Pigeons in Control of their Actions:

Learning and Performance in Stop-Signal and Change-Signal Tasks

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Abstract

In human participants, two paradigms commonly assumed to measure the executive-control processes involved in response inhibition are the Stop-Signal and Change-Signal tasks. There is, however, also considerable evidence that performance in these tasks can be mediated by associative processes. To assess which components of inhibitory response control might be associative, we developed analogues of these two tasks for pigeons. We trained pigeons to peck quickly at one of two keys of different colours to obtain a food reward. On some trials, the rewarded key was replaced (after a varying interval) by a signal of a different colour. For some birds, this was a Change Signal: pecking the signal had no effect, but pecking the usually unrewarded alternative key led to a reward, so the response had to be changed. For other birds, the change in colour was a Stop Signal: pecking the alternative key remained ineffective, but pecking the signal now led to a timeout instead of the usual reward, so responses had to be withheld. Pigeons succeeded in both tasks, but performance declined with increasing signal delay. The details of performance in both tasks were consistent with the independent horse-race model of inhibitory control often applied to studies of human participants. This outcome further suggests that stop-signal tasks of the kind used here might not be suitable for assessing top-down executive-control processes in humans.

Keywords: stop-signal task, inhibitory control, associative learning, pigeons

Response inhibition has recently become a topic of general interest because it is seen as a core feature of executive control. One of the most prominent models of the mechanisms underlying response inhibition is the independent horse-race model (Logan & Cowan, 1984; Verbruggen & Logan, 2008b, 2009b), which postulates that initiating a response and withholding a response are two independent processes that are triggered by the presentation of, respectively, a stimulus demanding the response, followed by a signal not to respond. Performance depends on the outcome of the "race" between these two processes - the process that is completed first determines whether the response is performed or stopped; an example of different outcomes of this race is shown in Figure 1. Verbruggen and Logan (2009b) successfully applied the independent horse-race model to several paradigms in which the response to the Go stimulus had to be withheld: one such paradigm is the Stop-Signal task, in which any response has to be inhibited so that no response of any kind is made. Another is the Change-Signal task, in which the occurrence of the signal indicates that an alternative response has to be executed instead. For example, in a Stop-Signal task, subjects might be instructed that a green dot will repeatedly be presented on screen, and that they should mouse-click on this green dot as soon as it appears. However, on some trials, the green dot might change to a red colour shortly after the start of the trial. If this happens, the subjects should withhold any response and instead wait for the trial to end. In a Change-Signal task, subjects might be instructed, when seeing the red dot, not to mouse-click on that dot but instead to move the mouse and click on a different target. In both these tasks, the appearance of a signal to inhibit a prepared response might activate global stopping processes (Mostofsky & Simmonds, 2008; Verbruggen & Logan, 2009b; Kenner, Mumford, Hommer et al., 2010; Boecker, Gauggel, & Drueke, 2013), regardless of whether that signal indicates that any response should be withheld or that the initial response has to be replaced by a different response. In the latter case, according to the model, the alternative response is prepared after the global inhibition process has been completed.

Interestingly, the horse-race model makes no assumptions about the involvement of executive control in response inhibition - and in fact, it has been proposed that response inhibition

in Stop-Signal and Change-Signal paradigms may be mediated (at least in part) by associative processes. In several studies, Verbruggen and colleagues (Verbruggen & Logan, 2008a, 2009a; Verbruggen, Best, Bowditch, Stevens, & McLaren, 2014; Best, Lawrence, Logan, McLaren, & Verbruggen, 2015) presented evidence that a stimulus that was consistently paired with the command to withhold a response eventually elicited automatic response inhibition. They argued that the effect could occur either because that stimulus became associated with the subsequent occurrence of the stop signal (and was thus indirectly associated with stopping), or because the stimulus became directly associated with the process that stopped the response. But if response inhibition in reaction to a signal can potentially be mediated via associative learning, can Stop-Signal and Change-Signal paradigms be regarded as valid instruments for measuring executive control? If associations played some part in response inhibition, even if it is limited in scope, the behaviour that is observed in such paradigms could not unambiguously be attributed to executive processes.

Executive functions are crucial for the planning of actions, which demands the ability to anticipate and select appropriate responses. Therefore, executive control - although perhaps not crucial for being able to react to a signal - might be necessary for the proactive preparation for the possibility that a response will have to be withheld. Bowditch, Verbruggen, and McLaren (2015) however found evidence to the contrary. They tested whether response inhibition could be cued associatively by presenting a range of coloured stimuli at the start of a trial; unbeknownst to their participants, these colour cues predicted the likelihood of a stop signal in the upcoming trial. Their results indicated that associations with stopping could extend to these cues: seeing the cue alone might indirectly facilitate or even directly initiate a stopping response even before any stop signal has appeared. Thus, as associative processes can affect response inhibition in advance of a signal, it is plausible that also behaviour that seemingly involves proactive planning might be, in some circumstances, reduced to associative processes.

Under conditions in which humans employ more reflective processes, pigeons have repeatedly demonstrated responding purely on the basis of stimulus-response associations (Lea,

Wills, Leaver et al., 2009; Meier, Lea, Forrest, Angerer, & McLaren, 2013; Meier, Lea, & McLaren, 2016a, 2016b; Wills, Lea, Leaver et al., 2009). Therefore, we assumed that their performance in Stop-Signal and Change-Signal tasks would also be governed mainly by associative processes. In the present experiment, we trained pigeons to perform a Stop-Signal or Change-Signal task similar to the tasks described above. We examined three questions:

Firstly, do the predictions of the independent horse-race model (see Figure 1) apply to the performance of pigeons? That is, does the model capture the effects of associative processes involved in response inhibition (even though it does not explicitly set out to do so)? Specifically, the independent horse-race model makes the following predictions (Verbruggen & Logan, 2009b):

- The probability that a response is incorrectly made in trials in which a signal is presented (henceforth referred to as Signal trials) is expected to increase with increasing interval between presenting the stimulus that indicated that a response should be executed and the arrival of the signal indicating it is now necessary to withhold that response. In the case of our study, we expect pigeons to show accurate response inhibition if the signal is presented shortly after the beginning of a trial, but to become increasingly less able to withhold or change their response as the interval between the appearance of the green dot at the start of a trial and its subsequent change to a red colour increases.
- In terms of response times, it is expected that these will be longer in Go trials, in which no signal appears and the prepared response is performed, compared to those performed incorrectly on Signal trials. Erroneous responses in Signal trials will primarily be made before or very shortly after the Stop signal appears, as a consequence of the process that initiates a response being completed before the inhibition process to stop the response. Pigeons will have more time to respond to the green dot on Go trials compared to Signal trials, in which the available time is limited by the change of the green dot to red.
- Similarly, the mean response time in Signal trials is expected to increase as the interval between the presentation of the stimulus indicating the requirement to make a response

and the presentation of the Stop signal increases. Specifically, the pigeons should become slower on average to make an (erroneous) response as the interval increases between the start of the trial with the presentation of the green dot and the appearance of the red dot signalling inhibition. As false responses to the green dot would mainly occur before or very shortly after the red signal appears, a longer interval would increase the time available to make an incorrect response before the signal appears, and in turn allow the response-time average to increase.

Secondly, we aimed to discern the limits of associative processes in mediating response inhibition. Provided that reactive response inhibition following a signal can be accomplished associatively, can the same be assumed about cued inhibitory control? If we present a cue that is stochastically related to the outcome (stopping or not stopping), will this cue come to deliver associatively-mediated inhibition in a similar fashion to that observed in experiments with humans (Bowditch et al., 2015)?

Lastly, we examined whether our assumptions about the involvement of associative processes in response inhibition also apply to Change-Signal tasks, in which the occurrence of the signal indicates that an alternative response has to be executed instead. Since Stop-Signal and Change-Signal tasks often use the same stimuli and very similar procedures, it seems logical to assume that they both involve the same inhibition mechanisms - the Change-Signal task has even been described as a mere "complication of the Stop-Signal paradigm" (Logan, 1994), in that stopping is followed by an additional process of initiating an alternative response. However, despite considerable support for this view, there are voices advocating two different response-inhibition processes as governing Stop-Signal and Change-Signal performance. Since one task requires the complete suppression of a response, whilst the other task requires the execution of an alternative action, Change-Signal tasks might elicit different inhibition processes than those involved in the mere stopping of a response (De Jong, Coles, & Logan, 1995; Aron & Verbruggen, 2008; Krämer, Knight, & Münte, 2010; Schall & Godlove, 2012; Boecker et al., 2013; Gulberti, Arndt, & Colonius,

2014) potentially making the Change-Signal task more cognitively demanding (or even requiring a level of cognitive control that pigeons are incapable of). Another possibility is that associative processes might facilitate performance in Change-Signal tasks such that the presentation of the Change signal immediately triggers the execution of the alternative response without the need to inhibit the Go response, so that only performance in the Stop-Signal task is entirely reliant on a response-inhibition process, while performance in the Change-Signal task is not. Verbruggen and Logan (2009b) claimed that the independent race model fitted their data from both Stop-Signal and Change-Signal paradigms, supporting the idea that they involve a common mechanism. We sought to test this claim in a novel subject species by assessing whether pigeons would show comparable levels of performance in the Stop-Signal and the Change-Signal tasks.

Methods

Subjects

Twelve pigeons (*Columba livia*) took part in this experiment. They were obtained as discards from local fanciers. Pigeons were housed together with other pigeons in an indoor aviary (2 x 1 x 2.5m) and were maintained at or above 80% of their free-feeding weight. The pigeons had previously taken part in unrelated studies but were naïve to the stimuli and the procedure of this experiment. Six pigeons completed the Stop-Signal task, the other six pigeons completed the Change-Signal task.

Apparatus

The pigeons were tested in eight identical 71x50.5x43.5cm operant chambers. Each pigeon was always tested in the same chamber. One of the long walls of the chamber was fitted with a 31x23.5cm (15") touch monitor (Model 1547L 1024x768 pixels TFT monitor, 0.3mm per pixel, CarrollTouch infrared detector, ELO Touchsystems Inc.) mounted 12cm above the grid floor of the chamber. Two 2.8-Watt white houselights were mounted to either side above the screen; below the screen, mounted 4cm above the chamber floor and directly below each house light, two 6x5cm apertures gave access to grain hoppers when solenoids were activated. The food hoppers were

illuminated by a 2.8-Watt light when activated and contained a 2:1 mixture of hemp seed and conditioner. A 50-Ohm loudspeaker mounted between the two food hoppers played white noise into the box and also indicated all effective pecks to target areas on screen with an immediate feedback beep. The interior of the box was monitored by a video camera attached to the short wall of the chamber opposite the chamber door. Contingencies were controlled and data collected using a PC computer running the Whisker system (Cardinal & Aitken, 2010), with client programs written in Microsoft Visual Basic.

Terminology

The following descriptions are used for different images presented to the subjects:

Go stimulus - One of two simultaneously presented response keys; for 7 pigeons, this key was filled in green, and for 5 other pigeons, it was filled in red. On Go trials, pecking the Go stimulus delivered a food reward. On Signal trials, the Go stimulus was eventually replaced by the Signal.

Signal - Also Stop Signal or Change Signal, depending on the relevant task. On Signal trials, the colour of the key presenting the Go stimulus changed from green to red (or from red to green depending on the colour assignments for the subject) after a variable stop-signal onset (SSO) interval. The occurrence of the Signal indicated that either, for the Stop-Signal task, no response should be carried out, or, for the Change-Signal task, instead of the key presenting the Signal/former Go stimulus, the alternative key could be pecked to obtain a food reward.

Go/Signal key - One of two keys presented on screen, which carried the Go stimulus/Signal.

Alternative key - A yellow key that was presented simultaneously with the Go/Signal key. In the Change-Signal task, it served as a pecking alternative to the Go/Signal key and pigeons could obtain a food reward if it was pecked in Change-Signal trials. In the Stop-Signal task, pecking it had no scheduled consequences.

Go response - Pecking the Go stimulus.

Go trial - A trial in which the Go stimulus was presented and the Go response had to be performed to obtain a food reward.

Signal trial - Also Stop-Signal trial or Change-Signal trial, depending on the relevant task. A trial in which the Go stimulus was eventually replaced by the Signal, indicating that the Go response should not be performed. Signal trials were further split into no-delay trials (in which the Signal appeared immediately at the start of the Signal trial) and delayed trials according to the relevant SSO.

SSO - Stop-Signal Onset interval. One of three intervals after which the Go stimulus was replaced by the Signal in Signal trials. The interval after which the Signal replaced the Go stimulus was either 25%, 50%, or 75% of the pigeon's mean Go-trial response time.

Go Cue - One of three cues presented before the start of a trial, which indicated that the following trial was likely to be a Go trial.

Neutral Cue - One of three cues presented before the start of a trial, which had no predictive value about the type of trial that followed.

Signal Cue - A cue presented before the start of a trial, which indicated that the following trial was likely to be a Signal trial.

Trial Procedure

The procedures of the Stop-Signal and the Change-Signal tasks were for the most part identical, with the critical difference being in the way responses were reinforced in signal trials; Figure 2 illustrates the trial procedure and reinforcement contingencies for the two tasks. In the full Change-Signal and Stop-Signal tasks (as shown in Figure 2), each trial began with the presentation of a white start key (75 pixels in diameter) presented in the centre of a black display to focus attention on the screen. Following two pecks at the start key, it was replaced by a smaller circular key (50 pixels in diameter) in the display centre that varied in appearance, to serve as a cue (its function is described below). A peck at this cue led to the addition of two circular response keys (each 50 pixels in diameter), whose centres were offset by 50 pixels to the left and the right side of the centre of the still visible cue. One of these keys, henceforth referred to as the Go/Signal key, was filled in red or green. For seven pigeons, green indicated that the current trial was a Go trial and red indicated a

Stop or Change trial; for the remaining five pigeons, the colour assignment was reversed. The other key was yellow and served as a pecking alternative to the red or green Go/Signal key. The locations of the Go/Signal key and the alternative key (left or right) were counterbalanced across trials.

Task Acquisition

Before performing the full task, pigeons went through several training stages to learn the correct response to each part of the task. During all training sessions, pecking the start key led directly to the presentation of the two response keys; that is, the cue was omitted from the display entirely during training.

Go Training. First, the pigeons received Go-training sessions, each consisting of 64 Go trials. A single peck at the Go stimulus resulted in the deletion of the stimulus display from the screen and presentation of a white reward key (75 pixels in diameter), which was centred 100 pixels from the lower edge of the screen and 100 pixels from the side of the screen that was closest to the stimulus. The purpose of the reward key was to position the subject close to the food magazine mounted below and to the side of that reward key. One peck at the reward key led to immediate access to that food magazine for 2.5 seconds; then, the next trial started after an inter-trial interval of 10 seconds. Pecks at the yellow alternative key had no scheduled consequences. If no pecks at the Go stimulus were made during the display presentation interval, the trial was terminated and the next trial started after the usual inter-trial interval.

Initially, the response display containing the Go/Signal key and alternative key was presented for 20 seconds in each trial. When overall performance in a session reached 85% or above (i.e., making a peck at the Go/Signal key in at least 55 of the 64 trials), the presentation time of the stimulus display was decreased in the following session; this was repeated systematically to reduce the presentation time from 20 seconds to 10, 8, 6, 4, 3 to 2.5 seconds as the lowest possible value. If performance was below 70% overall in a session, the presentation time was increased by a second for the following session. After an increase, the value was decreased again if the pigeon completed the next two sessions above 85%. Otherwise, training continued at the increased value until the

pigeon performed at 80% or above in two consecutive training sessions to pass this training stage. The stimulus presentation interval at which a pigeon passed the Go training was used as the stimulus presentation interval for all following sessions for that pigeon; the values are summarised in the Results section.

Go/Stop and Go/Change Training. Once the Go-training pass criterion was met, pigeons completed twenty Go/Stop or Go/Change training sessions. These sessions each consisted of 32 Go trials and 32 Stop-Signal or Change-Signal trials, presented in random order. While only one peck led to the presentation of the reward key during the Go training to facilitate task acquisition, now, two pecks at the Go stimulus were required in Go trials to obtain the reward key, because the first peck to the Go/Signal key (or any other key) might have been ballistic, i.e. launched irreversibly before the relevant stimulus appeared. If fewer than two pecks were made at the Go stimulus within the stimulus presentation interval, the trial was terminated and the next trial started after an inter-trial interval of 10 seconds. Any pecks at the yellow alternative key were ineffective on Go trials.

For reasons that will become apparent below, the remaining trials under these conditions will be referred to as no-delay Stop-Signal and no-delay Change-Signal trials. In these trials, instead of the Go stimulus, the Stop or Change signal was presented on the Go/Signal key; reinforcement contingencies varied between the Stop-Signal and the Change-Signal task.

In the Stop-Signal task, if a pigeon made no or only a single peck at the Signal on the Go/Signal key during the stimulus presentation interval, the trial terminated after completion of this interval and a new trial started after an inter-trial interval of 10 seconds. If the pigeon made a second peck at the Stop signal, it entered a delay period in which the signal remained on screen for four times the duration of the stimulus presentation interval (i.e., if the pigeon's stimulus presentation interval was 3 seconds, the delay period was set to 12 seconds), before the trial was terminated and a new trial started after an inter-trial interval of 10 seconds. During this delay period, pecking the Go/Signal key had no effect. The six pigeons completing the Stop-Signal task

reliably responded to at least 80% of Go trials and withheld a response on at least 80% of no-delay Stop-Signal trials at the end of the twenty training sessions.

In no-delay Change-Signal trials, two pecks at the yellow alternative key resulted in the immediate deletion of the response display and the presentation of the reward key closest to the alternative key, followed by access to the respective food magazine for 2.5 seconds before entering the inter-trial interval of 10 seconds. Any pecks at the Change signal presented on the Go/Signal key were ineffective for the duration of the display presentation interval; if one or no pecks at the alternative key were made during this interval, the trial was terminated and the next trial started after an inter-trial interval of 10 seconds. The six pigeons in the Change-Signal task successfully pecked the Go stimulus on at least 80% of Go trials and pecked the alternative key on at least 80% of no-delay Change-Signal trials by the end of the twenty training sessions.

Signal Training. Following the Go/Stop and Go/Change training, pigeons were given ten sessions in which, in addition to Go and no-delay Signal trials, they also experienced Signal trials in which the appearance of the signal was delayed. In these trials, after pecking the start key, the Go stimulus was initially presented on the Go/Signal key; it was subsequently replaced by the Stop or Change signal after one of three defined intervals (conventionally referred to as Stop-Signal Onset, or SSO, intervals): they were set to 25%, 50% and 75% of a pigeon's mean Go-trial response time (measured from the onset of the stimulus display to the second consecutive peck at the Go/Signal key or, for the Change-Signal task, the alternative key) in the previous session. That is, the absolute values of the SSOs in a given session depended on the pigeon's performance in the previous session; it could thus change from one session to the next. We established this tracking procedure in an effort to estimate the pigeons' ability to withhold a response at different stages of response preparation better than would be possible using arbitrarily chosen, fixed values, which might be too short or too long to necessitate any potential inhibitory control. Each of the three SSOs occurred equally often. The onset of the Stop or Change signal indicated that any pecking response towards the Go/Signal key should be withheld. If the Go/Signal key was pecked twice before the signal

appeared, the signal was presented and the response was coded as an incorrect response. Similarly, if, in the Change-Signal task, the alternative key was pecked twice before the signal onset, it was coded as a correct response; the second peck led to the immediate presentation of the reward key.

Each of the ten 64-trial Signal-training sessions consisted of 48 Go trials, four no-delay Signal trials, four 25%-delayed Signal trials, four 50% delayed Signal trials and four 75%-delayed Signal trials; that is, 75% of all trials were Go trials.

Cued Stop-Signal and Change-Signal Task

Following the Signal training sessions, the pigeons completed 30 further Signal sessions in which cues were presented prior to and during the stimulus display, as shown in Figure 2. As in the work of Bowditch et al. (2015), the cue predicted the likelihood of the occurrence of a signal on this trial. There were three distinct cues (see Table 1): the 'Go Cue' indicated that the trial that followed was most likely to be a Go trial. The Go Cue preceded 18 Go trials, three no-delay Signal trials and three delayed Signal trials (each one with a different SSO); that is, 75% of the trials following a Go Cue were Go trials and 25% were Signal trials. The 'Neutral Cue' indicated a 50% probability of a Go or Signal trial; it preceded twelve Go trials, six no-delay Signal trials and six delayed Signal trials (two trials of each SSO). Finally, the 'Signal Cue' indicated that the next trial was most likely to be a Signal trial. The Signal Cue preceded six Go trials, nine no-delay Signal trials and nine delayed Signal trials (three trials of each SSO); that is, 75% of the trials following this cue were Signal trials and 25% were Go trials.

The Go and Signal Cues were composed of vertically or horizontally orientated Gaussian grating patterns of high (21 cycles per 100 pixels) or low (7 cycles per 100 pixels) spatial frequency, 50 pixels in diameter. All four possible combinations of horizontal/vertical orientation of the grating and low/high spatial frequency were used and counterbalanced across pigeons such that the two cues that indicated either a 25% or a 75% likelihood of a Stop Signal on the current trial did not share any identical visual dimensions. For example, if one of the cues was made up of a horizontal grating pattern with a low spatial frequency, the complementary cue was a vertical pattern with a high

spatial frequency grating. The Neutral Cue that indicated a 50% likelihood of an upcoming Signal trial was always uniformly filled with grey. A single peck at the cue led to the addition of the Go/Signal key and alternative key to the display. From here on, the trial procedure matched that of an un-cued Signal trial as described for the Signal training sessions, with the exception that the cue remained visible on screen.

To highlight the function of the cues, the number of no-delay Signal trials was increased from ca. 6% of trials in the un-cued Signal training sessions to 25% of all trials in the cued sessions. Further, the ratio of Go trials was decreased to 50% of all trials in these sessions, to limit the overall duration of a session whilst presenting a sufficient number of Signal trials. Thus, each cued session consisted of 36 Go trials, 18 no-delay Signal trials and 18 delayed Signal trials.

Data Collection

To assess whether the predictions made by the independent horse-race model about the duration of Go and Stop processes apply to the behaviour of pigeons, and to examine the potential effect of cue information on the pigeons' ability to inhibit a response, we recorded the pigeons' error rates in response to each type of trial. Correct responses were defined as follows: for Go trials, pecking the Go/Signal key twice in succession (for Go trials in the Change-Signal task, doing so without previously pecking the alternative key); for Signal trials in the Stop-Signal task, pecking the Go/Signal key once or not at all; for Signal trials in the Change-Signal task, pecking the alternative key twice in succession without previously pecking the Go/Signal key. All other responses (including, in the Change-Signal task, missing responses) were coded as errors.

We also recorded response latencies of the first and the second peck, including the identity of the key that was chosen at the first and second peck. For the Change-Signal task, we additionally recorded the number of pecks at the alternative key and the latencies of the first and second peck at that key. Note that, although we collected information about the first peck at a key, we followed our previous practice in research with pigeons (e.g., Meier, Lea, & McLaren, 2016a, b) and focussed our analyses on the second consecutive peck (henceforth referred to as the "critical peck") made

towards a key, since the first peck to it might have been of a ballistic nature and thus not target-specific.

Results

The pigeons completed the Go training in a mean of 14 sessions (range: 7 to 28 sessions). Final stimulus presentation intervals ranged from 2.5 to 4 seconds for pigeons in the Stop-Signal group and from 4 to 5 seconds for pigeons in the Change-Signal group.

Signal-Dependent Performance

Conventionally, the human response-inhibition literature considers the probability of incorrectly responding on Signal trials, P(respond), and the latency to make a correct response to the Go stimulus on Go trials, to be the most informative measures of performance in stop-signal and change-signal paradigms. In the Stop-Signal task, the former measure, P(respond), is identical to the pigeons' error rates on Signal trials, which we report below. Change-Signal error rates additionally include trials in which fewer than two consecutive pecks at either key were made; therefore, we recoded Change-Signal trials in which no response was made as correct, to obtain a measure of P(respond) on Change-Signal trials. We used the recoded values of P(respond) in all subsequent analyses of error rates. For completeness however, we report both the uncorrected error rates that include trials with missing responses and P(respond), as the probability of responding to the incorrect key instead of the correct key, in Table 2.

Our analyses concentrate on the sessions of the cued Stop-Signal and Change-Signal tasks. Descriptive statistics for all dependent variables are summarised in Table 2. As part of our analyses focussed on response latencies, we assessed the skewness of the subset of data for which we had the most valid data points and therefore the most information about their distribution, namely the response latencies for Go trials (excluding trials in which no response was made). The data were moderately positively skewed in both the Stop-Signal (skewness of .81) and the Change-Signal group (skewness of 1.19). Therefore, we transformed all latency data to their natural logarithms before running the statistical analyses described below.

We analysed error rates and latencies to peck the Go/Signal key in Go trials, no-delay Signal trials and delayed Signal trials in two repeated-measures ANOVAs using Trial Type (Go, no-delay Signal, 25%-delayed Signal, 50%-delayed Signal, 75%-delayed Signal) as a within-subjects factor and Task (Stop-Signal or Change-Signal) as a between-subjects factor. For the Change-Signal task, we also recorded the latencies to peck the alternative key, which allowed us to compare the latencies to peck the correct key across trial types, using a repeated-measures ANOVA with Trial Type as a within-subjects factor. Where applicable, the reported results were subject to Huynh-Feldt corrections.

Errors in Go and Signal trials. Error rates (representing P(miss) on Go trials and P(respond) on Signal trials) are illustrated for each task in Figures 3A and 3B. They did not differ between the Stop-Signal and the Change-Signal tasks, $F(1,10)=2.13$; $p=.18$. The Trial Type greatly influenced error rates, $F(4,40)=37.82$; $p<.001$; $\eta_p^2=.79$; 95% CI: .73-.84, and the way that error rates depended on Trial Type was significantly affected by the task that pigeons performed, $F(4,40)=13.44$; $p=.002$, $\eta_p^2=57$; 95% CI: .31-.68.

Planned comparisons revealed that, for the Stop-Signal task, error rates on Go trials (P(miss),i.e., pecking the Go/Signal key once or not at all) were not significantly different from error rates on Stop-Signal trials (P(respond),i.e., pecking the Go/Signal key twice or more), all $p>.26$. For the Change-Signal task, however, performance was significantly different between Go trials (higher error rates) and all types of Change-Signal trials apart from 75%-delayed Change-Signal trials; comparison of Go to 75%-delayed Change-Signal: $p=.199$; all other $p\leq.026$. There was a significant quadratic trend over Signal trials for both tasks, both $p<.001$, due to the low number of errors for no-delay and 25%-delayed Signal trials (there was also a significant cubic trend in the Change-Signal task, $p=.009$). Error rates increased from no-delay Signal trials to 25%-delayed Signal trials to 50%-delayed Signal trials to 75%-delayed Signal trials in both the Stop-Signal task and the Change-Signal task. Comparing each Trial Type between the two tasks, error rates in terms of P(respond) differed significantly between the Stop-Signal and the Change-Signal task only for 50%-delayed and 75%-

delayed Signal trials, both $p \leq .001$; all other comparisons between Signal trials: $p \geq .34$. As reported in Table 2, P(respond) was lower in the Change-Signal task than in the Stop-Signal task for these two types of Signal trials. This potentially indicates that the pigeons in the Change-Signal task, which had to opportunity to make a response to the alternative key, learned to avoid making an incorrect response to a high level of accuracy (i.e. there was a floor effect across all Change-Signal SSOs). However no such learning occurred in the pigeons in the Stop-Signal task, which were forced to withhold any pecking response. Error rates in terms of P(miss) on Go trials, though higher in the Change-Signal task, were not significantly different between the two tasks, $p=.10$.

Latency to peck the Go/Signal key. The log-transformed latencies of the critical peck towards the Go/Signal key (for the Change-Signal task, without having previously pecked the alternative key) are illustrated in Figures 4A and 4B. Data for the Go trials shown are for correct responses, those for the other trial types are incorrect responses. Note that only four of the pigeons completing the Stop-Signal task and two pigeons completing the Change-Signal task responded incorrectly in at least one trial of each type of Signal trial, and thus produced analysable latencies for every trial type. For those six pigeons, response latencies did not differ significantly between tasks, $F(1,4)=2.58$; $p=.18$. However, the factor Trial Type did affect latencies significantly, $F(4,16)=10.84$; $p<.001$; $\eta_p^2=.73$; 95% CI: .32-.81, and the task that pigeons performed somewhat influenced the effect of Trial Type on response times, $F(4,16)=3.17$; $p=.042$; $\eta_p^2=.44$; 95% CI: .00-.59, in that pigeons in the Stop-Signal task showed lower latencies in 25%-delayed Signal trials than pigeons in the Change-Signal task, $p=.017$ (Figure 4), and there was a marginally significant difference between tasks for Go trials, $p=.050$; all other comparisons: $p \geq .11$.

Planned comparisons between trial types (regardless of task) showed that latencies of correct responses in Go trials and of incorrect responses to the Go/Signal key in no-delay Signal trials were significantly longer than those in the three types of delayed Stop-Signal trials, all $p \leq .025$. The latency to incorrectly peck the Go/Signal key in no-delay Signal trials however did not differ significantly from latencies in Go trials, $p=.30$. Note that the number of Signal trials in which the

pigeons incorrectly responded to the Go/Signal key is very low; it only happened in 799 of the 12932 (6.2%) Signal trials, which resulted in very high variability in the data.

Latency of correct responses in the Change-Signal task. The data of the Change-Signal task allowed us to assess response latencies to make a correct choice from the moment of the signal (rather than the Go stimulus) onset. For this analysis, we considered only those trials in which both a pigeon's first and second peck were made towards the correct key (Go/Signal key on Go trials, alternative key on Change-Signal trials) and occurred after the onset of the Change signal. We subtracted the SSO of each type of Change-Signal trial from the latency of the critical peck. Latencies did not differ significantly between the five Trial Types, $F(4,20)=0.73$; $p=.58$.

Cue-Dependent Performance

In addition to the effects directly related to the signal, we estimated changes in performance depending on the cues that were presented in advance of a trial by examining the probability to respond in Signal trials, P(respond), the probability of missing a response in Go trials, P(miss), and the pigeons' latencies to respond to the Go stimulus in Go trials. P(respond) and P(miss) correspond to the pigeons' error rates in Signal trials and Go trials, respectively. The results for all four dependent variables are shown in Figure 5; descriptive statistics are summarised in Table 3. The data were analysed in repeated-measures ANOVAs using Cue Type (Go Cue, Neutral Cue and Signal Cue) and Session (blocked sessions 1-10, 11-20, 21-30) as within-subjects factors and Task (Change-Signal or Stop-Signal task) as a between-subjects factor. Where applicable, the reported results were subject to Huynh-Feldt corrections.

P(respond) on Signal trials. As shown in Figure 5A, the task that pigeons completed affected their likelihood of making a response during a Signal trial, $F(1,10)=11.08$; $p=.008$; $\eta_p^2=.53$; 95% CI: .06-.73, in that pigeons in the Stop-Signal task showed a greater probability of responding incorrectly to the Go/Signal key than those in the Change-Signal task. However, there was no significant difference in performance between the cue types that were presented, $F(2,20)=0.22$, $p=.81$, or between

sessions, $F(2,20)=0.77$; $p=.48$. There were also no significant interactions between any factors, all $p \geq .21$.

P(miss) on Go trials. As shown in Figure 5B, the probability of missing a response on Go trials was not significantly influenced by the task that pigeons completed, $F(1,10)=3.92$; $p=.076$, nor by the presented cue type, $F(2,20)=1.09$; $p=.36$, nor by the session, $F(2,20)=0.77$; $p=.48$. There was a significant interaction between the factors Task and Cue Type, $F(2,20)=5.03$; $p=.017$; $\eta_p^2=.34$; 95% CI: .01-.54; pigeons completing the Change-Signal task were more likely to miss a response in Go trials following a Signal Cue, the pigeons in the Stop-Signal task had the lowest probability to miss a Go response when a Signal Cue was shown.

Latency to peck the Go/Signal key on Go trials. As shown in Figure 5C, the pigeons' log-transformed latencies to correctly respond to the Go stimulus were not affected by the cue type presented, $F(2,20)=1.58$; $p=.23$, nor by the session, $F(2,20)=0.84$; $p=.46$, nor was there a significant interaction between the two factors, $F(4,40)=0.59$, $p=.66$. Pigeons doing the Change-Signal task were somewhat slower to peck the Go/Signal key than pigeons in the Stop-Signal task, $F(1,10)=4.78$; $p=.054$; $\eta_p^2=.32$; 95% CI: .00-.61. The interaction between the factors Task and Session was marginally significant, $F(2,20)=3.50$; $p=.050$; $\eta_p^2=.26$; 95% CI: .00-.48; the pigeons in the Change-Signal task became slower as the experiment went on, whereas those in the Stop-Signal task did not.

Discussion

In the present study, we aimed to answer the following questions: firstly, do the predictions made by the independent horse-race model of response inhibition (Verbruggen & Logan, 2009b) apply to performance that is governed purely by associative processes? Secondly, do pigeons use information about the likelihood that a signal will occur in an upcoming trial to improve their ability to inhibit a response? And thirdly, are these effects, if present at all, found not only in Stop-Signal tasks, in which the occurrence of a signal indicated that pigeons had to inhibit any response, but also in Change-Signal tasks, in which pigeons had to execute an alternative response instead of the

initially prepared one when the signal appeared? As the answer to the last question provides an important logical foundation for the other two questions, we shall address this one first.

Stop-Signal task vs. Change-Signal task

The pigeons completing the Change-Signal task appeared to be more successful in avoiding making an incorrect response at the Go/Signal key in Signal trials, compared to the pigeons completing the Stop-Signal task, which seemed to struggle to withhold a response when the Signal onset interval was very long. This was likely due to the different response contingencies between tasks: the pigeons in the Change-Signal task were permitted to redirect their pecking response to an alternative key, while the pigeons in the Stop-Signal task were forced to wait without performing any active response. Nonetheless, the pattern of performance was broadly comparable for the pigeons completing either task across most of the variables we examined, and the effects discussed below were found to similar degrees in both tasks. We are thus confident that the associative processes governing pigeons' learning were similar in both tasks.

Signal-dependent performance

The performance of pigeons in both the Stop-Signal and the Change-Signal task matched the predictions made by the independent horse-race model, which assumes that the process of initiating a response and the process of inhibiting a response are independent mechanisms, and that behaviour is determined by the process that is completed first. Based on these assumptions, one can expect to observe that performance (successful stopping) should decrease with increasing signal delay. This was the case for our pigeons: errors increased from Signal trials without a delay in signal onset to trials in which the signal appeared after a delay of 25% of their mean response times to trials with a 50% delay to trials with a 75% delay. Less obviously, the independent horse-race model predicts that response latencies should be shorter for Signal trials than for Go trials, which was the case for pigeons in both tasks (albeit a bit more evident in the Stop-Signal task than in the Change-Signal task). The logical explanation for this finding is that errors in Signal trials (i.e., making a response that should not be made) mainly occur when the response is made quickly. The average

latency for Go trials includes not only trials with fast responses but also trials in which more time was needed or available to respond. By contrast, in Signal trials, if an erroneous response is not made quickly, then it will not be made at all. Taken together, these results provide evidence that the independent horse-race model is largely consistent with associatively-mediated response inhibition, both in the Stop-Signal and the Change-Signal task.

Another question we addressed was whether the Stop-Signal and Change-Signal tasks engage the same inhibition mechanisms, or whether the mechanisms differ between tasks, either in such a way that the Change-Signal task requires a more complex level of inhibitory control than the Stop-Signal task, or that it requires less (or perhaps no) inhibitory control. The pigeons' performance was mostly comparable in the two tasks; their ability to perform response inhibition was no more or less successful in the Change-Signal task than it was in the Stop-Signal task.

We also considered whether the process of executing the alternative response in the Change-Signal task was preceded by a process of inhibiting the initially indicated Go response. If this was so, then it would be possible to directly assess the duration of stopping the initial response and changing to the alternative response in the Change-Signal task. We did this by comparing the latencies to respond to the correct key in Go trials to those in Change-Signal trials. The pigeons took equally long to respond to the correct key in no-delay Change-Signal trials and Go trials, which is not surprising - it is unlikely that the subjects initially prepared the Go response in no-delay Change-Signal trials, since they were never exposed to the stimulus associated with a Go in these trials. Instead, they probably only prepared and carried out one response option in these trials (pecking the alternative key). After subtracting the delay of the signal onset from the latencies of delayed Change-Signal trials, latencies to respond to the correct key were of comparable duration across all Change-Signal trials. Thus, to a first approximation, the process of responding to the signal appears to be of a fixed length, which would be the result predicted by the race model. This outcome is interesting. On the one hand, it confirms that the execution of the alternative response is triggered immediately upon signal onset and independent of the process that initiates the Go response. On

the other hand, it implies that there was little difference in latencies between trials in which only one response had to be executed (be it responding to the Go stimulus in Go trials, or pecking the alternative key in no-delay Change-Signal trials) and delayed Change-Signal trials in which, presumably, the initial Go response had to be inhibited and replaced by the alternative response.

This phenomenon is not unknown in the human literature, where it has raised the question of whether a separate process of inhibiting the Go response is indeed needed before an alternative response can be initiated (cf. Boecker et al., 2013). Logically, the latencies to make a correct response would be expected to be of comparable length in both Go and Change-Signal trials (measured from the moment of presenting the colour that signals the respective response) only if the associative retrieval of the alternative response on Change-Signal trials can replace the Go response at the same time as a process that actively inhibits that Go response. However, if the inhibition of the Go response has to precede the initiation of the alternative response, the latencies to respond in delayed Change-Signal trials (from the moment the signal appears) might be longer than the latencies in Go trials and no-delay Change-Signal trials. In that case, the latencies in delayed Change-Signal trials might also be longer than those in delayed Stop-Signal trials, in which only the inhibition process, but no additional response-initiation process, is performed. But interestingly, Change-Signal response times and estimated Stop-Signal response times are often similar in length (cf. Boecker et al., 2013), indicating that the duration of the behavioural adjustment in signal trials is predominantly determined by the inhibition mechanism and not by the process of response initiation.

Verbruggen, Schneider, and Logan (2008) explicitly addressed the issue of whether performance in Change-Signal tasks relies on response inhibition and concluded that, in accordance with the independent horse-race model, the inhibition process is indeed a necessary mechanism to stop the Go response on Signal trials, but that because the inhibition process is performed independently of the process to initiate a response, both processes can occur in parallel, so that no additional time is needed to initiate the alternative response once the inhibition process is

completed. The pigeons in our experiment took approximately equally long to make a response after the signal appeared in all Change-Signal trials, regardless of signal delay. Furthermore, we found that the response times in delayed Change-Signal trials were not significantly longer than those in delayed Stop-Signal trials (although the very low number of analysable trials for the Stop-Signal task might prevent a meaningful interpretation of this result). Taken together, the pigeon data appear to support Verbruggen, Schneider, and Logan's (2008) assumption that the response-inhibition process could be performed in parallel with an independent response-initiation process. However, given the above considerations, it is currently not clear whether the pigeons' performance in our Change-Signal task did indeed involve an inhibition process at all, or whether the observed response patterns were due to the automatic retrieval of signal-response associations. The specific procedure of our experiment might even have facilitated the absence of an inhibition process: unlike in studies with human participants, who typically performed the Go response and the alternative response with different hands or fingers and could thus potentially carry out both responses simultaneously, the pigeons could only ever execute one response at the same time - either peck the Signal or peck the alternative key. To test this possibility, it might be advisable to test humans under similar conditions as the pigeons, or to devise a paradigm that allows pigeons to perform both responses simultaneously and therefore unambiguously necessitates the inhibition of one response.

Cue-dependent performance

Pigeons showed no indication of altering their behaviour when provided with information about the likely nature of an upcoming trial. That is, performance was similar regardless of whether the cue predicted a high or low likelihood of the appearance of a signal in the upcoming trial. Although the graphs in Figure 5 might suggest that the presentation of a predictive cue influenced the pigeons' ability to inhibit an unwanted response, the data are too variable to carry any statistical meaning.

Sufficient evidence for a differentiation between the cues would have been the following: longer response times towards the Go/Signal key or a greater probability of missing a response in Go

trials when the Signal Cue was presented (compared to presenting the Go Cue), or a greater probability of pecking at the Go/Signal key in Signal trials in the presence of the Go Cue (compared to presenting the Signal Cue). However, the pigeons did not demonstrate any of these effects, and consequently, we have no discernible evidence that pigeons differentiated between the cues that predicted with varying probabilities whether the next trial would be a Signal trial. Clearly, additional research into the abilities of pigeons to attend to informative cues is necessary, and a promising way forward in this regard might be to target the reliability of the predictive cues. Bowditch, Verbruggen, and McLaren (under review) suggest that associatively-mediated cued inhibitory control is most readily achieved by supplying 100% predictive cues rather than 75% predictive cues, as were used in the current study.

However, one can only speculate about what this finding implies about the cognitive requirements for exerting cue-based response inhibition. There is so far no concrete evidence that pigeons are not able to utilise the cues; it may be that they simply did not do so with our current procedure, the amount of training we gave or the particular timings that we used. Although pigeons do not always attend to information that would reduce the ambiguity of a problem (Roberts, Feeney, McMillan et al., 2009; Smith, 2009), they are able to do so under the right circumstances (Dinsmoor, Sears, & Dout, 1976; Silberberg & Fantino, 2010; Zentall & Stagner, 2012). The results of this part of our study therefore indicate that cue-dependent response inhibition, although potentially mediated by associative learning as the research of Bowditch et al. (2015) suggests, is not acquired as easily or quickly with our procedures as the response inhibition following an explicit signal.

Conclusions and implications

Although Stop-Signal and Change-Signal tasks are common instruments for examining executive control in humans, it has recently been proposed that associative processes may be involved in response inhibition in these tasks. Indeed, we found that pigeons - assumedly mainly associative creatures - were able to inhibit a response when signalled to do so in both tasks and, as

predicted by the independent horse-race model of inhibitory control, doing so became increasingly difficult with increasing signal onset interval. Our pigeons did not detectably adjust their behaviour in response to cues predicting the likelihood that the response will have to be withheld. Taken together, these findings support the independent horse-race model.

Although the pigeons did not show any signs of proactive response inhibition, they succeeded rather impressively in inhibiting an action in response to a Stop signal, an ability that is typically regarded as indicative of executive control (Mostofsky & Simmonds, 2008; Verbruggen & Logan, 2009b; Kenner et al., 2010; Boecker et al., 2013). Overall, these results strongly question whether response inhibition based on external signals does in fact require top-down executive control. Furthermore, they confirm that performance in line with the independent horse-race model does not imply that executive-control processes are involved in achieving response inhibition (Verbruggen & Logan, 2008b, 2009b; Verbruggen et al., 2014; Best et al., 2016; Bowditch et al., 2016). This may have wider implications for the use of Stop-Signal and Change-Signal tasks as a measure of top-down executive control in humans, especially if the Change-Signal task, at least in the format used in our study, might be performed without any involvement of inhibitory processes, which would make it inadequate for the assessment of this cognitive ability. The possibility that performance in these tasks might be mediated, even to a large degree, by associative processes must be considered when interpreting the behavioural patterns from such experiments.

However, our results may highlight the importance of discriminating between passive response inhibition in reaction to a Stop signal and proactive inhibition in advance of such a signal: Our pigeons succeeded only in the former, but showed no evidence of the latter. If this pattern persists in future work, it might provide evidence for an alternative focus in the assessment of response inhibition. Proactive inhibition depends on an individual's ability to perform preparatory behavioural adjustments that occur in anticipation of the arrival of a Go stimulus or signal and might therefore be a more suitable measure of executive-control processes than reactive response inhibition.

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Table 1. Number of trials of each trial type (and percentage of Go trials) that followed the presentation of a Go Cue, Neutral Cue and Signal cue.

	Trial Type				
Cue	Go	Signal - no delay	Signal - 25% delayed	Signal - 50% delayed	Signal - 75% delayed
Go Cue	18 (75%)	3	1	1	1
Neutral Cue	12 (50%)	6	2	2	2
Signal Cue	6 (25%)	9	3	3	3

Table 2. Descriptive statistics of errors, latency to peck the Go stimulus, and latency of correct responses (Change-Signal task only) depending on Trial Type. Note the different sample sizes for the latency analyses; for all other analyses, *N*=6.

		Trial Type				
Measure		Go	Signal - no delay	Signal - 25% delayed	Signal - 50% delayed	Signal - 75% delayed
Stop-Signal Task						
Errors	Mean %	16.5	0.2	1.8	12.8	34.8
	Std. Error	5.0	2.7	2.5	2.0	2.5
Latency to peck the Go/Signal key twice *(N=4)*	Mean ms	1709	2469	757	848	1079
	Std. Error	190	523	117	79	93
	Number of valid trials	3647	12	15	94	259
	% of all trials of this type	84.3	0.6	2.1	13.1	35.9
Change-Signal Task						
Errors	Mean %	30.2	24.7	36.0	49.2	61.3
	Std. Error	5.4	3.9	3.8	2.7	2.6
Errors recoded as P(respond)	Mean %	30.2	1.5	1.8	4.8	12.3
	Std. Error	5.4	0.9	0.9	1.3	2.3
Latency to peck the Go/Signal key twice *(N=2)*	Mean ms	2112	2033	1615	1385	1354
	Std. Error	217	702	414	147	159
	Number of valid trials	1180	49	20	32	57
	% of all trials of this type	55.0	4.6	5.6	9.0	16.0
Latency of correct response (SSO subtracted)	Mean ms	1140	1135	1068	1078	1067
	Std. Error	66	71	54	57	43
	Number of valid trials	4513	2443	698	549	414
	% of all trials of this type	69.9	75.6	64.6	51.1	38.6

Table 3. Means [and standard errors] of P(respond) on Signal trials, P(miss) on Go trials, and latencies to correctly respond to the Go stimulus, depending on Cue Type (Go, Neutral and Signal Cue) and Test Sessions (three test blocks of ten sessions, in which the Go and Signal Cues predicted the occurrence of a signal on the following trial to 75% accuracy).

		Sessions		
Measure	Cue	1-10	11-20	21-30
Stop Signal Task				
P(respond)	Go Cue	0.08 [0.01]	0.10 [0.02]	0.08 [0.02]
	Neutral Cue	0.07 [0.01]	0.07 [0.01]	0.09 [0.01]
	Signal Cue	0.08 [0.01]	0.09 [0.02]	0.10 [0.07]
P(miss)	Go Cue	0.18 [0.05]	0.21 [0.08]	0.12 [0.04]
	Neutral Cue	0.16 [0.05]	0.21 [0.08]	0.12 [0.03]
	Signal Cue	0.18 [0.04]	0.19 [0.08]	0.09 [0.03]
Latency to peck the Go/Signal key twice	Go Cue	1561 [124]	1661 [147]	1562 [142]
	Neutral Cue	1616 [139]	1741 [163]	1537 [122]
	Signal Cue	1591 [135]	1670 [171]	1598 [162]

(continued overleaf)

Change-Signal Task				
P(respond)	Go Cue	0.04 [0.01]	0.05 [0.01]	0.03 [0.02]
	Neutral Cue	0.05 [0.02]	0.04 [0.01]	0.03 [0.01]
	Signal Cue	0.04 [0.01]	0.05 [0.02]	0.03 [0.01]
P(miss)	Go Cue	0.26 [0.06]	0.31 [0.06]	0.30 [0.09]
	Neutral Cue	0.30 [0.05]	0.29 [0.07]	0.32 [0.09]
	Signal Cue	0.33 [0.05]	0.34 [0.05]	0.34 [0.08]
Latency to peck the Go/Signal key	Go Cue	1924 [124]	1979 [147]	2112 [142]
	Neutral Cue	1941 [139]	1972 [163]	2114 [119]
	Signal Cue	2076 [141]	2036 [154]	2130 [157]

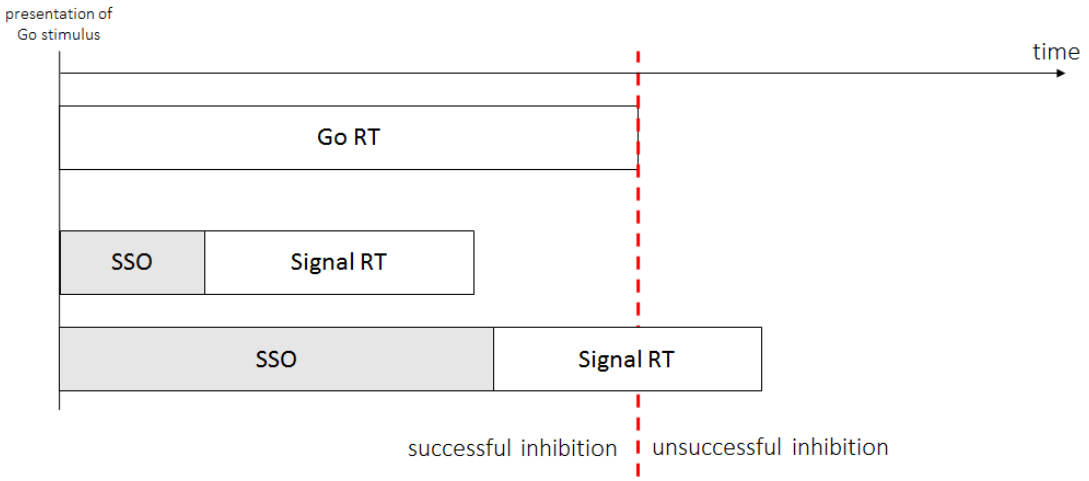


Figure 1. An illustration of the independent horse-race model. For Go trials, the time to make a correct response to the Go/Signal key (Go RT) is determined by the length of the Go process. On Signal trials, a second process is triggered by the presentation of the Signal, which is presented at the end of the Stop-Signal Onset (SSO) interval. The Signal RT is determined by the length of the inhibition process, which runs independently of the Go process. The time taken to inhibit a Go response in Signal trials is the sum of the SSO and the Signal RT. If the cumulative time is less than required to complete the Go process, inhibition is successful (this may be the case if the SSO is very short, as illustrated by the second bar; the bar does not cross the red dotted line and so no response will be emitted); if the cumulative time of SSO and Signal RT takes longer than the Go process, inhibition of the Go response is unsuccessful (this may be the case if the SSO is very long, as illustrated by the third bar; it crosses the red dotted line and hence a Go response will be made).

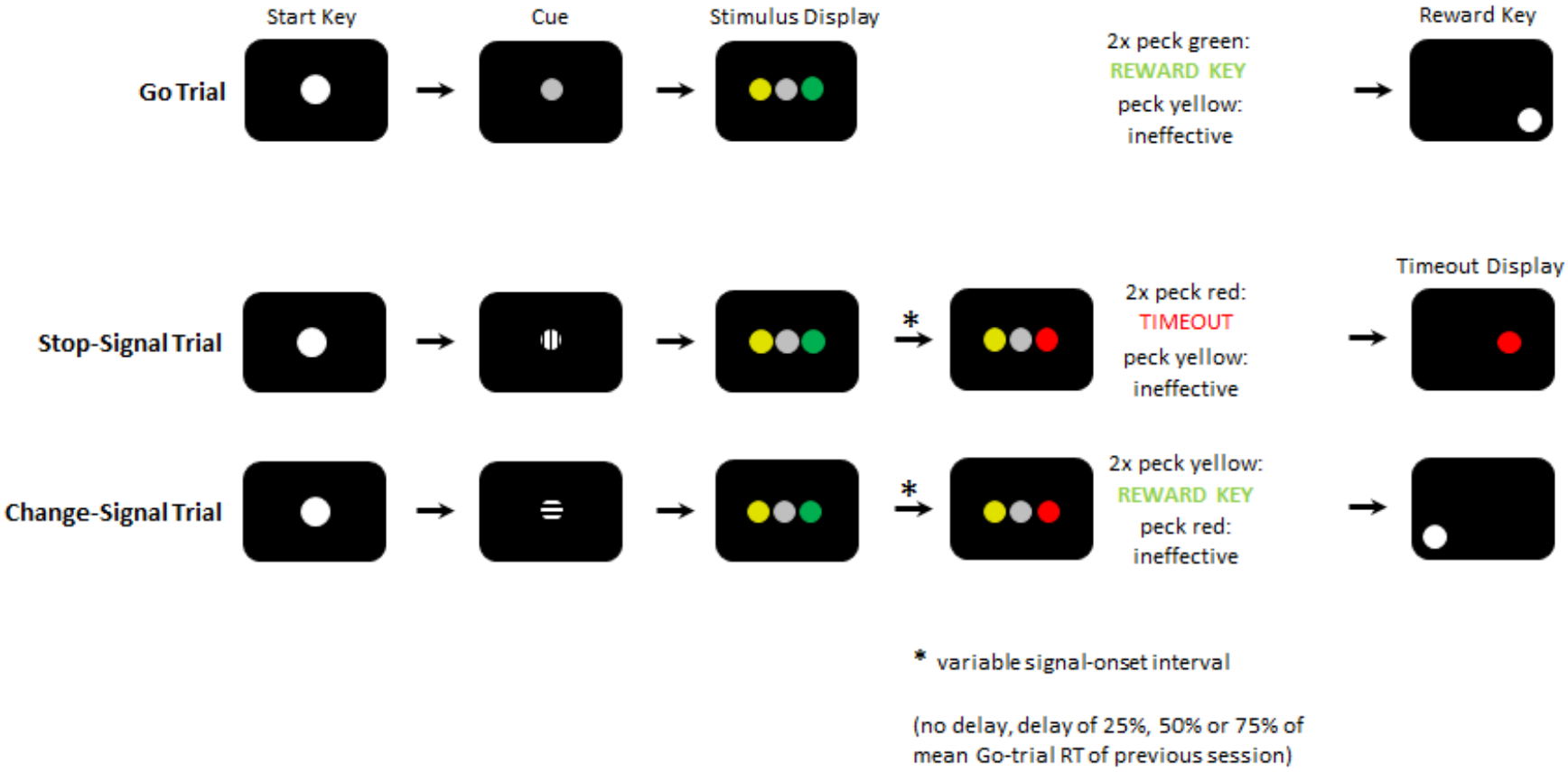

Start Key
Cue
Stimulus Display
Reward Key
Go Trial
2x peck green:
REWARD KEY
peck yellow:
ineffective
Timeout Display
Stop-Signal Trial
*
2x peck red:
TIMEOUT
peck yellow:
ineffective
Change-Signal Trial
*
2x peck yellow:
REWARD KEY
peck red:
ineffective
* variable signal-onset interval
(no delay, delay of 25%, 50% or 75% of
mean Go-trial RT of previous session)

Figure 2. Procedure of Go and Signal trials and the corresponding reinforcement contingencies in the Change-Signal and Stop-Signal task. 36 trials per session were Go trials, 36 trials were Signal trials. After the subject pecked the start key, one of three cues was shown; see text for details. One peck at the cue led to the presentation of the stimulus display, which contained the alternative key (yellow), the cue (grey) and the Go/Signal key carrying the Go stimulus (green) or the Signal (red). Note that, in Signal trials, the Go stimulus was presented first on the Go/Signal key and was replaced by the Signal after a variable stop-signal onset interval. For Go trials, following two pecks at the Go/Signal key carrying the Go stimulus (green), the reward key was shown on the side of the screen closest to the Go/Signal key. One peck at the reward key operated the food magazine mounted directly below that key. For Change-Signal trials, two pecks at the alternative key also resulted in the presentation of a reward key on the side of the alternative key. For Stop-Signal trials, two pecks at the Go/Signal key imposed a timeout period, during which only the Signal was shown on screen. Any other pecks had no scheduled consequences.

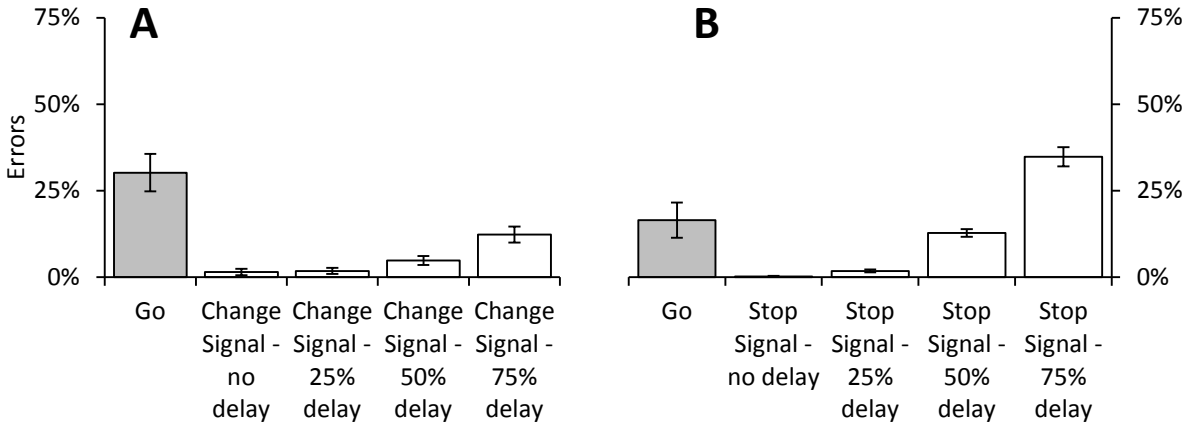


Figure 3. Error rates in % depending on Trial Type in *A)* the Change-Signal task and *B)* the Stop-Signal task. For Go trials (grey bars), error rates correspond to P(miss). For Signal trials (white bars), error rates correspond to P(respond). Error bars represent standard errors.

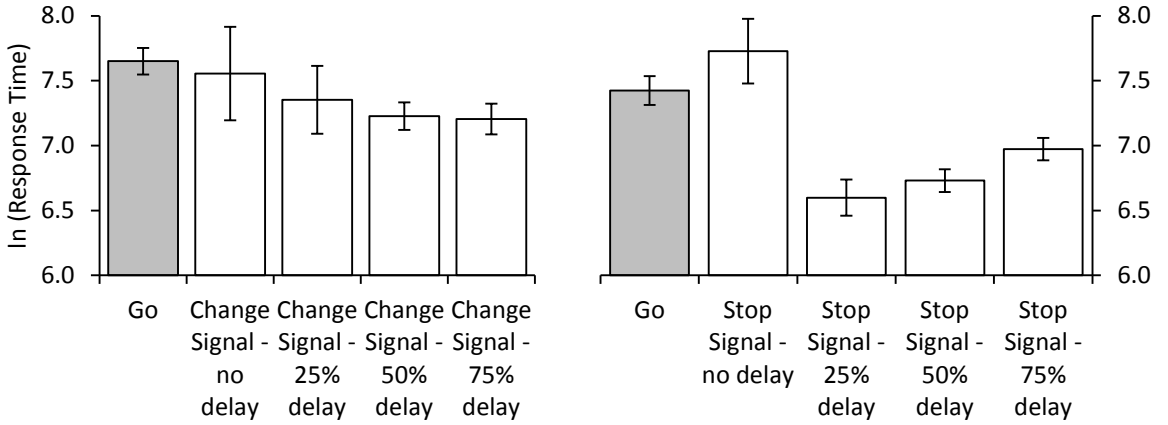


Figure 4. Log_e-transformed latencies of the second peck that is made at the Go/Signal key, depending on Trial Type, in *A)* the Change-Signal task (given that there have not been any pecks to the alternative key) and *B)* the Stop-Signal task. Error bars represent standard errors.

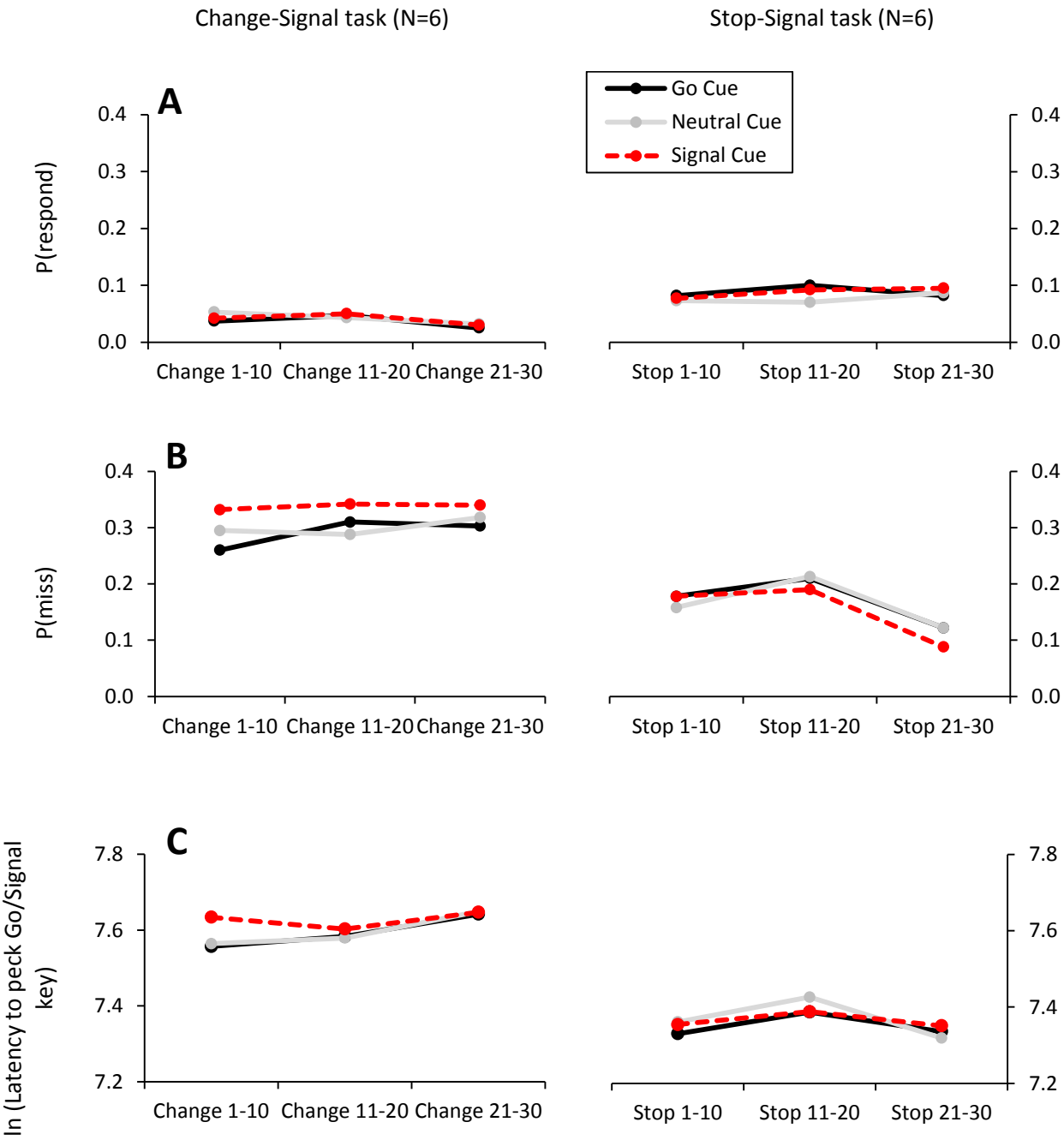
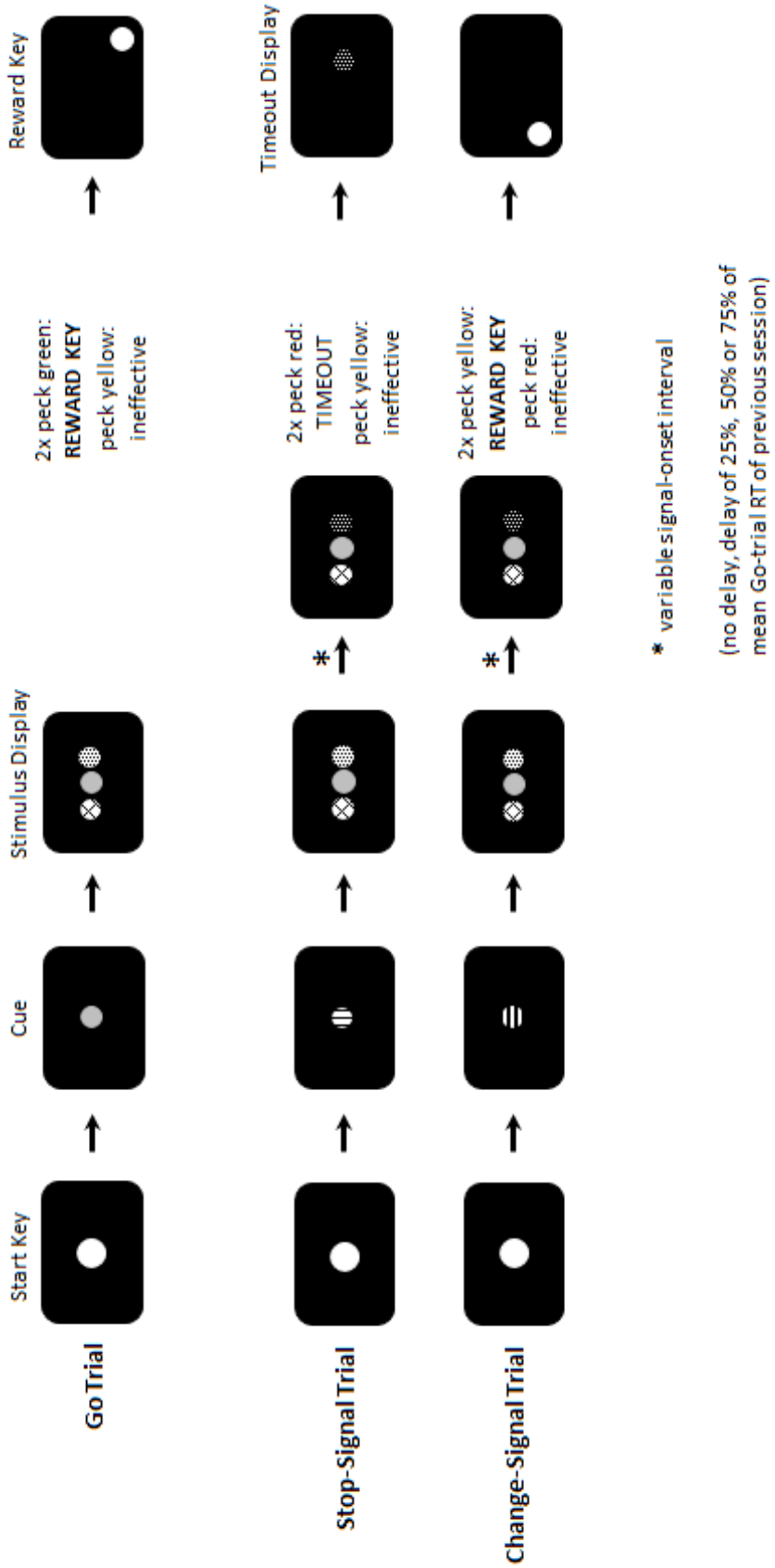


Figure 5. *A)* The overall probability of pecking at the Go/Signal key on Signal trials, P(respond), *B)* the probability of missing a response to the Go/Signal key on Go trials, P(miss), and *C)* the $\log_e$-transformed latency to peck the Go/Signal key on Go trials, depending on the cue that was shown in a trial (Go, Neutral, or Signal cue), across 30 cued sessions (in three blocks for easier visualisation).



Supplementary: Black and white version of Figure 2.