


Divided control by past behavior, present stimuli, and future outcome value in a concurrent-chains procedure

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Abstract

When multiple stimuli appear to signal behavior–reinforcer contingencies, control may be divided between those stimuli. Such divided stimulus control depends in part on the value of the outcome to the organism, with stimuli signaling more valuable outcomes exerting stronger control. The present experiment investigated how divided control by past and present stimuli interacts with outcome value. Pigeons responded in a concurrent-chains procedure in which one terminal link ended with two food deliveries after 8 s and the other link ended with six food deliveries after 48 s. Outcomes were signaled by the response producing terminal-link entry (past behavior) as well as keylight stimuli during initial links (past signals) and terminal links (present signals). When these sources of stimulus control conflicted, past behavior exerted strong control over terminal-link responding, overshadowing control by past signals. Some control by present signals was also evident, particularly at later times in terminal links. Additionally, stimuli signaling pigeons' more preferred outcome (smaller-sooner reinforcer) exerted stronger control than stimuli signaling the less preferred (larger-later) outcome. These findings highlight the importance of subjective outcome value in stimulus control and demonstrate that egocentric stimuli can exert enduring behavioral control even when other less transient discriminative stimuli occurred in the recent past or present.

KEYWORDS

conflicting information, consequence control, intertemporal choice, pigeon, stimulus control

When a behavior is followed by an appetitive consequence (a *reinforcer*) in the presence of a stimulus, that stimulus normally comes to control the rate or probability of the behavior (Terrace, 1966). Such *stimulus control* arises due to the correlation between the stimulus, behavior, and reinforcer delivery (Baum, 1973). This correlation allows the stimulus to “signpost” (Shahan, 2010) future reinforcer conditions. As a result, behavior changes when the stimulus is presented again in the future (for example, response rates increase if the stimulus signals an increase in reinforcer rates). As the correlation between the stimulus and reinforcer availability strengthens, so too does stimulus control. Thus, stimuli that are more highly correlated, and thus more reliable,

signposts of future reinforcer conditions tend to exert stronger control over behavior (e.g., Cowie et al., 2017; Davison & Elliffe, 2010; McLinn & Stephens, 2006; Shahan & Podlesnik, 2006, 2007).

Stimulus control depends not only on the actual correlation but also on the extent to which subjects can discriminate correlations between stimuli, behaviors, and consequences. Indeed, control by arranged contingencies is weaker when the stimulus or response producing a reinforcer is difficult to discriminate from other stimuli or responses (e.g., Miller et al., 1980). Even in the absence of manipulations that degrade stimulus or response discriminability, subjects may still make errors in discrimination—as reinforcers obtained following one

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stimulus or response may be *misallocated* to a different stimulus or response (e.g., see Cowie et al., 2017; Davison & Jenkins, 1985; Davison & Nevin, 1999). Such misallocation may occur because of perceptual or memory failures (e.g., difficulty perceiving or remembering the stimulus or response that produced a reinforcer; see e.g., Cowie et al., 2017). Therefore, the presence of a stimulus that reliably signals future reinforcer conditions does not guarantee that the stimulus will exert strong control over behavior. Instead, the strength of stimulus control is mediated by subjects' ability to discriminate the arranged contingencies accurately. To the extent that misallocation occurs, discriminated contingencies will deviate from arranged contingencies, resulting in weaker than expected stimulus control.

Control by one stimulus is also determined by the extent to which *other* stimuli appear to signpost future events. The stimuli among which control is divided (Davison & Elliffe, 2010; Gomes-Ng et al., 2023; Shahan & Podlesnik, 2006, 2007) can include somewhat unreliable signposts for future contingencies (e.g., Davison & Cowie, 2019) and stimuli that are no longer present (e.g., Cowie et al., 2017). For example, in a matching-to-sample (MTS) task in which subjects are presented with a sample stimulus and then choose its matching comparison, performance in the current trial may be affected by the sample that was presented in the previous trial (*proactive interference*; e.g., Edhouse & White, 1988; Moise, 1976; White et al., 2004). Similarly, Cowie et al. (2017) found that control by reliable key-color stimuli, which signaled the definite next-food location, was imperfect because less reliable past stimuli (food deliveries, which signaled the likely next-food location) continued to exert some control over choice. That is, despite the presence of a perfectly reliable stimulus signaling the location of the next food delivery, preference for that location was not exclusive because stimulus control was *divided* between the reliable present stimulus and a less reliable past stimulus. Likewise, in humans, prior instructions often exert strong control over behavior, and such instructional control persists even when the instructions are incongruent with current contingencies (e.g., Fox & Kyonka, 2017; Galizio, 1979; Hackenberg & Joker, 1994; Podlesnik & Chase, 2006).

Past behavior may be a particularly salient discriminative stimulus (Davison, 2018; Gomes-Ng et al., 2019, 2022; Jones & Davison, 1998; Killeen, 1978; Urcuioli, 1984, 1985). For example, Urcuioli (1984, 1985) arranged different response requirements (e.g., fixed ratio vs. differential reinforcement of low rate) for different sample stimuli in an MTS procedure and found that comparison choice was exclusively controlled by sample-specific response patterns (see also Urcuioli & Honig, 1980). Even when differential sample responding is not required, idiosyncratic differential sample behavior may develop during sample-stimulus presentation (e.g., orienting toward a particular location), and such

behavior may control comparison choice at the expense of control by the sample stimulus itself (see, e.g., Gomes-Ng et al., 2019). Indeed, Cowie et al. (2020) and Gomes-Ng et al. (2022) found that in a concurrent-chains schedule in which the initial-link keys produced access to terminal links differing in reinforcer delay and magnitude, terminal-link response patterns were primarily controlled by the response that had produced terminal-link entry, whereas compound stimuli that signaled the reinforcer delay and magnitude exerted much weaker control. These findings suggest that the organism's own behavior in the recent past may be more salient than, and thus overshadow, other past or present external stimuli.

Finally, stimulus control also appears to depend on the subjective value of the outcome. Conditions that alter the value of a reinforcer or punisher (*motivating operations*) influence the strength of control by stimuli that signal the availability of that outcome (for discussions, see Edwards et al., 2019; Poling et al., 2020). After food deprivation, stimuli that signal food availability exert stronger control over behavior than stimuli signaling water availability, whereas the reverse is true if subjects are instead water deprived (Hull, 1933; Leeper, 1935). Similarly, pre-session feeding weakens subsequent control by stimuli signaling food availability (Bizo & White, 1995; Ward & Odum, 2006). Even when deprivation or satiation does not occur, the characteristics of the outcome itself may influence its reinforcing effectiveness and thus stimulus control. For example, Cowie et al. (2020) recently found that stimuli signaling access to pigeons' more preferred reinforcer (in their procedure, a smaller reinforcer delivered sooner) exerted stronger control over choice than stimuli signaling access to a less preferred reinforcer (a larger reinforcer delivered later; see also Gomes-Ng et al., 2022).

These findings indicate that stimulus control is subjective in nature (Cowie et al., 2020). That is, its strength depends not only on the arranged correlation between stimulus, behavior, and consequence but also on what the organism discriminates about that relation, about relations signaled by stimuli (including the organism's behavior) in the recent past, and on the subjective value of the consequence to the organism (see also Killeen & Jacobs, 2017). At present, few studies have examined how these components interact to determine stimulus control. Therefore, the present experiment investigated how control by past and present stimuli interacts with subjective outcome value in a concurrent-chains procedure. We arranged a systematic replication of Cowie et al. (2020) and Gomes-Ng et al. (2022) in which each trial was separated into an initial-link period (the recent *past*) and a terminal-link period (the *present*) and trials ended with either two food deliveries after an 8-s delay (smaller-sooner reinforcer) or six food deliveries after a 48-s delay (larger-later reinforcer). Thus, terminal links led to outcomes that differed in value. Consistent with previous work (Cowie et al., 2020; Gomes-Ng et al., 2022; see

also Baum & Rachlin, 1969; Davison, 1988), we assessed subjective outcome value by examining initial-link choice. Stronger preference for one alternative suggests that its outcome is of greater subjective value. Across trials, outcomes were signaled by the initial-link response producing terminal-link entry (i.e., past behavior) and by additional colored stimuli during initial and terminal links (i.e., past and present external stimuli). These sources of stimulus control conflicted in some trials (e.g., initial-link and terminal-link stimuli differed), allowing us to examine the extent to which past behavior, past external stimuli, and present external stimuli each controlled behavior during terminal links.

METHOD

Subjects

Five adult pigeons (*Columba livia*; age and sex unknown), numbered 112 to 116, served as subjects in Conditions 1 and 2. A sixth pigeon, numbered 111, was added in Conditions 3 and 4. Pigeon 116 was removed from the experiment during Condition 4 due to a health issue. Pigeons were maintained at $85\% \pm 15\%$ g of their free-feeding bodyweight, with supplementary feeding of mixed grain occurring at approximately 9:30 a.m. each morning. Water and grit were always available. All pigeons, excluding 111, had previous experience in concurrent-chains procedures (Cowie et al., 2020; Gomes-Ng et al., 2022).

Apparatus

Each pigeon was housed in an individual cage ($375 \times 375 \times 370$ mm [height \times depth \times width]), which also served as the experimental chamber. Two perpendicular wooden perches were elevated above the cage floor. The operant panel contained three circular 20-mm diameter plastic response keys spaced 100 mm apart horizontally. Keys could be illuminated red, green, or yellow. Pecks to the keys exceeding 0.1 N of force were recorded. Sixty mm above the perches, below the center keylight, was a square magazine aperture measuring 40×40 mm. A hopper, filled with wheat, was located behind the magazine aperture. When a reinforcer was delivered, the keylights were extinguished, the magazine aperture was lit, and the hopper was raised for 1.2 s, providing access to wheat. Successive hopper presentations were separated by 0.3 s during which the hopper lowered to refill. Cages were kept in a colony room where the pigeons could see and hear other pigeons in the room during the experiment. The colony room operated on an automatic light–dark cycle (lights on at 12 a.m. and off at 4 p.m. daily), with experimental sessions occurring at 2 a.m. daily. The experiment was controlled, and experimental events were

automatically recorded by a computer running MED-PC IV in a neighboring room. No human entered the colony room during experimental sessions.

Procedure

We arranged a concurrent-chains schedule in which the pigeons chose between two alternatives, one delivering a small reinforcer after a short delay and the other delivering a large reinforcer after a long delay (as in Cowie et al., 2020, and Gomes-Ng et al., 2022). In different trial types and conditions, different discriminative stimuli signaled the outcome of each trial (i.e., whether a smaller-sooner [SS] or larger-later [LL] reinforcer was arranged). These stimuli included (a) the response (SS or LL) producing terminal-link entry, (b) a compound discriminative stimulus during initial links, (c) a compound stimulus during terminal links, and (d) a brief stimulus signaling the response that produced terminal-link entry (only in Conditions 3 and 4). Experimental sessions ran daily starting at 2 a.m. and lasted for 60 trials or until 85 min had elapsed, whichever occurred first.

There were two types of conditions: *unsigned-peck* conditions (Conditions 1 and 2) in which the response producing terminal-link entry was not signaled and *signed-peck* conditions (Conditions 3 and 4) in which the response producing terminal-link entry was signaled during the first 4 s of terminal links. Each pair of conditions differed only in the locations of the side keys that produced entry to the smaller-sooner (SS) and larger-later (LL) terminal links (see Table 1). Reversing the key locations in this manner enabled us to assess the replicability of our results as well as to separate preference for a particular terminal link (e.g., SS) from bias toward a particular key location (e.g., right key).¹

Conditions 1 and 2 (unsigned-peck conditions)

In Conditions 1 and 2 (unsigned-peck conditions), trial outcomes were signaled by the response (SS or LL) producing terminal-link entry (hereafter, “TL-entry response”) and by compound discriminative stimuli that were present during initial and terminal links. In each session, 44 trials were reinforced and 16 trials were unreinforced. These were split evenly between trial outcomes (SS or LL) and trial types (uncued and cued; described below). Figure 1 depicts the structure of each trial type in Conditions 1 and 2.

¹Due to experimenter error, Pigeon 116’s key location did not reverse between Conditions 1 and 2. This only minimally affects our findings because we could still compare initial-link choice in Conditions 1 and 2 with choice in Condition 3 for this pigeon (as initial links were identical across conditions). Also, the focus of the current manuscript is on the stimuli controlling responding during terminal links rather than initial-link choice per se.

TABLE 1 Smaller-sooner (SS) stimulus, SS-peck stimulus, and SS key location across pigeons and conditions.

Pigeon	SS stimulus	SS-peck stimulus	Key location of SS			
			C1	C2	Baseline & C3	C4
111	Red-Fast	Red	-	-	-	Right
112	Green-Slow	Green	Right	Left	Right	Left
113	Red-Fast	Red	Right	Left	Right	Left
114	Green-Slow	Green	Left	Right	Left	Right
115	Red-Fast	Red	Left	Right	Left	Right
116	Green-Slow	Green	Left	Left	Right	-

Note: SS Stimulus = compound stimulus (red-fast or green-slow) during initial and terminal links in cued trials (the LL stimulus was the other compound, e.g., green-slow for Pigeons 111, 113, and 115). SS-peck stimulus = color (red or green) signaling which key produced SS terminal-link entry in signaled-peck conditions (LL entry was signaled by the other color). C1 and C2 = unsignaled-peck conditions; C3 and C4 = signaled-peck conditions. The baseline condition ran in between Conditions 2 and 3 and arranged only uncued and cued trials. Due to a programming error, Pigeon 116's SS key location did not reverse between Conditions 1 and 2.

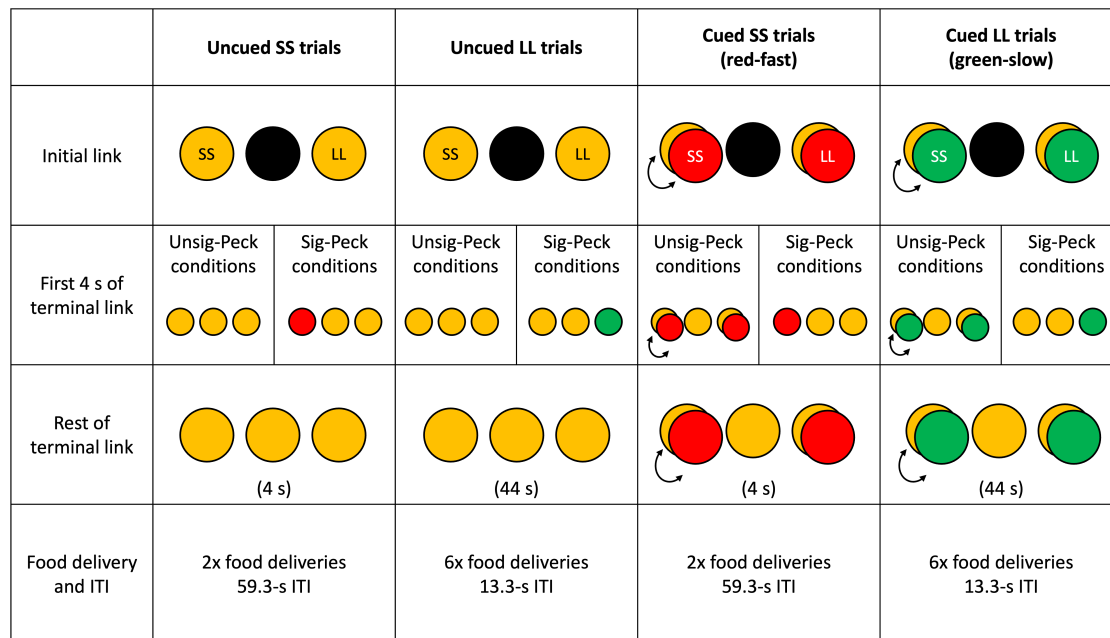


FIGURE 1 Initial-link and terminal-link stimuli in uncued and cued trials. In this example, the left key produces entry to the SS terminal link and the right key produces entry to the LL terminal link; the red-fast stimulus signals an SS outcome and the green-slow stimulus signals an LL outcome. Double-ended arrows indicate that the stimulus was a compound that alternated at a fast or slow frequency. In each trial, only one side key produced entry to its respective terminal link. The only difference between unsignaled-peck (unsig-peck) and signaled-peck (sig-peck) conditions was the stimuli during the first 4 s of terminal links. The side keys either continued displaying the initial-link stimuli (unsig-peck conditions) or the response producing terminal-link entry was lit red or green (sig-peck conditions). Thereafter, the initial-link stimuli were presented on the side keys for the remainder of the terminal link. The SS trials ended with 2 food deliveries after a total delay of 8 s, and LL trials ended with 6 food deliveries after a delay of 48 s.

Uncued trials

In *uncued* trials (left two panels of Figure 1), only the TL-entry response signaled trial outcomes. In these trials, both side keys were lit yellow. One side key produced entry to the SS terminal link, and the other key produced entry to the LL terminal link (counterbalanced across pigeons; Table 1). Terminal-link entry was dependently scheduled (Stubbs & Pliskoff, 1969) according to variable-interval (VI) 10-s schedules. After the VI schedule arranged entry, the trial outcome (and thus the response producing terminal-link entry) was selected probabilistically ($p = .50$), with the

constraint that each outcome was experienced equally often within a session. After a response to the key selected for terminal-link entry, the center key was lit yellow to signal the start of the terminal link (the side keys remained lit but inoperative during terminal links). In the SS link, a center-key response resulted in two reinforcer deliveries after an 8-s delay (i.e., a fixed-interval [FI] 8-s schedule). In the LL link, center-key responding resulted in six reinforcer deliveries after a 48-s delay (i.e., FI 48-s schedule). Terminal links ended with an intertrial interval during which the keylights remained darkened. The duration of the intertrial

interval was adjusted such that the total duration of the terminal link was always 70 s.

Cued trials

Cued trials were identical to uncued trials, except that the TL-entry response (SS or LL) was also differentially signaled with a compound stimulus (right two panels of Figure 1) during initial links. Specifically, the side keys alternated between red and yellow every 0.1 s (“red-fast”) or between green and yellow every 0.9 s (“green-slow”) to signal which terminal link would be presented (i.e., the trial outcome). The red-fast stimulus signaled the SS link, and the green-slow stimulus signaled the LL link for odd-numbered pigeons (111, 113, and 115). The reverse was arranged for even-numbered pigeons (112, 114, 116). The compound stimulus also remained present on the side keys throughout terminal links.

In cued trials, the TL-entry response and the compound stimuli during initial and terminal links always provided congruent information about trial outcomes. Thus, it is not possible to determine which stimuli exerted greater control in these trials, because control by any or all of the stimuli would be expected to produce similar behavior. Thus, after 30 sessions with uncued and cued trials, we introduced *conflicting* trials for 20 sessions.

Conflicting trials

In *conflicting* trials, stimuli signaled incongruent outcomes. This allowed us to determine the division of

control between the different stimuli. Figure 2 shows the structure of conflicting trials. Conflicting trials began in the same way as cued trials, with either the red-fast or green-slow stimulus presented on the side keys during initial links. As in cued trials, entry into the terminal links was dependently scheduled so that in half of trials the LL key produced entry into the terminal link. Unlike cued trials in which one compound stimulus always signaled SS-key entry and the other stimulus signaled LL-key entry, in half of conflicting trials the initial-link compound stimulus signaled the incorrect TL-entry response. In these trials, the compound stimulus and entry response provided conflicting information about trial outcomes. For example, if the red-fast stimulus was presented during the initial link, the SS key produced entry in half of such trials and the LL key produced entry in the other half. Additionally, upon terminal-link entry, the compound stimulus on the side keys changed to the other stimulus. That is, if the initial-link stimulus signaled an SS outcome (e.g., red-fast), then upon terminal-link entry the stimulus changed to that signaling an LL outcome (e.g., green-slow), and vice versa. Hereafter, for brevity, we term these “SS-to-LL” and “LL-to-SS” trials, respectively. Thus, there were four types of conflicting trials: SS-to-LL trials in which an SS response produced terminal-link entry, SS-to-LL trials in which an LL response produced entry, LL-to-SS trials in which an SS response produced entry, and LL-to-SS trials in which an LL response produced entry. Terminal links in

	SS-to-LL trials SS key entry		SS-to-LL trials LL key entry		LL-to-SS trials SS key entry		LL-to-SS trials LL key entry	
Initial link								
First 4 s of terminal link	Unsig-Peck conditions 	Sig-Peck conditions 	Unsig-Peck conditions 	Sig-Peck conditions 	Unsig-Peck conditions 	Sig-Peck conditions 	Unsig-Peck conditions 	Sig-Peck conditions
Rest of terminal link (110 s)								
Food delivery and ITI	No food 26-s ITI		No food 26-s ITI		No food 26-s ITI		No food 26-s ITI	

FIGURE 2 Initial-link and terminal-link stimuli in conflicting trials. In this example, the left key produces entry to the SS terminal link, the right key produces entry to the LL terminal link, the red-fast stimulus signals an SS outcome, and the green-slow stimulus signals an LL outcome. Double-ended arrows indicate that the stimulus was a compound that alternated at a fast or slow frequency. In each trial, one side key was randomly chosen to produce terminal-link entry. Upon terminal-link onset, the stimuli on the side keys changed from red-fast to green-slow, or vice versa in unsignaled-peck conditions. In signaled-peck conditions, the TL-entry response was lit red or green during the first 4 s of terminal links, after which the other compound stimulus was presented. Terminal links lasted for a total of 114 s and ended without food delivery.

conflicting trials lasted for 114 s, ended without a reinforcer delivery, and were followed by a 26-s intertrial interval. There were four conflicting trials per session, which replaced four of the unreinforced trials (one each of Uncued SS, Uncued LL, Cued SS, and Cued LL).

Conditions 3 and 4 (signaled-peck conditions)

Before beginning Condition 3, all pigeons were returned to a baseline condition with only uncued and cued trials for 30 sessions. The side keys producing SS and LL entry were reversed in the baseline condition (Table 1).

Conditions 3 and 4 were identical to Conditions 1 and 2, except that the response that had produced entry to the terminal link was signaled during the first 4 s of terminal links (signaled-peck conditions). At the start of the terminal link in Conditions 3 and 4, the side key producing terminal-link entry was lit either red or green. For odd-numbered pigeons (111, 113, and 115), the side key was lit red if the SS key produced terminal-link entry and green if the LL key produced terminal-link entry. The reverse was arranged for even-numbered pigeons (112, 114, and 116). After 4 s, this “keypeck” signal was removed and the terminal-link stimulus (two yellow keys in uncued trials, the red-fast or green-slow stimulus in cued trials, or the other compound stimulus in conflicting trials) was presented for the remainder of the terminal link.

Data analysis

Analyses of un signaled-peck conditions (Conditions 1 and 2) and the baseline condition included data from Pigeons 112 to 116. Pigeon 111 joined the experiment in Condition 3, so data for all six pigeons were included in the analyses for that condition. Pigeon 116 was removed from the experiment before Condition 4, so only data for Pigeons 111 to 115 were analyzed for Condition 4. All the analyses were programmed in Python 3.7.

Initial-link choice

We examined the effects of subjective outcome value by analyzing initial-link choice (Cowie et al., 2020; Gomes-Ng et al., 2022; see also Baum & Rachlin, 1969; Davison, 1988). We first assessed the effects of key-location bias on initial-link choice (i.e., a bias toward one side key regardless of trial outcomes or initial-link signals) by comparing pairs of conditions arranging the same contingencies but different SS and LL key locations (see Table 1). Next, we quantified control by trial outcomes and by initial-link signals by calculating two summary measures of preference, *outcome control* and *signal control* (see Cowie et al., 2020).

Outcome control

Stronger preference for a specific outcome (e.g., SS) regardless of which side key produced that outcome or the initial-link signals would suggest that the preferred outcome was more subjectively valuable than the other outcome. Put simply, the pigeons may have preferred one side key *because of* the outcome (SS or LL) it produced. Table 2 shows how responses to the SS and LL keys during initial links were separated based on the actual (uncued and cued trials) or signaled (conflicting trials) trial outcome for calculations of outcome control. Each cell in Table 2 represents the number of responses, denoted by $B_{x|y}$, to key x (columns) when the actual or signaled trial outcome was y (rows).

To quantify outcome control, we used the following equation:

$$\text{Outcome control} = 0.5 \cdot \log \left(\frac{B_{SS|SS \text{ trial}}}{B_{LL|SS \text{ trial}}} \cdot \frac{B_{SS|LL \text{ trial}}}{B_{LL|LL \text{ trial}}} \right), \quad (1)$$

where the $B_{x|y}$ terms correspond to the response counts shown in Table 2. For example, for uncued and cued trials, $\frac{B_{SS|SS \text{ trial}}}{B_{LL|SS \text{ trial}}}$ represents the ratio of SS/LL responses in trials ending in an SS reinforcer, whereas in conflicting trials this ratio represents responses in trials that were *signaled* (by the initial-link signal) to end in an SS reinforcer. Likewise, $\frac{B_{SS|LL \text{ trial}}}{B_{LL|LL \text{ trial}}}$ represents the ratio of SS to LL responses in trials ending in or signaled to end in an LL reinforcer. Because some response counts were zero (i.e., the pigeons never responded to one alternative), we added 0.5 to all counts for calculations of Equation 1 (Hautus, 1995). More positive values of Equation 1 indicate more responses to (and thus stronger preference for) the SS key, and more negative values indicate more responses to the LL key. Thus, this measure reflects the extent to which choice was controlled by the trial outcomes themselves (i.e., the extent to which the pigeons preferred a particular outcome; subjective outcome value).

Signal control

In cued and conflicting trials, a compound stimulus signaled the trial outcome during initial links. To measure control by the initial-link signal, we used the following equation:

TABLE 2 Response counts used for calculations of outcome and signal control.

Actual or signaled trial outcome	Response to key	
	SS	LL
SS	$B_{SS SS \text{ trial}}$	$B_{LL SS \text{ trial}}$
LL	$B_{SS LL \text{ trial}}$	$B_{LL LL \text{ trial}}$

Note: Responses in uncued and cued trials were separated according to the actual outcome. Responses in conflicting trials were separated according to the outcome signaled by the initial-link signals.

$$\text{Signal control} = 0.5 \cdot \log \left(\frac{B_{SS|SS \text{ trial}} \cdot B_{LL|LL \text{ trial}}}{B_{LL|SS \text{ trial}} \cdot B_{SS|LL \text{ trial}}} \right). \quad (2)$$

Equation 2 is similar to Equation 1 (see also Table 2), except that now the numerator contains responses to the key that was signaled by the compound stimulus. Thus, in Equation 2, more positive values indicate more responses to the key that was signaled to produce terminal-link entry and thus stronger control by the signals. Values closer to zero or below zero indicate little to no control by the signal.

Terminal-link responding

Our primary objective was to assess sources of stimulus control during terminal links. As in initial links, multiple stimuli may have controlled responding during terminal links: (a) The response that produced terminal-link entry (past *behavior*), (b) the red-fast or green-slow stimulus present during initial links (past *signals*), (c) the red-fast or green-slow stimulus present during terminal links (present *signals*), and (d) the 4-s red or green stimulus signaling the TL-entry response in signaled-peck conditions.

To analyze terminal-link responding, responses to the center key (i.e., the active key) during terminal links were aggregated into 1-s time bins, and we used these response counts to calculate response rates in each bin (number of responses in a bin divided by the number of times that bin was reached). Because absolute response rates differed between pigeons, trials, or conditions, we standardized terminal-link response rates by calculating the proportion of peak responding (i.e., *relative* response rates). This enabled us to directly compare terminal-link responding across different trials and conditions.

Fixed-interval performance in individual trials can be characterized by two periods of responding, one in which response rates are low, followed by a period in which response rates are high. The time at which response rates transition from low to high (the *change-point*) provides a measure of temporal discrimination (Cheng & Westwood, 1993; Church et al., 1994). Thus, in addition to visual analysis of response patterns in terminal links, we computed changepoints using a method described by Gallistel et al. (2004). Briefly, this method involves considering each response made during a trial as a putative changepoint. The algorithm compares response rates before that putative changepoint with response rates after that changepoint. If the difference exceeds a specified decision criterion, then a significant changepoint is recorded.² We used a binomial test to compare response rates before and after the putative

changepoint and an odds ratio of 20:1 (corresponding to $p < .05$) as the decision criterion. Trials with fewer than three responses ($N = 173$; 2.25% of trials) were excluded from the changepoint analyses.

Statistical analyses

We compared initial-link choice and median changepoints across conditions and trial types using Bayesian hypothesis tests (Wagenmakers, Love, et al., 2018; Wagenmakers, Marsman, et al., 2018) in JASP (JASP Team, 2018). Bayesian tests are advantageous because they quantify the strength of the evidence for the null or alternative hypothesis with a Bayes Factor (BF_{10}), which reflects the likelihood of H_1 relative to H_0 given the obtained data. This can provide greater confidence in analytic results. A BF_{10} value of 1 indicates no evidence for the null or alternative hypothesis, whereas values greater than 1 (less than 1) indicate support for the alternative (null) hypothesis. Values above 3 (less than 0.33) indicate moderate support for the alternative (null) hypothesis, values above 10 (less than 0.1) indicate strong support, and values above 100 (less than 0.001) indicate extremely strong support for H_1 (H_0).

RESULTS

Initial-link choice

Acquisition

Figure 3 shows the mean proportion of responses to the LL key during initial links in uncued and cued trials across the 50 sessions of each condition. The vertical line denotes the 30-session mark, after which conflicting trials were introduced. The data in Figure 3 are representative of individual-pigeon data. Initial-link choice followed similar patterns in both unsignaled-peck conditions and in both signaled-peck conditions. Thus, data were replicable across pigeons and across conditions arranging the same contingencies.

In general, initial-link choice stabilized (ceased to change systematically) within the first 10 to 15 sessions of each condition (Figure 3). The only exception was Condition 3, in which choice was already stable at the start of the condition because of the preceding baseline condition. Overall, choice in uncued trials shifted toward the SS key across sessions and stabilized in slight favor of the SS key. In cued trials, choice shifted toward the signaled key (i.e., toward the SS key in Cued-SS trials, and toward the LL key in Cued-LL trials) and stabilized in strong favor of that key. Such preference for the signaled key was stronger in Cued-SS than in Cued-LL trials. Introducing conflicting trials in the last 20 sessions of each condition had little influence on choice in uncued and cued trials.

²Although more than one changepoint may be recorded in a trial (e.g., if response rates transition from low to high or vice versa multiple times), we only analyzed the first changepoint in each trial (i.e., the time at which response rates *first* transitioned from low to high).

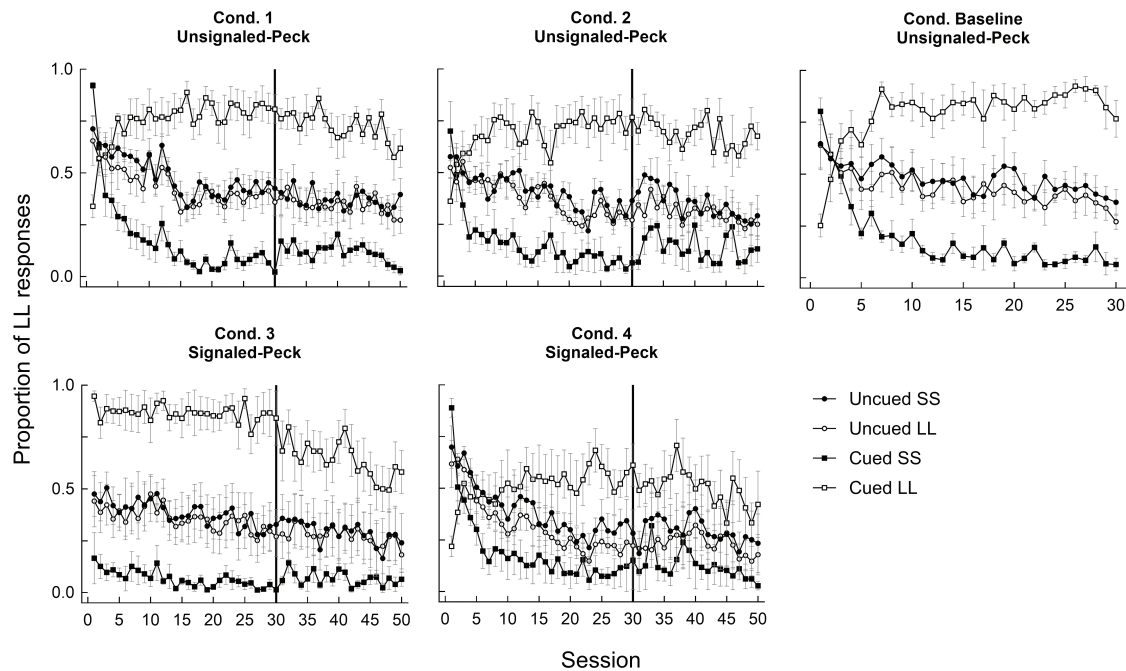


FIGURE 3 Mean initial-link choice across sessions in each condition. The top row shows data from unsignaled-peck conditions, and the bottom row shows data from signaled-peck conditions. Data are averaged across pigeons, and the error bars show the SEM.

Even where small changes in choice during the last 20 sessions of each condition were apparent, these did not produce changes in overall preference for an alternative (e.g., if choice favored the LL key, it continued to do so). Subsequent analyses use data from the last 10 sessions of each condition so that comparisons between unsignaled, signaled, and conflicting trials use stable data from the same sessions.

Key-location bias

Figure 4 shows the proportion of LL responses for pairs of conditions arranging the same contingencies but different locations of the SS and LL keys. Note that pairs of conditions were not available for Pigeon 111 (who completed only Condition 4) or Pigeon 116 (who completed Conditions 1 to 3, but the key locations did not reverse between Conditions 1 and 2 due to an experimenter error). Therefore, we will focus on the other four pigeons here.

The differences in the proportion of LL responses between pairs of conditions in Figure 4 reflect key-location biases. Key-location biases were generally small (i.e., they did not result in a difference in the *direction* of preference) and idiosyncratic (i.e., not all pigeons were biased toward the same key). Indeed, despite such biases, control by trial outcomes and by the initial-link signals was also apparent, as choice differed between trial types and for each trial type the overall *direction* of preference tended to be the same for pairs of conditions. That is, the pigeons generally preferred the SS key in uncued trials

and the key signaled to produce terminal-link entry in cued and conflicting trials (the only exception was Pigeon 112 in Uncued-LL and Cued-LL trials in signaled-peck conditions).

These patterns (Figure 4) were supported by statistical analysis. A Bayesian repeated-measures ANOVA with condition (unsignaled-peck, signaled-peck), SS-key location (Left, Right), and trial type (Uncued, Cued SS, Cued LL, Conflicting SS-to-LL, Conflicting LL-to-SS) as within-subjects factors indicated strong support for a model containing only the effects of condition, trial type, and their interaction ($BF_{10} = 9.62 \times 10^7$, error % = 5.84). Analysis of effects across models indicated that this was driven by the effect of trial type ($BF_{incl} = 5.41 \times 10^7$), whereas condition ($BF_{10} = 1.60$) and the interaction term ($BF_{10} = 1.95$) had very weak effects, and there was no evidence for an effect of SS-key location ($BF_{incl} = 0.95$). Thus, initial-link choice depended primarily on the presence or absence of compound stimuli signaling trial outcomes. The type of condition and location of the SS key had no systematic effect on initial-link choice.

Outcome and signal control

To better quantify control by trial outcomes and by initial-link signals, we calculated measures of outcome and signal control (Equations 1 and 2, respectively). Effectively, these measures capture the extent to which trial outcomes controlled initial-link choice (regardless of the initial-link signals) and the extent to which initial-link

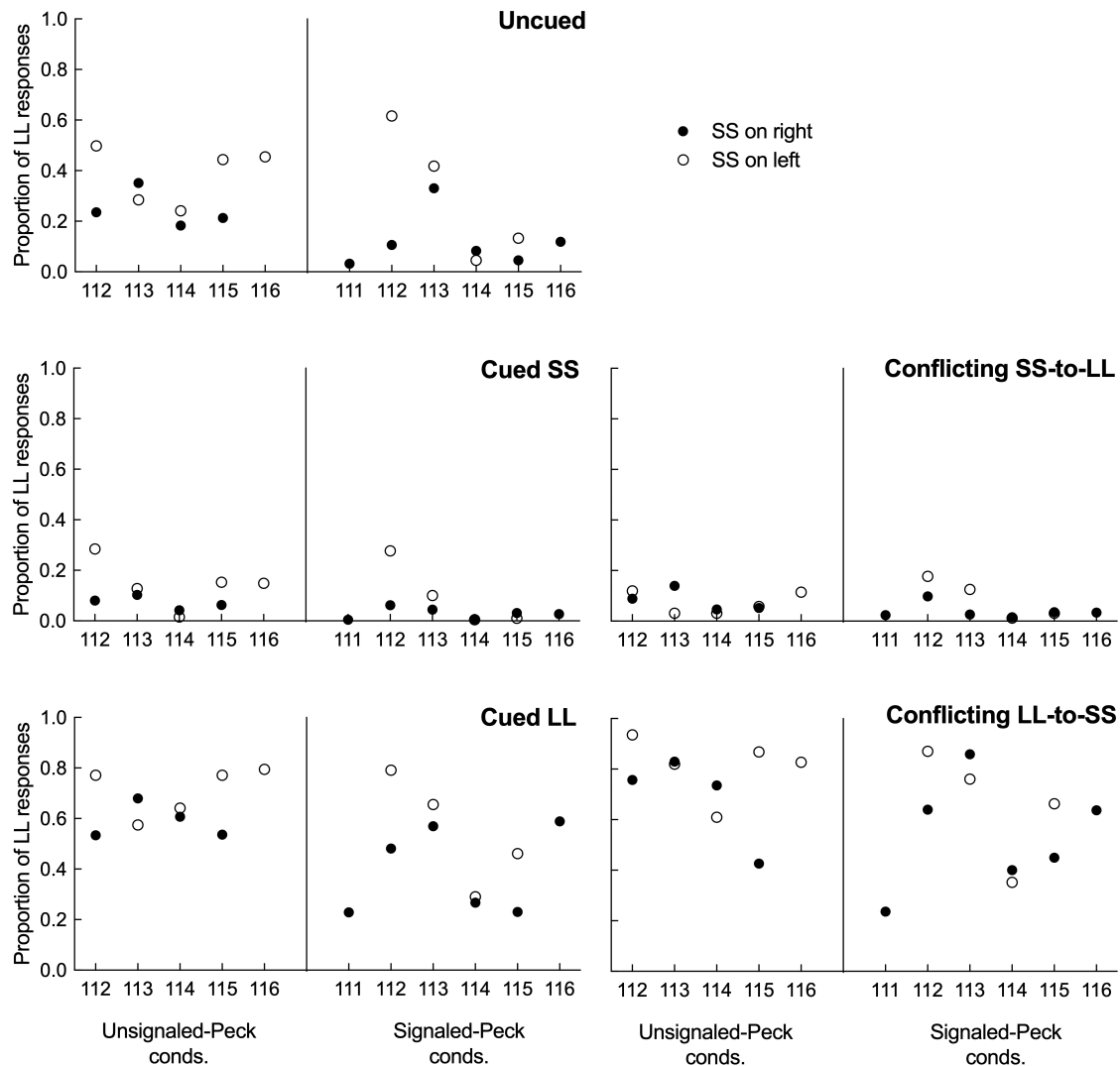


FIGURE 4 Initial-link choice for pairs of conditions arranging different SS and LL key locations. Filled data points show data from conditions where the SS key was on the right, and unfilled data points show data from conditions where the SS key was on the left. Pairs of conditions were not available for Pigeons 111 and 116.

signals controlled choice (regardless of trial outcomes). Figure 5 shows these measures for individual pigeons (data points) and averaged across all pigeons (bars). Although data from conflicting trials are shown separately from cued trials in Figure 5, these trials were effectively identical during initial links (see Figures 1 and 2).

In uncued trials, the initial-link side keys always remained yellow. Measures of outcome control (Equation 1) were positive in these trials, reflecting an overall preference for the SS key (Figure 5). When colored compound stimuli signaled trial outcomes in cued and conflicting trials, outcome control was similarly positive. In these trials, measures of signal control (Equation 2) were also positive, reflecting a preference for the key that was signaled to produce terminal-link entry. Values of signal control were larger than outcome control; thus, the initial-link signals exerted greater (but not exclusive) control over choice than did trial outcomes. Thus, initial-link choice was jointly controlled by preference for an outcome

and by the initial-link discriminative stimuli when such stimuli were present. The strength of control by trial outcomes and by initial-link signals did not differ systematically between conditions or trial types; Bayesian repeated-measures ANOVAs with condition and trial type as within-subjects factors indicated no support for models containing either factor for both outcome control and signal control (all models $BF_{10} < 1.05$). This is unsurprising, given that the SS and LL outcomes were the same in all conditions and that the initial-link signals in cued and conflicting trials were identical.

Terminal-link responding

There were several potential sources of stimulus control in terminal links: Past behavior (the response producing terminal-link entry), past initial-link signals (compound stimuli signaling an SS or LL outcome during initial

links), and present terminal-link signals (compound stimuli signaling an SS or LL outcome during terminal links). Additionally, in signaled-peck conditions, the response that had produced terminal-link entry was lit during the first 4 s of terminal links. We will first consider responding in uncued and cued trials—in which past behavior and signals provided congruent information about trial outcomes—and then we will consider responding in conflicting trials. Because only the center key was operative during terminal links, we combined data across replication conditions for analyses of terminal-link responding. Terminal-link responding for individual pigeons in each condition are shown in the Appendix (Figures A1–A6).

Uncued and cued trials

Figure 6 shows mean relative response rates across time in terminal links in uncued and cued trials. When the SS key produced terminal-link entry, response rates

increased rapidly in the first few seconds of terminal links and reached a maximum at about 8 s. There were few differences between Uncued-SS and Cued-SS trials or between unsignaled-peck and signaled-peck conditions. Thus, signaling trial outcomes had little effect on response-rate patterns when the SS key produced entry. In contrast, when the LL key produced terminal-link entry, patterns of responding depended on whether additional initial-link and terminal-link signals were present. When no such signals were available (uncued trials in unsignaled-peck conditions; filled data points in the left panel of Figure 6), response rates reached a peak at about 8 s and then gradually decreased before increasing again. That is, the pigeons appeared to behave “as if” an SS reinforcer would be delivered (akin to a “default” SS strategy), even though the LL key had produced terminal-link entry. This suggests some control by elapsed time (i.e., by “what usually happens now”); the yellow side keys signaled that food would be delivered at either 8 s or 48 s, and both durations controlled

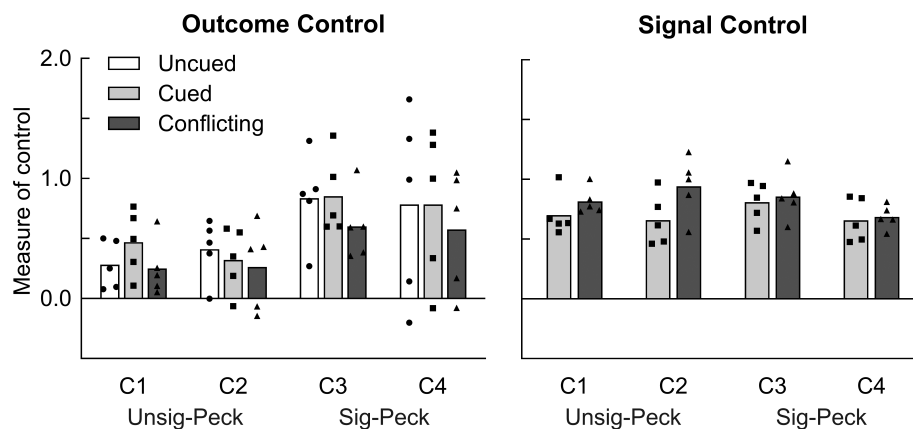


FIGURE 5 Control by trial outcomes and by initial-link signals. Data points show individual pigeon data, and bars show group-mean data. The left panel shows outcome control (Equation 1), and the right panel shows signal control (Equation 2). Unsig-Peck = unsignaled-peck conditions; Sig-Peck = signaled-peck conditions.

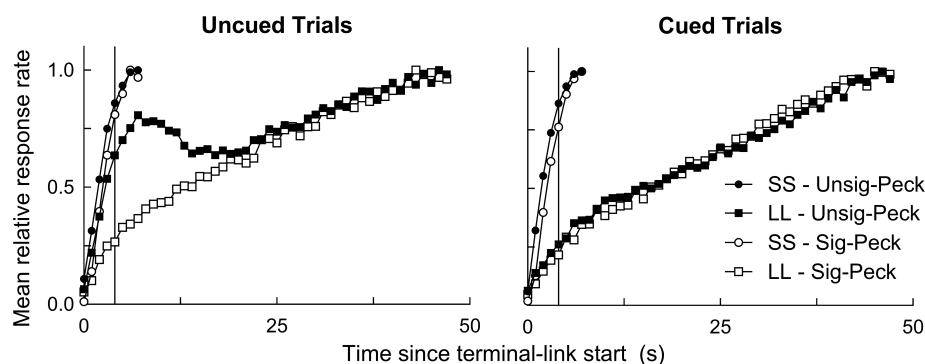


FIGURE 6 Terminal-link responding in uncued and cued trials. Data are averaged across pigeons. The left panel shows data from uncued trials, and the right panel shows data from cued trials. Filled symbols show data from unsignaled-peck conditions, and unfilled symbols show data from signaled-peck conditions. The vertical line at 4 s denotes the time at which the stimulus signaling the TL-entry response was removed in signaled-peck conditions.

responding. Some control, albeit weak, by the key producing terminal-link entry was also apparent. The initial increase in response rates was slightly slower, and the peak at 8 s was smaller in trials where the LL key produced terminal-link entry (filled squares in Figure 6, left panel) than in trials where the SS key produced entry (filled circles Figure 6, left panel). When additional signals were present (cued trials as well as uncued trials in signaled-peck conditions), no peak at 8 s was apparent in LL trials; instead, response rates increased gradually throughout terminal links. These response patterns suggest some control by elapsed time (as evidenced by the smaller peak at 8 s in Uncued-LL trials), by the TL-entry response (as evidenced by the differences between SS and LL trials), and by past and present signals (as evidenced by the differences between trials with and without initial- and terminal-link signals).

Conflicting trials

In conflicting trials, past behavior, past (initial-link) signals, and present (terminal-link) signals provided incongruent information about trial outcomes. Figure 7 shows

terminal-link responding in conflicting trials. Response rates in Cued-SS and Cued-LL trials are also shown (in gray) for comparison. Greater similarity between response patterns in conflicting trials and in Cued-SS (or -LL) trials reflects stronger control by the stimuli signaling SS (or LL) trial outcomes. In general, response rates in conflicting trials tended to increase during the first few seconds of terminal links and reached a peak at about 8 s before decreasing and then increasing again. Although the peak at 8 s appears consistent with a default SS strategy (as in Uncued-LL trials in unsignaled-peck conditions; see Figure 6), its height and time depended on the TL-entry response, past signals, and/or present signals, indicating control by the discriminative stimuli signaling trial outcomes.

SS-to-LL trials

In SS-to-LL trials (Figure 7, upper panels), initial-link stimuli signaled that the trial would end in an SS reinforcer, whereas terminal-link stimuli signaled that the trial would end in an LL reinforcer. In some trials, the SS key produced terminal-link entry; in other trials, the LL key produced entry. The TL-entry response clearly modulated the height of the peak at 8 s. A prominent peak,

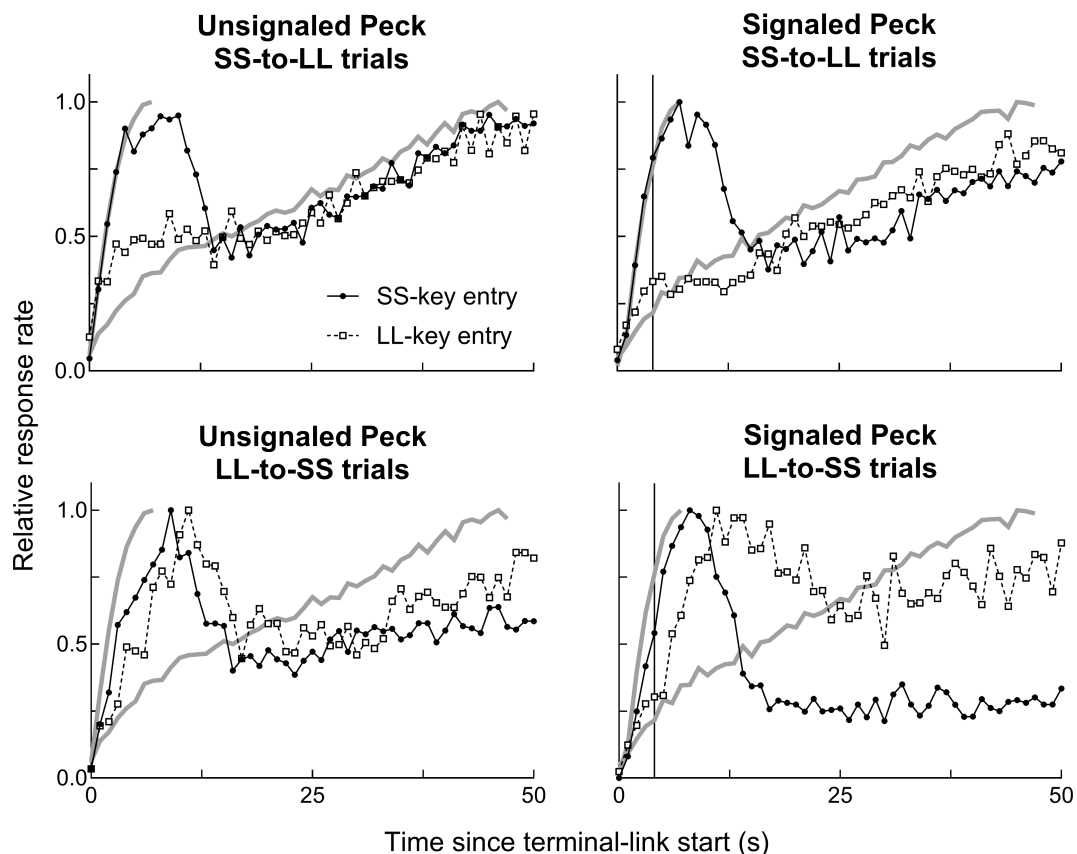


FIGURE 7 Terminal-link responding in conflicting trials. Data are averaged across pigeons. Solid gray lines show mean relative response rates in Cued-SS and Cued-LL trials for comparison. Filled circles show data from trials in which the SS key produced entry, and unfilled squares show data from trials in which the LL key produced entry. The vertical line at 4 s denotes the time at which the stimulus signaling the TL-entry response was removed in signaled-peck conditions.

similar to Cued-SS trials, was evident when the SS key produced entry, but the peak was much smaller when the LL key produced entry (Figure 7, top row). There was little difference between unsignaled-peck and signaled-peck conditions, although the height of the peak was slightly smaller in signaled-peck conditions when the LL key produced entry. Thus, control by past behavior was evident, and the strength of such control was similar regardless of whether the TL-entry response was signaled or unsignaled. That response rates peaked at 8 s—despite the present LL signal and even when the LL key produced terminal-link entry—also suggests some control, albeit weak, by the past SS signal. After about 12 s, response rates converged regardless of the TL-entry response and thereafter followed a pattern similar to that of the Cued-LL trials. These response patterns at later times are consistent with control by the present LL signal and by elapsed time (which signaled that the food delivery would occur at 48 s). Thus, control by past behavior and past signals decreased over time such that the present LL signal and elapsed time appeared to control responding at later times.

LL-to-SS trials

In LL-to-SS trials, the initial-link stimuli signaled that the trial would end in an LL reinforcer, whereas terminal-link stimuli signaled that the trial would end in an SS reinforcer. In such trials, a prominent peak in responding close to 8 s was apparent, reflecting strong control by the present SS signal at early times (Figure 7). Control by the past LL signal was also evident, as the time of the peak was always later than in Cued-SS trials. Additionally, the time of the peak was later when the LL key produced entry than when the SS key produced entry, consistent with some control by past behavior.

In contrast to SS-to-LL trials—in which responding at later times was strongly controlled by the present LL signal (Figure 7, upper panels)—the present SS signal appeared to exert weak control over responding at later times in LL-to-SS trials (Figure 7, lower panels). Specifically, in unsignaled-peck conditions, response rates in LL-to-SS trials converged regardless of the TL-entry response after about 12 s and then appeared to increase slightly, although not to the same extent as Cued-LL trials. This suggests that responding at later times was controlled primarily by elapsed time (which signaled that food would likely be delivered at 48 s), with weak control by the present SS signal (which may have decreased response rates slightly relative to Cued-LL trials). In contrast to unsignaled-peck conditions, response rates in LL-to-SS trials in signaled-peck conditions remained differential with respect to past behavior, with greater responding when the LL key produced entry than when the SS key produced entry. Therefore, control by past behavior endured when the TL-entry response was briefly signaled at the start of terminal links in LL-to-SS trials. Even so, the present SS signal still modulated responding

at later times, as response rates did not follow the same pattern as Cued-LL trials (not even when the LL key produced entry).

Changepoint analysis

Figure 8 shows median changepoints—the first time at which response rates changed from low to high—in terminal links. These changepoints reflect sources of stimulus control at earlier times in terminal links (i.e., when response rates were initially increasing). In line with visual analysis of response patterns across time (Figures 6 and 7), changepoints in Uncued-SS and Cued-SS trials were earlier than in Uncued-LL and Cued-LL trials, and this difference appeared to be larger when additional (congruent) stimuli signaled trial outcomes, consistent with control by the initial- and terminal-link signals. In conflicting trials, changepoints tended to be earlier when the SS key produced terminal-link entry, reflecting control by past behavior. In unsignaled-peck conditions (unfilled bars in Figure 8), changepoints appeared to be earlier in SS-to-LL trials than in LL-to-SS trials, perhaps due to control by the past SS signal in the former and past LL signal in the latter. Signaling the TL-entry response during the first 4 s of terminal links in signaled-peck conditions (filled bars in Figure 8) shifted changepoints later relative to unsignaled-peck conditions and to a greater extent when the LL key produced entry.

A Bayesian repeated-measures ANOVA with condition (unsignaled-peck, signaled-peck), TL-entry response (SS or LL), and trial type (uncued, cued, Conflicting SS-to-LL, Conflicting LL-to-SS) as within-subjects factors indicated that there was very strong support for the model containing all main effects and interaction terms ($BF_{010} = 50.35$, error % = 4.87). Analysis of effects across all models revealed that there was moderate evidence for an effect of the key producing entry ($BF_{incl} = 7.34$), but there was only anecdotal support for condition ($BF_{incl} = 2.27$), trial type ($BF_{incl} = 2.43$), and the two-way interaction terms ($1.74 < BF_{incl} < 2.92$). There was moderate support for a three-way interaction between condition, TL-entry response, and trial type ($BF_{incl} = 4.75$). We followed up this three-way interaction with separate Bayesian repeated-measures ANOVAs

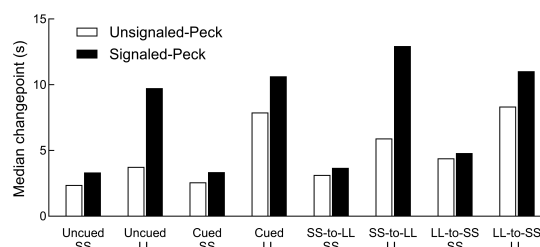


FIGURE 8 Median changepoints. Unfilled bars show data from unsignaled-peck conditions, and filled bars show data from signaled-peck conditions. SS and LL indicate the response that produced terminal-link entry.

for each condition (with TL-entry response and trial type as within-subjects factors), which revealed weak evidence for an effect of either factor in unsignaled-peck conditions (all models $BF_{10} < 3.6$) but strong support for a model containing the TL-entry response in signaled-peck trials ($BF_{10} = 10.06$, error % = 1.24). Thus, in summary, the response producing terminal-link entry had the strongest effect on changepoints and this effect was much larger when that response was signaled during the first 4 s of terminal links.

Summary of main results

Initial-link choice was controlled by trial outcomes and by stimuli signaling outcomes when such stimuli were present (cued trials). During terminal links, responding was jointly controlled by past behavior, past signals, and present signals (Figures 6 and 7). When trial outcomes were not differentially signaled by additional stimuli (uncued trials in unsignaled-peck conditions), elapsed time exerted some control, as response rates peaked at 8 s regardless of the response producing terminal-link entry. Nevertheless, some control by past behavior was also evident because the peak was smaller when the LL key produced entry than when the SS key produced entry. When trial outcomes were differentially signaled by additional compound stimuli, these signals exerted strong (but not exclusive) control over responding.

When signals provided conflicting information about trial outcomes (conflicting trials), stimulus control was divided between past behavior, past (initial-link) signals, and present (terminal-link) signals (Figure 7). Specifically, the response peak at around 8 s was more prominent (SS-to-LL trials) or closer to 8 s (LL-to-SS trials) when the SS key produced terminal-link entry, reflecting control by past behavior. Some control by past signals was also apparent, albeit weak. An early response peak was always evident in SS-to-LL trials (consistent with the past SS signal), and the peak time in LL-to-SS trials was always later than in Cued-SS trials (consistent with the past LL signal). Control by past behavior and past signals was strongest at early times in terminal links, probably because those signals had occurred in the recent past.

Control by present signals in conflicting trials depended on elapsed time. Specifically, present signals appeared to exert the strongest control when they were *congruent* with elapsed time. The present LL signal exerted strong control at later times in SS-to-LL trials, whereas the present SS signal exerted strong control at earlier times in LL-to-SS trials (Figure 7). In contrast, when present signals were *incongruent* with elapsed time (an LL signal at earlier times, or an SS signal at later times), responding was more strongly controlled by other available stimuli. In SS-to-LL trials, responding at early times was controlled by past behavior and past signals (which had just recently occurred), whereas in LL-to-SS

trials, responding at later times was controlled by either elapsed time (when past behavior and past signals were more distant in time, in unsignaled-peck trials) or by the response producing terminal-link entry (when that response had been recently signaled, in signaled-peck trials). Thus, stimulus control appeared to *shift* from past behavior and past signals at earlier times to present (or recently presented) signals and elapsed time at later times in terminal links.

DISCUSSION

The present experiment investigated divided control by past behavior, past signals, and present signals in a concurrent-chains procedure. In each trial, the outcome (a smaller-sooner or larger-later reinforcer) could be signaled by the response producing terminal-link entry (past behavior), by a compound stimulus during initial links (past signals), and by a compound stimulus during terminal links (present signals). Elapsed time during terminal links served as an additional stimulus signaling what was likely to happen (i.e., food at 8 s or 48 s). Additionally, in some conditions, a brief stimulus signaled the response that had produced terminal-link entry. To separate sources of stimulus control during terminal links, we arranged conflicting trials in which signals provided incongruent information about trial outcomes. There were three main findings in this experiment. First, outcome value influenced stimulus control. Stimuli that signaled the more preferred (SS) outcome exerted stronger control than stimuli signaling the less preferred (LL) outcome. Second, past behavior competed with other stimuli for control over terminal-link responding. Our third finding was that control by past behavior and past signals declined across time and control by present signals—including by the passage of time itself—increased.

Our findings replicate Cowie et al. (2020) and Gomes-Ng et al. (2022), both of whom also arranged a concurrent-chains procedure with SS and LL outcomes that were sometimes signaled by red-fast and green-slow stimuli. Like us, both Cowie et al. and Gomes-Ng et al. found that initial-link choice was jointly controlled by outcome value and by a compound stimulus signaling the trial outcome and that past behavior exerted strong control over terminal-link responding. However, unlike these past studies—which arranged either no signals during terminal links (Cowie et al., 2020) or the same signals during initial and terminal links (Gomes-Ng et al., 2022)—we arranged *different* initial- and terminal-link signals in conflicting trials in the present experiment. This allowed us to examine how past behavior, past signals, and present signals combined to control responding during terminal links. The present findings provide further evidence that control by past discriminative stimuli (here, past behavior and past signals) may endure for some

time, even when such stimuli conflict with stimuli in the present (here, present signals; see also Cowie et al., 2017).

Outcome value influences stimulus control

The notion that stimulus control depends on outcome value is not new (see, e.g., Edwards et al., 2019; Laraway et al., 2003; Michael, 1993; Poling et al., 2020, for discussions). It is well established that the reinforcing or punishing effectiveness of an outcome depends on *motivating operations*—on conditions that alter the value of the outcome and the organism's motivation to respond for that outcome. For example, food deprivation establishes food as a valuable (and thus more effective) reinforcer and also increases the subject's motivation to respond for food reinforcers. As a result, stimuli that signal food availability exert stronger control over behavior than stimuli signaling other less valuable reinforcers (e.g., Bizo & White, 1995; Hull, 1933; Leeper, 1935; Ward & Odum, 2006; see Edwards et al., 2019, for a recent discussion on motivating operations and stimulus control).

Similarly, Cowie et al. (2020) showed that stimuli signaling more *preferred* outcomes exerted stronger control over choice than stimuli signaling less preferred outcomes. Our results replicate and extend these findings; here, preference for the signaled key in cued and conflicting trials was stronger when that key led to the more preferred (SS) outcome than when it led to the less preferred outcome (Figure 5). In terminal links, signaling the response that produced terminal-link entry in signaled-peck conditions had no effect on responding in Uncued-SS trials, whereas it did in Uncued-LL trials. This provides further evidence that past stimuli signaling the SS reinforcer exerted longer lasting control than did past stimuli signaling the LL reinforcer. Additionally, response rates in all types of terminal links peaked at around 8 s (although this peak was small in some trials or conditions), again suggesting control by stimuli signaling the more preferred SS outcome, even when other stimuli (past behavior or present signals) signaled a different outcome.

These findings have important implications for how we conceptualize the fundamental unit of behavior, which has traditionally considered the correlations between stimuli, behavior, and outcomes to be the critical determinant of stimulus control. Such correlations are certainly important for establishing discriminative control, but they do not (and cannot) operate in isolation from the organism (see also Killeen & Jacobs, 2017). Indeed, stimulus control depends on the organism's ability to accurately detect correlations between stimuli, behavior, and outcomes (e.g., Davison & Nevin, 1999). Even if such correlations are detected, a stimulus that signals outcome availability may only control behavior to the extent that the signaled outcome is valuable to (that is, wanted or needed by) the organism and to the extent

that the organism is sufficiently motivated to respond for that outcome. Thus, our findings join others in highlighting the importance of centering the organism within the three- (or four-, including the motivating operation) term contingency (see, e.g., Cowie et al., 2020; Dallery et al., 2015; Killeen & Jacobs, 2017; Poling et al., 2017).

The present experiment, together with Cowie et al. (2020) and Gomes-Ng et al. (2022), demonstrates the utility of the concurrent-chains procedure for investigating how outcome value modulates stimulus control. However, these three studies all arranged the same outcomes—two food deliveries after an 8-s delay or six food deliveries after a 48-s delay—so the extent to which outcome value influences stimulus control with other combinations of reinforcer magnitude and delay remains unclear. Future studies could manipulate the magnitude and delay ratios across conditions to investigate the replicability and generality of our results. This would provide further insight into the conditions under which outcome value does or does not influence stimulus control.

Reliable stimuli exert nonexclusive control

A growing body of evidence shows that exclusive (or selective) control by a single stimulus is rare. Even when a stimulus signals the definite location of the next reinforcer, choice is not necessarily exclusive toward that location (e.g., our Figures 3 and 4; Cowie et al., 2017, 2020; Davison & Cowie, 2025; Davison & Jones, 1998; Gomes-Ng et al., 2018, 2022). Likewise, in the present experiment, compound stimuli reliably signaled the key that would produce terminal-link entry in cued trials, yet initial-link choice never favored that key exclusively. Such nonexclusive preference may be an artifact of the procedure that we used to arrange terminal-link entry. We arranged a dependent VI schedule during initial links, and this may have reduced the likelihood of exclusive choice because the terminal-link-entry key was chosen by the schedule rather than by the subject (Stubbs & Pliskoff, 1969). In our view, it seems unlikely that the dependent VI schedule was responsible for nonexclusive choice in cued trials because in these trials the key producing terminal-link entry was definitively signaled; that is, there were effectively two types of cued trials—Cued-SS trials in which all terminal-link entries were produced by pecks to the SS key and Cued-LL trials in which all entries were produced by pecks to the LL key. Thus, unlike uncued trials, there was no need to respond to both schedules to determine which key would produce entry in cued trials. Alternatively, the absence of a changeover delay (a brief period between switch responses) may have resulted in the pigeons alternating their responses between the side keys (Stubbs & Pliskoff, 1969). This also seems unlikely given that other studies have found nonexclusive choice even with a changeover delay and when one alternative never delivers

reinforcers (Davison & Cowie, 2025; Davison & Jones, 1998).

Instead, nonexclusive choice despite the presence of reliable stimuli may reflect the effects of subjective outcome value, alongside adaptive constraints on choice (Cowie et al., 2020). To elaborate, exclusive choice may be fundamentally maladaptive because it limits the organism's exposure to the range of contingencies operating in the current environment. Conversely, nonexclusive choice ensures that the organism experiences the contingencies arranged at each alternative—for example, reinforcers at one alternative and their absence at another—and may also facilitate adaptation to changes in contingencies by ensuring that the organism can detect such changes when they occur. Thus, a tendency toward nonexclusive choice may have evolved to facilitate adaptation in dynamic environments. In other words, nonexclusive choice in experimental contexts may reflect the influence of the organism's evolutionary history (see Cowie et al., 2020; Racey et al., 2011, for related discussions).

Past behavior as a discriminative stimulus

To what extent did past behavior serve as a discriminative stimulus in the present experiment? Although the peak in responding at 8 s in Uncued-LL trials in un signaled-peck conditions (Figure 6) appears inconsistent with control by past behavior, the differences between the height of the peak in Uncued-SS and Uncued-LL trials indicate that past behavior exerted at least some control over responding (perhaps in combination with control by elapsed time, which signaled that food would occur at 8 s and 48 s). Control by past behavior was also evident in conflicting trials, with more prominent response peaks (SS-to-LL trials) or peaks closer to 8 s (LL-to-SS trials) when the SS key produced terminal-link entry than when the LL key produced entry. These patterns suggest that past behavior controlled responding even when other discriminative stimuli in the recent past or in the present signaled trial outcomes. In contrast, control by past signals was much less obvious. At first glance, this is somewhat surprising, especially given that past behavior was a more transient stimulus (a peck to the key producing terminal-link entry) than past signals, which were presented on the side keys for the entire initial-link duration.

Why did past behavior exert stronger control than past signals? One possibility is that egocentric stimuli, especially those involving a response to a side key (as in our procedure), may produce enduring differences in body positioning (e.g., orienting toward one side of the operant panel). Such differences in body positioning—which may arise incidentally when location-based responses are arranged—effectively bring the past behavior stimulus into the present and thus may be the

mechanism by which a past response continues to control present responding (Cowie et al., 2020; Gomes-Ng et al., 2019, 2022; Urcuioli, 1984, 1985; Weaver et al., 1999). If so, control by past behavior may be partly related to the arrangement of the operant panel in the sense that some arrangements may be more likely to promote changes in body positioning (e.g., if the left and right keys are farther apart). To test this, the distance between the left and right keys could be manipulated in a future experiment. If control by past behavior is stronger with farther distances between the keys, this would suggest that body position plays a role. Alternatively, to isolate the effects of the SS or LL response itself from the effects of body position, the keys could be arranged vertically (i.e., top and bottom) or non-location-based stimuli (e.g., colors) could be used to signal the SS and LL alternatives.

Another mechanism that may have contributed to strong control by past behavior in the present experiment is stimulus *reliability*. Stimuli that are, appear to be, or have in the past been more reliable predictors of reinforcers tend to exert stronger control over behavior (e.g., Davison, 2018; Davison & Elliffe, 2010; Dube & McIlvane, 1997; Gomes-Ng et al., 2023; McLinn & Stephens, 2006; Rubi & Stephens, 2016; Shahan & Podlesnik, 2006, 2007). In our procedure, trial outcomes were predictable based on past behavior in uncued and cued trials (i.e., all trials, except for the four conflicting trials in the latter 20 sessions of each condition), whereas past signals predicted trial outcomes only in cued trials (i.e., in about 50% of trials). That is, the pigeons effectively had double the experience with past behavior as a discriminative stimulus relative to past signals. Therefore, past behavior may have appeared to be a more reliable predictor of trial outcomes than past signals, resulting in stronger control by past behavior. To test this suggestion, a future replication of our study could arrange equal experience with past behavior and signals (e.g., by varying the proportion of uncued to cued trials) or could manipulate the relative reliabilities of past behavior and signals (e.g., by arranging trials in which these stimuli incorrectly signal trial outcomes). If these manipulations weaken control by past behavior, this would lend support to our suggestion that past behavior was indeed a more reliable predictor of trial outcomes than, and thus overshadowed control by, past signals in the current study.

A rapidly growing body of evidence shows that reinforcers are discriminative stimuli that signal future outcomes (see Cowie, 2018, 2020; Cowie & Davison, 2016, for reviews). Our findings add to this evidence by showing that behavior, too, may serve as a discriminative stimulus that competes with—and under some conditions, may completely overshadow—other stimuli (see also Davison, 2018; Killeen, 1978; Zentall et al., 2008). Similar results were reported by Davison (2018), who recently demonstrated that behavior–reinforcer contingencies compete with external stimuli for control in much

the same way as two external stimuli may compete for stimulus control. The implication here is that when both stimuli and behavior are differential with respect to reinforcer availability—as, for example, in a concurrent schedule where different stimuli and behaviors may be correlated with different reinforcer rates—there is a trade-off between control by the stimulus–reinforcer relation and by the behavior–reinforcer relation (Davison, 2018).

Shifting stimulus control from past to present

Stimuli in the past can only continue to control behavior to the extent that they can be accurately remembered. When such stimuli are forgotten, control typically shifts toward other discriminative stimuli in the present (e.g., Cowie et al., 2011, 2017). Here, control by past behavior was most apparent during the first 10 to 12 s of terminal links, after which present signals and elapsed time appeared to control responding. The strength of control by present signals at later times (i.e., after 12 s) appeared to depend on their congruency with elapsed time, which also provided some signal about the likelihood of a reinforcer occurring. To elaborate, consider the times at which reinforcers were delivered in our procedure (8 s and 48 s). Stimuli that signaled SS outcomes were only ever presented for about 8 s (because the reinforcer was then delivered), whereas stimuli signaling LL outcomes were present at both 8 s and 48 s. Thus, the pigeons had experience with long presentations of the LL signal but not with the SS signal. As a result, in conflicting trials, a present LL signal at later times was congruent with elapsed time (SS-to-LL trials), whereas a present SS signal at later times was incongruent with elapsed time (LL-to-SS trials).

Signaling past behavior appeared to prolong control by past behavior only when present signals conflicted with elapsed time (Figure 7). Why did past behavior appear to exert enduring control in LL-to-SS trials in signaled-peck conditions but not in the other trials or conditions? It seems unlikely that memory for past behavior was superior in LL-to-SS trials in signaled-peck conditions. There is no a priori reason why past behavior would be more memorable in those trials than in other trials or conditions. The differential responding at later times in LL-to-SS trials in signaled-peck conditions may reflect the influence of another egocentric cue: response rates. Response rates at about 12 s were still differential with respect to past behavior in LL-to-SS trials in signaled-peck conditions but not in the other trials or conditions. Therefore, response rates themselves may have served as an additional discriminative stimulus guiding future responding (in a sense, “continue responding at this low (or high) rate”; see e.g., Urcuioli, 1984, 1985, for examples of response patterns as discriminative stimuli). These findings tentatively suggest that when stimuli in

the present provide conflicting information about future outcomes, other stimuli may incidentally come to control behavior, perhaps because such incidental stimuli help to reduce the degree of uncertainty about future outcomes (Dall & Johnstone, 2002; Dall et al., 2005).

Conclusions

Stimulus control appears to be somewhat subjective in nature. It depends on the value of the outcome to the organism; on what the organism discriminates about stimulus–behavior–outcome relations; and on the organism’s ability detect other apparently relevant stimuli, including remembered discriminative stimuli from the recent past. Our findings serve as an important reminder not to overlook the organism’s disposition, sensory or memory capacities, and learning history. Some or all of these may dictate which stimuli exert the strongest control over behavior. Moreover, it is rare that a single stimulus will ever exert total exclusive control over behavior. Instead, other stimuli in the environment, whether deliberately or incidentally arranged, may also exert some control.

Our findings clearly highlight the importance of considering the discriminative properties of the organism’s own behavior. Our findings add to the evidence suggesting that behavior itself is a particularly salient stimulus that may overshadow control by other exteroceptive stimuli. Perhaps this is because emitting an operant behavior requires some degree of attending to that behavior, whereas external stimuli often require the organism to orient toward and observe the stimulus (Dinsmoor, 1985). More colloquially, the organism’s own behavior is probably more difficult to ignore than a localized visual stimulus. Furthermore, after emitting a behavior (e.g., a left-key response), other egocentric stimuli, such as body positioning or the current rate of responding, may help to bridge the gap between the behavior and the outcome, whereas such bridging may not necessarily occur with an external stimulus (see also Wiles et al., 2023). Therefore, even when behavior is not intentionally arranged to be a discriminative stimulus, discriminative control may develop—and compete with control by other, arranged external stimuli—if behavior is differential with respect to outcomes. This corroborates previous research demonstrating that stimulus control is not limited to the physical properties of a stimulus (e.g., color) but may also include its spatial or temporal location as well as behavior directed toward that stimulus (e.g., Iversen, 1997; Iversen et al., 1986; Lionello & Urcuioli, 1998; Urcuioli, 2008).

Thus, although researchers or practitioners of behavior analysis may arrange external stimuli to signal contingencies (e.g., key colors, verbal prompts), a precise understanding of how those stimuli affect behavior requires considering the range of *other* stimuli that are present within the broader environment as well as stimuli that may be generated by the

subject themselves (i.e., egocentric stimuli). Indeed, stimulus control is likely to be divided between the various stimuli in the present or the recent past that are, or appear to be, differential with respect to outcomes. Such division may be adaptive, reducing uncertainty about future outcomes and ensuring outcomes can still be predicted even if one stimulus changes or disappears from the environment (Dall et al., 2005; Dall & Johnstone, 2002). Of course, this divided control also can reduce (or eliminate) control by researcher- or practitioner-arranged stimuli (see Rincover & Koegel, 1975, for an applied example). Thus, the stimuli that we expect to control behavior may not necessarily be the stimuli that control behavior the most strongly (or, in extreme cases, at all).

AUTHOR CONTRIBUTIONS

Stephanie Gomes-Ng and Tess Austin share first authorship for this article.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS APPROVAL

This experiment was conducted under Approval 001396, granted by The University of Auckland Animal Ethics Committee.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDIX A

A.1 Terminal-link response rates for individual pigeons

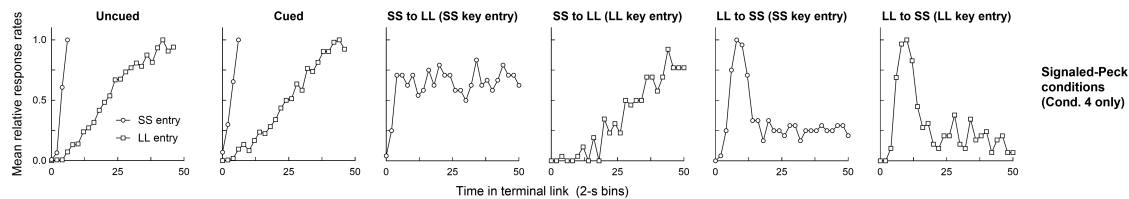


FIGURE A1 Terminal-link responding for Pigeon 111 (Condition 4 only). Circles show data from trials in which the SS key produced entry, and squares show data from trials in which the LL key produced entry. Unfilled data points show data from replication conditions (i.e., Conditions 2 and 4). The top row shows data from unsigned-peck conditions, and the bottom row shows data from signaled-peck conditions. Pigeon 111 only completed Condition 4.

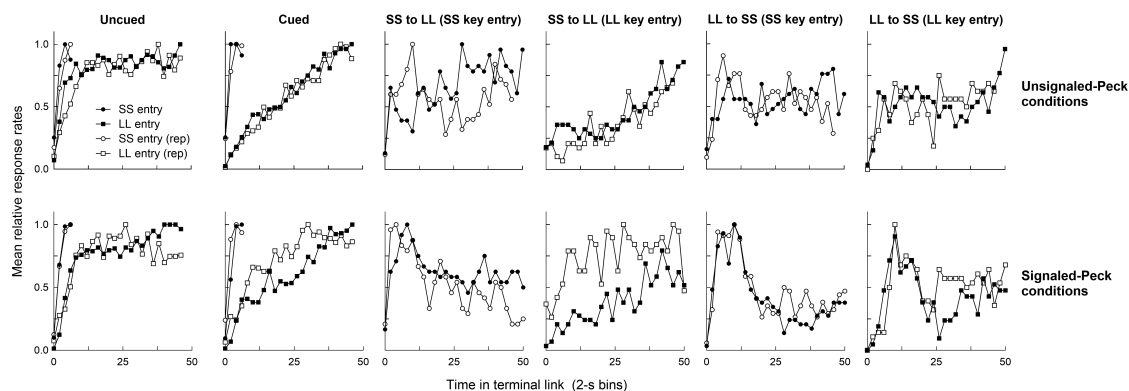


FIGURE A2 Terminal-link responding for Pigeon 112. Circles show data from trials in which the SS key produced entry, and squares show data from trials in which the LL key produced entry. Unfilled data points show data from replication conditions (i.e., Conditions 2 and 4). The top row shows data from unsigned-peck conditions, and the bottom row shows data from signaled-peck conditions.

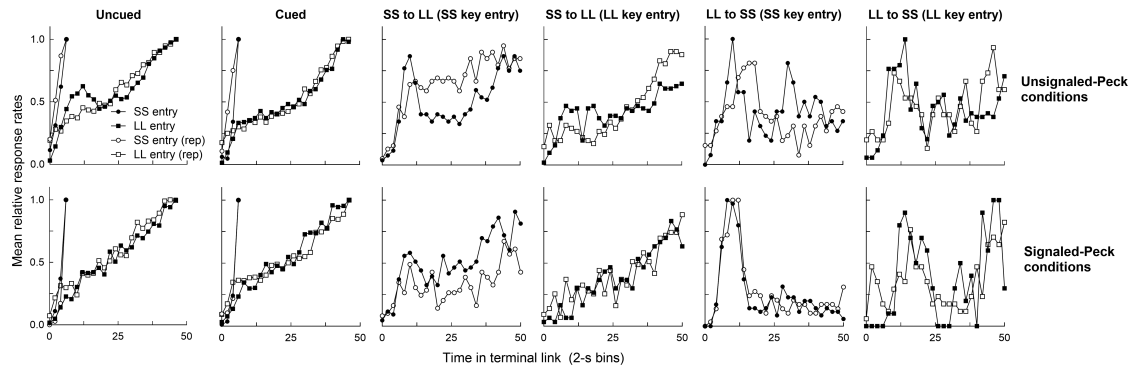


FIGURE A3 Terminal-link responding for Pigeon 113. Circles show data from trials in which the SS key produced entry, and squares show data from trials in which the LL key produced entry. Unfilled data points show data from replication conditions (i.e., Conditions 2 and 4). The top row shows data from unsigned-peck conditions, and the bottom row shows data from signed-peck conditions.

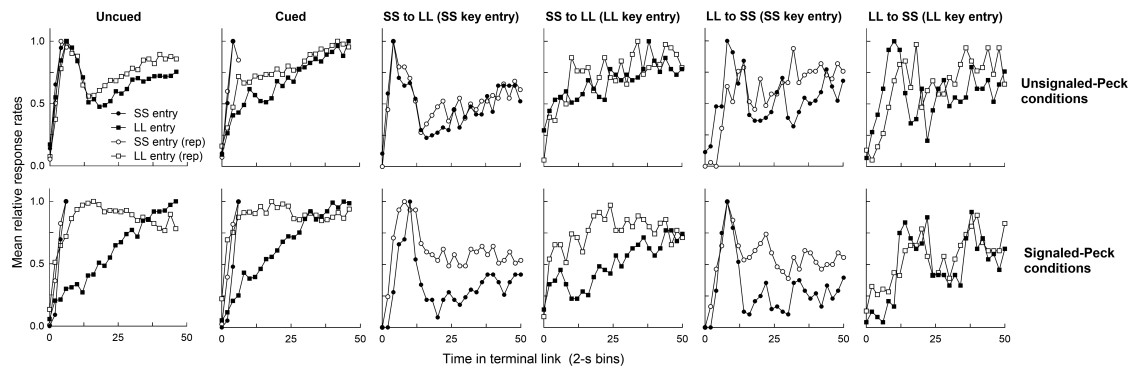


FIGURE A4 Terminal-link responding for Pigeon 114. Circles show data from trials in which the SS key produced entry, and squares show data from trials in which the LL key produced entry. Unfilled data points show data from replication conditions (i.e., Conditions 2 and 4). The top row shows data from unsigned-peck conditions, and the bottom row shows data from signed-peck conditions.

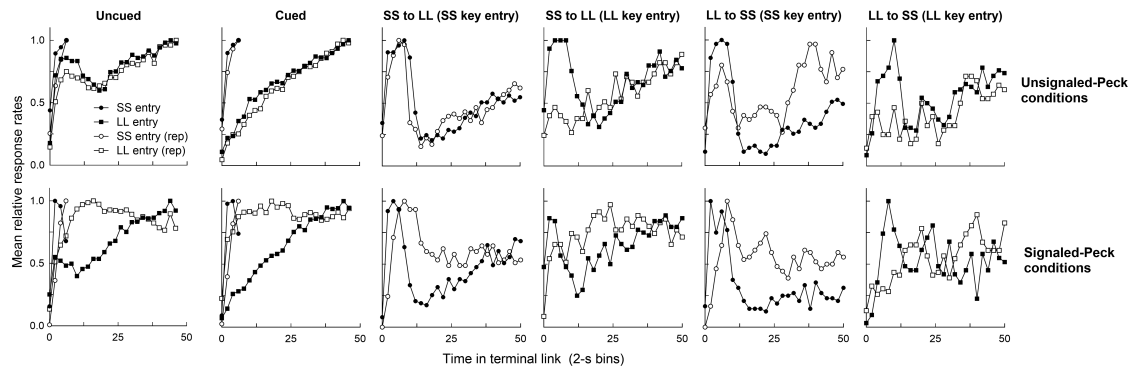


FIGURE A5 Terminal-link responding for Pigeon 115. Circles show data from trials in which the SS key produced entry, and squares show data from trials in which the LL key produced entry. Unfilled data points show data from replication conditions (i.e., Conditions 2 and 4). The top row shows data from unsigned-peck conditions, and the bottom row shows data from signed-peck conditions.

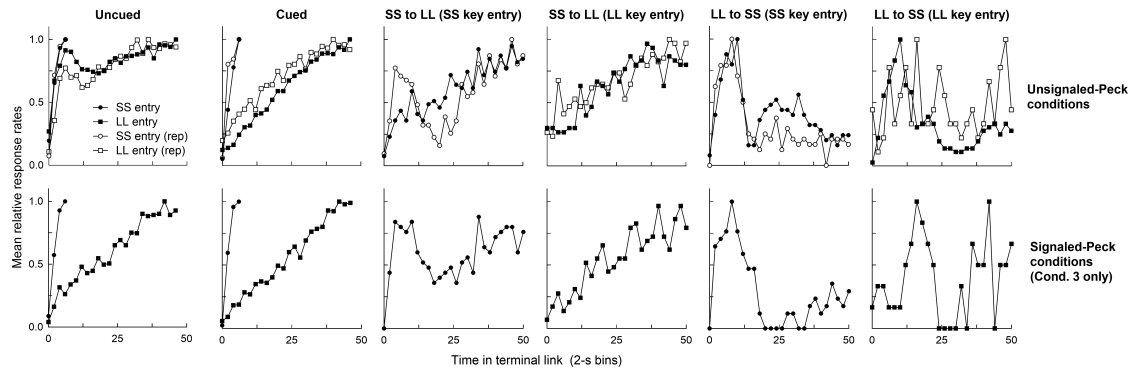


FIGURE A6 Terminal-link responding for Pigeon 116 (Conditions 1 to 3 only). Pigeon 116 only completed Conditions 1 to 3. Circles show data from trials in which the SS key produced entry, and squares show data from trials in which the LL key produced entry. Unfilled data points show data from replication conditions (i.e., Conditions 2 and 4). The top row shows data from unsigned-peck conditions, and the bottom row shows data from signaled-peck conditions.