a red and the other with a green hue (comparisons). One comparison was correct following the 2-s sample, and the other comparison was correct following the 6- and 18-s samples. The correct comparison for each sample was counterbalanced across pigeons. After a peck to either comparison, the two comparison keylights were turned off. If the response was correct, reinforcement was delivered and then the ITI started; if the response was incorrect, the ITI started immediately. A correction procedure was in effect: following an incorrect response, the trial was repeated; after three consecutive incorrect responses, only the correct comparison was presented.

The birds began each session at approximately 80% of their free-feeding weight. To minimize feeding outside the experimental session, reinforcement duration was adjusted individually and varied from 1.5 to 6 s across animals.

Each session comprised 64 trials (excluding correction trials), 32 2-s sample trials, 16 6-s sample trials, and 16 18-s sample trials. These values meant that each comparison was the correct choice the same number of times in each session. Across trials, the location of the comparisons varied randomly with the constraint that each comparison was presented the same number of times on each side key. Training lasted a minimum of 15 sessions, and it continued until the pigeon met a criterion of at least 80% correct responses to each sample in a session (excluding correction trials), for five consecutive sessions, or until a maximum of 30 sessions was completed.

Testing

Each session included three types of trials: regular training trials, no-sample test trials, and dark-ITI test trials. The training trials remained exactly as during the Training phase. On the no-sample trials, the center key was not illuminated and the comparisons immediately followed the ITI (i.e., at houselight offset). On the dark-ITI trials, all procedural details remained as on the training trials except that the houselight was not turned on during the ITI.

The three types of trials were arranged in blocks. A training block included 16 training trials (8×2 , 4×6 , 4×18 s). A no-sample block included 8 no-sample trials randomly interspersed among 8 training trials (4×2 , 2×6 , 2×18 s), for a total of 16 trials. No reinforcers were delivered on no-sample trials. Lastly, a dark-ITI block included 16 training trials (8×2 , 4×6 , 4×18 s) in which the ITI preceding the sample was spent in darkness. On dark-ITI trials, correct responses were reinforced.

Every test session comprised four 16-trial blocks, for a total of 64 trials. The first and third blocks were always training blocks; the second and fourth blocks were either no-sample and dark-ITI blocks, respectively, or dark-ITI and no-sample blocks, respectively. The order of the no-sample and dark-ITI blocks alternated across days. On the first day, their order was counterbalanced across pigeons with half experiencing one order, and the other half the other order. Testing lasted 10 sessions.

Results

Training

The birds completed the training phase in 26 sessions on the average (range 15–30). Although six birds did not meet the criterion of 80% correct responses to each sample for five consecutive days, they clearly learned the discrimination, for percent correct following each sample on the last five sessions averaged 78% or above. Overall, during the last five sessions of training, matching accuracy averaged 90% (range 84–97%) on 2-s trials, 85% (range 78–93%) on 6-s trials, and 95% (range 93–100%) on 18-s trials.

Testing

During the test phase, performance on training trials remained similar to the training phase: matching accuracy over the 10 test sessions averaged 94% (range 88–98%), following 2-s samples, 85% (range 73–97%), following 6-s samples and 97% (range 91–99%), following 18-s samples. There were no significant differences between the training and testing phases for 2-s trials, $F(1,9) = 3.77$, $P = .084$, $\eta_G^2 = .17$, 6-s trials, $F(1,9) = .01$, $P = .928$, $\eta_G^2 < .001$, or 18-s trials, $F(1,9) = 1.49$, $P = .253$, $\eta_G^2 = .04$. We conclude that testing did not disrupt baseline performance.

On no-sample test trials, nine pigeons preferred the “short” comparison (average 73%; range 45–93%). A t test confirmed that this preference differed significantly from 50%, $t(9) = 4.56$, $P = .001$, Cohen’s $d_z = 1.44$, 95% CI for d [.52, 2.33] (d_z , standardized mean difference effect size, see, e.g., Cohen 1988, p. 48; Lakens 2013). Performance on no-sample trials was also significantly different from performance on 2-s sample trials, $t(9) = 3.77$, $P = .004$, Cohen’s $d_z = 1.19$, 95% CI [.35, 2.00].

Figure 2 shows the results from training trials and dark-ITI trials. Removing the houselight illumination during the ITI reduced accuracy only following the 2-s samples. This visual impression was confirmed by statistical analyses: A paired-sample t test revealed that when the ITI was darkened correct choices following the 2-s samples decreased significantly ($t(9) = 5.19$, $P = .001$, $d_z = 1.64$, 95% CI [.65, 2.59]),

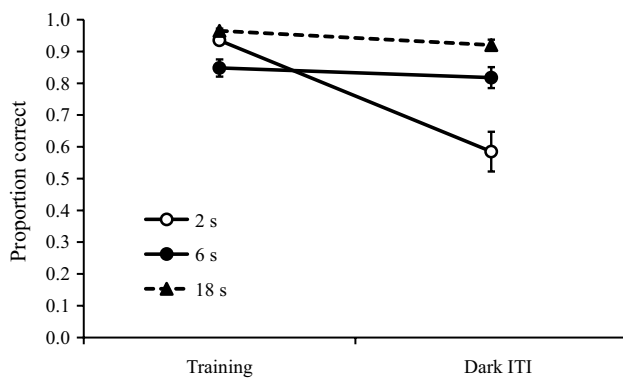


Fig. 2 Mean (with SEM) proportion correct to each sample duration during testing, in training trials (left side) and in dark-ITI test trials (right side)

but for the other samples, the changes were not significant (6-s samples, $t(9) = 1.70$, $P = .124$, $d_z = .54$, 95% CI $[-.14, 1.19]$; 18-s samples, $t(9) = 2.00$, $P = .077$, $d_z = .63$, 95% CI $[-.07, 1.30]$).

The two types of test differed in their reinforcement contingencies: No-sample trials were never reinforced, whereas correct responses on dark-ITI trials were. It is possible that extinction in one case and reinforcement (if correct) in another would induce changes during testing. To assess them, we compared performance in the first and the last five sessions of testing with a t test for related samples. The results for the dark-ITI trials revealed a significant increase in overall correct responses, $t(9) = 3.01$, $P = .015$, Cohen's $d_z = .95$, 95% CI $[.18, 1.69]$. Performance was most affected following 2-s samples, so learning could be most impactful on these trials. Therefore, we ran the same analysis for 2-s trials separately and found similar results: There was a significant increase in correct responses, $t(9) = 6.87$, $P < .001$, Cohen's $d_z = 2.17$, 95% CI $[.99, 3.32]$. The results for the no-sample trials revealed no difference between the first and the last sessions, $t(9) = 1.55$, $P = .155$, Cohen's $d_z = .49$, 95% CI $[-.18, 1.14]$.

Discussion

Pigeons were trained in a symbolic matching-to-sample task with the objective of analyzing the nature of stimulus control exerted by sample and houselight, namely to assess whether there was a trade-off in the combination of the two stimuli. To that end, two tests were run, each consisting in the removal of one of the stimuli under scrutiny: no-sample and dark-ITI tests. Starting with the no-sample test, there was a preference for the “short” key, a result that replicates our previous findings (Pinto and Machado 2015, 2017) and suggests that the houselight exerted control over responding

(cf. Table 1). However, if the pigeons' responses were based exclusively on the houselight, an even stronger preference for the “short” comparison would be expected. The range of results suggests that the sample stimulus also controlled choice. Thus, the no-sample test indicates that the pigeons seemed to be making use of both sample and houselight to learn the task. On the dark-ITI test, the percentage of “long” responses increased when the ITI was not illuminated, a result also consistent with control by the houselight (cf. Table 1).

If both the houselight and the center keylight (sample) controlled choice, then we may ask about the nature of their joint control. In what follows, we make three assumptions, the first two in line with classic selective-attention models (Lovejoy 1968; Mackintosh 1965; Sutherland and Mackintosh 1971; Zeaman and House 1963): (a) The two stimuli compete in the sense that the more a pigeon relies on one, the less it relies on the other; (b) on a given trial, the pigeon relies on only one of the two stimuli; and (c) to estimate the relative effect of each stimulus, we also assume that on *no-sample trials* the percentage of choices of the “short” key correlates positively with the influence of the houselight, whereas on *dark-ITI trials* the percentage of correct responses following 2-s samples (that is, choices of the “short” key) correlates positively with the influence of the sample keylight (see Table 1). This last assumption means that across pigeons, the higher the relative influence of the houselight, the higher the preference for the “short” key on no-sample trials, and, conversely, the higher the relative influence of the sample, the higher the percentage of correct responses following 2-s samples on dark-ITI trials.

These assumptions imply that the probability of choosing the “short” comparison given a no-sample trial, $P(\text{“short”} | \text{no-sample trial})$ —a measure of houselight influence—and the probability of choosing the “short” comparison correctly given a Dark-ITI trial, $P(\text{“short”} | \text{Dark-ITI, 2-s trial})$ —a measure of sample influence—should be negatively correlated, reflecting the trade-off between the two sources of stimulus control.

Figure 3 shows the individual results on the two tests. As predicted, there was a negative correlation between performance on the two trial types (with one exception, signaled with an unfilled circle, discussed below): A Pearson's correlation of $-.64$ was significant ($P = .03$). A one-sided permutation test confirmed this result, i.e., of 10,000 random permutations, only 3% yielded a negative correlation more extreme than the observed value.

Pigeon PG29 was the exception. It showed high values on both axes, a result inconsistent with the assumed competition or trade-off between the two stimuli. PG29 was the only pigeon whose matching accuracy following 2-s samples on dark-ITI trials remained above 80%, the learning criterion. This result suggests a strong reliance on sample onset

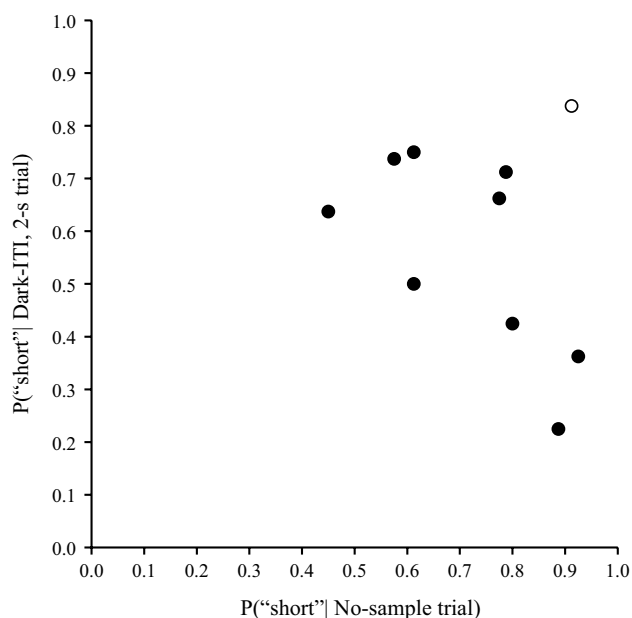


Fig. 3 Proportion of choices to the “short” key in no-sample test trials (x axis) plotted against proportion of correct responses following 2-s samples in dark-ITI test trials (y axis). Each data point refers to the performance of one pigeon. The empty circle identifies pigeon PG29

as a time marker. However, the .91 proportion of “short” responses on the no-sample trials suggests a strong reliance on the houselight as well. Hence, it seems that this pigeon may have learned to use both stimuli simultaneously.

To summarize, the results were consistent with the hypothesis that animals were attending to two different stimuli, the white keylight and the houselight that signaled the ITI. This result confirms that, in a symbolic matching-to-sample timing task, two stimuli can jointly control responding. Of the 10 birds, one seemed to rely on the two stimuli simultaneously. For the remaining animals, the data seem to suggest a trade-off in the use of the two stimuli.

The reinforcement contingencies differed between the two tests, for reinforcement was delivered on dark-ITI trials (provided the response was correct), but not on no-sample trials. This difference can be problematic because on the dark-ITI trials new learning could occur, thus contaminating our measure of stimulus control. One alternative would be to conduct both tests in extinction. However, extinction on dark-ITI trials poses its own problems such as disrupting the temporal control exerted by the sample, perhaps bringing choice proportions closer to indifference. In that case, it would not be possible to determine whether any differences between the dark-ITI trials and the training trials would reveal the effect of the houselight offset or the change in the reinforcement contingencies during testing. Perhaps a better approach would be to compare the test results across different training and testing conditions (e.g.,

testing with the same contingencies as during training versus testing in extinction; training with partial reinforcement and then testing with the same partial, but non-differential reinforcement).

The group data revealed a significant difference in performance between the first and last five sessions of the dark-ITI test, a difference consistent with additional learning during testing. Besides this general learning effect, reinforcement during dark-ITI tests could have affected also how attention was divided between the houselight and the sample keylight. Hence, a finer analysis of the effect of reinforcement during dark-ITI tests can be instructive regarding the nature of joint stimulus control. Assuming a trade-off between houselight and sample, reinforcement on dark-ITI trials could have changed how much the pigeons relied on each stimulus. This is because when responding was based on the houselight, pigeons would be reinforced in a seemingly random fashion (because correct responses would correlate with sample duration, not with presence or absence of the houselight). Thus, pigeons could have learned that the houselight was no longer a reliable predictor of reinforcement. Therefore, and because the sample duration continued to be a reliable indicator of what response was to be reinforced, pigeons could have learned to attend less to the unreliable houselight and more to the reliable sample duration. The following analyses will include only the pigeons that seemingly made use of the trade-off strategy (that is, pigeon PG29—signaled with an empty circle in Fig. 3—was excluded).

A change in attention favoring the sample would have two major consequences: an increase in correct responses following 2-s samples on dark-ITI trials and a decrease in choices of the “short” comparison on no-sample trials (as per Table 1). Regarding the dark-ITI trials, as shown before, there was an improvement in matching accuracy to 2-s samples, but this result could be due solely to continued learning of the task during testing. Hence, the increase in correct responses following 2-s samples, although consistent with an increased reliance on the sample, is not conclusive evidence of a switch in attention. On the other hand, on no-sample trials there was no reinforcement, so a decrease in preference of the “short” comparison would be more robust evidence of an increased reliance on the sample stimulus. Even though no difference was found when all animals were included in the analysis, when PG29 was excluded, there was a significant decrease: average choices of “short” were 74% in the first five sessions and 68% in the last five sessions, $t(8) = 2.72$, $P = .026$, Cohen’s $d_z = .91$, 95% CI [.10, 1.67].

In sum, even though the effect of testing limits the conclusions that can be derived from directly contrasting performance between the two tasks, the evidence collected is suggestive of a trade-off between sample and houselight (for 9 out of the 10 pigeons tested). First, the effects of testing, suggesting a change in focus is consistent with a trade-off,

where the reliance on one stimulus correlates negatively with the reliance on the other. Second, even though the negative correlation between the measures derived from the two tests became more pronounced with testing, in the initial sessions, there was already a negative trend, albeit nonsignificant ($r = -.41$; $P = .13$), that could be suggestive of a trade-off.

Not all stimuli in the environment acquire control over responding, and if one assumes that it is more taxing to attend to two stimuli (or two aspects of a stimulus) than to a single stimulus, why would an animal attend to two redundant stimuli? It is possible that the benefit of having more than one source of information may compensate the additional cost. Moreover, the way a task is set up may facilitate the acquisition of control by more than one stimulus. In the present study, the finding that the houselight also was attended to may be explained by its salience: The houselight is a strong light that illuminates the whole box. Johnson and Cumming (1968) manipulated the intensity of one element in a compound visual stimuli and found that the higher the intensity of that element during training, the stronger its control over responding during testing (see also Gaitan and Wixted 2000 for a detection theory based on stimulus salience).

When joint control does occur, it is likely to differ across subjects; that is, the degree of competition between stimuli may vary and different stimulus control topographies may develop (Mackintosh 1975; McIlvane and Dube 2003). In light of the trade-off model, differences in performance reveal the differences in the use of the available information, suggesting that whereas some birds rarely attended to the houselight, others may have been influenced mostly by that stimulus. Similarly, Reynolds (1961) found that, when trained with a white triangle in a red background, one pigeon attended to the red hue and the other to the triangle. In a separate task, a side lamp was illuminated with either green or yellow (which differed in brightness, the yellow being brighter than the green), to indicate which element of the compound stimulus would provide reinforcement. Test trials revealed that neither bird attended to the color of the lamp light and responded based on its intensity. With a red side lamp as bright as the green, pigeons responded as if a green lamp was present; with a white lamp brighter than the yellow, pigeons responded as if a yellow lamp was present; finally, with a dim yellow light, pigeons responded as if a green lamp was present.

When a task includes correlated stimuli, it is important to ask not only which stimuli will be used to solve the task but also how the stimuli interact. For instance, a conditioned response or the rate of operant responding may be higher in the presence of a combination of stimuli (each conditioned/trained separately) than in the presence of each stimulus individually (summation effect: Weiss 1964; Wolf 1963).

On the other hand, it has been found that matching accuracy is lower when a compound sample is presented than when a single-element sample is presented (element superiority effect: Maki and Leith 1973). That is, combining the elements seems to strengthen their individual effects in the first case, but to weaken them in the second case.

In conclusion, the present results stress the importance of taking into account the potential sources of stimulus control inherent in a procedure, of understanding better how multiple stimuli interact when controlling behavior, and of identifying the variables that may explain seeming individual differences in learning strategy.

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Compliance with ethical standards

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

Ethical approval This research was conducted in agreement with European (Directive 2010/63/EU) and Portuguese law (Ordinance 1005/92 of October 23), and was approved by the Directorate-General for Food and Veterinary, the Portuguese national authority for animal health (Reference 0421/000/000/2013).

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