Express saccades during a countermanding task

Steven P. Errington & Jeffrey D. Schall

Department of Psychology, Vanderbilt Vision Research Center, Center for Integrative & Cognitive Neuroscience, Vanderbilt Brain Institute, Vanderbilt University, Nashville, Tennessee 37240, USA

Corresponding author:
Jeffrey D. Schall Ph.D.
Department of Psychology
PMB 407817
2301 Vanderbilt Place,
Vanderbilt University,
Nashville,
TN 37240-7817
(615) 322-0868
jeffrey.d.schall@vanderbilt.edu

ABSTRACT

Express saccades are rapid saccadic eye movements that can accurately redirect gaze to behaviorally relevant stimuli in the visual environment. This behavior can be commonly observed when the fixation spot disappears at a consistent, short interval before a target spot appears at a repeated location. While seemingly automatic, whether cognitive control can govern express saccade production has not been investigated. Here we report the production and manipulation of express saccades under unfavorable conditions in a saccade countermanding task necessitating cognitive control. To perform this task, we trained two monkeys to fixate a central spot and, following a variable amount of time, saccade to a target stimulus at one of two fixed locations (no-stop trials) presented simultaneously with the disappearance of the fixation dot. On a minority of trials, the fixation point reappeared instructing the monkeys to cancel their planned saccade to the peripheral target (stop-signal trials). Monkeys earned fluid reward for generating saccades to targets on no-stop trials and for maintaining fixation on stop-signal trials. Monkeys and humans adapt to the stop-signal trials by increasing saccade latencies. However, in two macaque monkeys we observed a significant fraction of trials with saccade latencies < 100 ms, resulting in a bimodal distribution of saccadic latencies. Target timing derived from regularities of the fixation interval (foreperiod) was used by some monkeys in some sessions to adapt regular but not express saccade latencies. Furthermore, simulations revealed by varying express saccade production, monkeys could maximize the opportunity for reward. To determine whether monkeys exploited this opportunity, reward contingencies for express saccade were changed. When unrewarded, significantly fewer express saccades were produced. This was confirmed in two other monkeys. This study highlights an unexpected manifestation of cognitive control through release of very short latency responses.

Keywords: Express Saccades, Reward, Cognitive Control

INTRODUCTION

Saccade latency is a manifestation of visual, motor, and cognitive processes (Carpenter 1988). Saccade latency is longer in tasks with spatiotemporal uncertainty about target location and presentation time and becomes shorter with less uncertainty. When stimulus timing and location is predictable and visual fixation is released, express saccades with latencies of approximately 80 ms in macaques and 100 ms in humans, approaching the lower limits imposed by conduction delays in the oculomotor system, are produced (Boch and Fischer 1986; Boch et al. 1984; Fischer and Boch 1983; Schiller et al. 2004).

Express saccades are typically tested through the gap paradigm with a 100-200 ms asynchrony between fixation spot disappearance and target appearance (Saslow 1967). This paradigm yields a high proportion of express saccades because of the removal of fixation point before target onset, a predictable target location, and a predictable target presentation time around 200 ms after fixation point removal (Fischer and Ramsperger 1984; Pare and Munoz 1996). The effects of waiting time, also known as foreperiod, on response time has been described many times (Drazin 1961; Klemmer 1956; Naatanen 1970; Niemi and Näätänen 1981). Nevertheless, the countermanding task has none of the features that would encourage production of express saccades.

Other evidence suggests express saccades have a learned component (Bibi and Edelman 2009; Fischer et al. 1984; McPeek and Schiller 1994). Express saccades are rarely made during the initial phases of training when subjects are unfamiliar with the parameters of the task, and become more frequent as training progresses (Pare and Munoz 1996). Of course, learning depends on reward contingencies, and non-human primates are adept at optimizing reward rate by exploring different behavioral strategies and task parameters (Feng et al. 2009).

Here we reported a serendipitous observation of frequent express saccades produced by particular monkeys performing a saccade countermanding task. The observation was unexpected because, by design, the countermanding task has: no gap between fixation spot disappearance and target onset, the time of target appearance is thought to be unpredictable, and saccade latencies in the task are generally slowed in comparison to simple reaction time tasks. In spite of these unfavorable conditions we observed express saccades on a considerable proportion of trials. We will describe the characteristics of express saccades in this task and the factors that encourage and discourage their

production. However, being incidental findings that were not the focus of the investigations, we acknowledge limitations of interpretation and suggest future experimental designs that could address them.

METHODOLOGY

Animal Care. Data were collected from 3 male bonnet macaques (Macaca radiata, 6.9 to 8.8 kg), and 1 female rhesus macaque (Macaca mulatta, 6.0 kg). Animal care exceeded policies set forth by the USDA and Public Health Service Policy on Humane Care and Use of Laboratory Animals and all procedures were carried out with supervision and approval from the Vanderbilt Institutional Animal Care and Use Committee. Titanium headposts were surgically implanted to facilitate head restraint during eye tracking. Surgical methods have previously been described in detail (Godlove et al. 2011).

Data Acquisition. Experiments were carried out in darkened, sound attenuated rooms. During testing, monkeys were seated comfortably 43 to 47 cm from a CRT monitor (~48 x 38°, 70Hz) in enclosed polycarbonate and stainless-steel primate chairs and head restrained using surgically implanted head posts. Stimulus presentation, task contingencies related to eye position, and delivery of liquid reinforcement were all under computer control in hard real time (TEMPO, Reflective Computing, Olympia, WA). With the exception of the 70 Hz screen refresh rate, task timing was controlled at 500 Hz. Stimulus sizes and eccentricities were calculated automatically by the stimulus presentation program based on subject to screen distance to allow for increased precision between primate chairs and recording room setups. Stimuli were presented using computer-controlled raster graphics (TEMPO Videosync 640 x 400 pixel resolution, Reflective Computing, Olympia, WA). Stimuli had a luminance of 3.56 cd/m^2 (fixation point and stop-signals) or 2 cd/m^2 (targets) on a 0.01 cd/m^2 background.

Behavioral Task. Behavior and electrophysiological signals were recorded during the countermanding (i.e., stop-signal) task (Figure 1). Additional details about the behavioral training regime and task have been described previously (Hanes et al. 1998; Hanes and Schall 1995). Trials were initiated when monkeys fixated a centrally presented square which subtended 0.34° of visual angle. After

a variable foreperiod, the center of the central fixation point was extinguished leaving a white outline. A target subtending 3° of visual angle simultaneously appeared at 10° to the left or right of the fixation. For two monkeys (F & H) foreperiods were randomly sampled from a uniform distribution. For two other monkeys (Eu & X) foreperiods were randomly sampled from an approximately non-aging, exponentially decaying distribution. On no-stop trials (Figure 1, top), no further visual stimuli were presented. Monkeys were required to make a saccade to the target and hold fixation to obtain reward. Correct trials were rewarded with several drops of juice. On stop trials (Figure 1, bottom), the center of the fixation point was re-illuminated after a variable delay providing a “stop-signal” which instructed the monkeys to cancel their impending eye movements and maintain central fixation. In practice, two trial outcomes were then possible. If monkeys successfully withheld the eye movement and maintained fixation for a period of time, they obtained a juice reward. These trials were designated as "canceled”. If monkeys were unable to inhibit the movement, no rewards were given, and the trial was termed “non-canceled”. The stop-signal delay (SSD) or time between target and stop-signal presentation determines the probability with which movements can be successfully countermanded (Logan and Cowan 1984). An initial set of SSDs was selected for each recording session based on the experimenter's knowledge of the animal's past performance. SSD was then manipulated using either an adaptive staircasing algorithm which adjusted stopping difficulty based on accuracy, or by randomly selecting one of the defined SSD’s. In the staircasing design, when subjects failed to inhibit responses, the SSD was decreased by a random step of 1, 2, or 3 stop-signals increasing the likelihood of success on the next stop trial. Similarly, when subjects were successful in inhibiting the eye movement, the next SSD was increased by a random step of 1, 2, or 3 decreasing the future probability of success. This procedure was used to ensure that subjects failed to inhibit action on ~50% of stop trials overall. Plots showing the probability of responding at each SSD (inhibition functions) were constructed and monitored online to ensure adequate performance.

Eye Tracking. Eye position data were acquired, calibrated, and streamed to the Plexon computer using the EyeLink 1000 infrared eye-tracking system (SR Research, Ontario, Canada). This system has an advertised resolution of 0.01°. Online, gaze was monitored using digital fixation windows. The size of

these windows was determined by the experimenter based on the quality of the eye tracker calibration. Typically, subjects were allowed 1° of stimulus fixation error online. For final trial classification and analysis, saccade initiation and termination were detected offline using a custom algorithm implemented in the MATLAB programming environment (MathWorks, Natick, MA). Saccade starting and ending times were defined as periods when instantaneous velocity was elevated above $30°s^{-1}$. The eye tracking procedures we employed allowed us to reliably detect saccades > 0.2° in amplitude.

RESULTS

These results are based on 425 sessions of saccade countermanding obtained from two monkeys (Monkey F: 110 sessions; Monkey H: 315 sessions) plus an additional 29 sessions of saccade countermanding in two other monkeys to compare training histories and reward contingencies (Monkey Eu: 12 sessions; Monkey X: 17 sessions). Collectively, monkeys completed 298,238 trials (Monkey F: 77,438; Monkey H: 186,984; Monkey Eu: 11,583; Monkey X: 22,233).

Prevalence of express saccades across monkeys and task conditions. While performing the saccade countermanding task, monkeys F and H produced saccades with very short latencies which led to bimodal or multi-modal latency distributions. In single behavioral sessions and across sessions, saccades with latencies ≤ 100ms comprised a separate mode in the distributions. Express saccades comprised an average of 6% of the total latency distribution and ranged from 0% to 66% across sessions. Express saccades were prominent in both monkeys. In one example session for monkey F, there were 522 trials, 100 of which were successfully canceled, and 422 of which had a saccade generated (357 no-stop trials, 65 non-canceled). The response distribution for this session was clearly multimodal (Figure 2A, top) with express saccades produced in 174 (41.2%) saccade trials. Across the session, the median saccade latency was 143 ms (IQR 104 ms - 276 ms), and median express saccade latency was 82.5 ms (IQR: 79 ms – 87 ms). A similar pattern of multimodality in response times was present in an example session for monkey H (Figure 2A, bottom). In 310 trials, 58 were successfully canceled and 252 had a saccade generated (145 no-stop trials, 107 non-canceled). Express saccades were produced in 40

(15.9%) saccade trials. Across the session, the median response time (saccade latency) was 126 ms (IQR 104 ms - 276 ms) and the median express saccade latency was 92 ms (IQR: 88 ms – 96 ms).

This finding is consistent when looking across multiple sessions. Across 110 sessions, monkey F had a valid outcome on 49,602 trials, in which saccades were generated in 38,982 trials (32,992 no-stop, 5,990 non-canceled, 10,620 canceled). The response distribution was clearly multimodal (Figure 2B, top). Median saccade latency across these trials was 248 ms (IQR: 157 – 318 ms). Express saccades were elicited in 4,707 (12.0%) saccade trials. The median express saccade latency was 87 ms (IQR: 82 ms – 92 ms). Similarly, monkey H had a valid outcome on 120,666 trials, in 90,347 of which an eye movement was elicited (73,750 no-stop, 16,597 non-canceled, 30,319 canceled). Again, the response time distribution was multimodal (Figure 2B, bottom) with a median saccade latency of 328 ms (IQR: 256 – 420 ms). Express saccades were elicited in 4,061 (4.5%) saccade trials. The median express saccade latency was 92 ms (IQR: 91.93 ms – 96 ms).

This pattern of response times was also examined in data collect from two other monkeys who had completed 29 sessions (Monkey Eu: 12 sessions; Monkey X: 17 sessions) of saccade countermanding. These sessions had 26,511 trials with a valid eye movement (Monkey Eu: 8,469 trials; Monkey X: 18,042 trials). For both monkeys, the saccade latency distributions were unimodal, with no evidence of an express saccade mode in example sessions or across all sessions (Figure 2C & D). Median saccade latency across response trials was 264 ms (IQR: 217 – 356 ms) for monkey Eu, and 225 ms (IQR: 188 – 282 ms) for monkey X. Express saccades were elicited in only 107 trials, comprising only 0.40% of all saccade latencies. Monkey Eu produced 42 (0.49%) express saccades, with a median express saccade latency of 68 ms (IQR: 62 – 78 ms). Monkey X produced 65 (0.36%) express saccades, with a median express saccade latency of 93 ms (IQR: 80 – 97.25 ms).

Varying experimental design influences express saccade production. Both monkeys had sessions in which stop-signal delay was varied through a staircasing procedure and sessions in which it was randomly selected from a fixed set of values.

Monkey F had 64/110 sessions (58.18%) in which stop-signal delay was varied through a staircasing procedure, and 46/110 (41.82%) in which stop-signal delay varied randomly. There was no

significant difference in the proportion of express saccades produced between these two experimental designs, $t(108) = -0.6906$, $p = 0.4913$. Additionally, there was no significant difference in the proportion of stop trials the monkey experienced between these two experimental designs, $t(108) = 1.6250$, $p = 0.1071$. Monkey H had 163/315 sessions (51.75%) in which stop-signal delay was varied through a staircasing procedure, and 152/315 (48.25%) in which stop-signal delay varied randomly. In contrast to Monkey F, monkey H produced more express saccades in staircased sessions (15.68% ± 10.84%) compared to fixed sessions (5.04% ± 5.24%), $t(313) = -10.9690$, $p < 10\text{-}5$. Furthermore, there were significantly fewer stop trials in fixed sessions (34.59% ± 10.10%) compared to staircased sessions (44.62% ± 9.60%), $t(313) = -9.0361$, $p < 10\text{-}5$. Monkey Eu and X both experienced sessions in which SSD's were varied through a staircasing procedure, and thus no comparisons between experimental designs could be made.

Foreperiod variation and express saccade production. Given that express saccades occur more often when the timing of a target presentation is predictable, we examined saccade latency as a function of the foreperiod between fixation at the central cue and target presentation. For each session we quantified the beginning, end, median, and duration of the foreperiods.

Monkey F experienced a uniform foreperiod distribution ranging from ~420 to ~630ms in the majority of sessions (mean ± SD range: 202.71 ± 4.47 ms, n = 84/110 sessions, Figure 3A). Monkey H experienced two foreperiod distributions in the experiment. First, monkey H experienced an early uniform distribution, ranging from ~350 to ~675 ms (301.55 ± 13.00 ms, n = 31/315 sessions, Figure 3B). Second, monkey H experienced a later uniform distribution, ranging from ~760 to ~2275 ms (1490.00 ± 44.36.2 ms, n = 157/315 sessions, Figure 3C). This distribution occurred most frequently in staircased sessions (154/157, 98.09%). The pattern of foreperiods across other sessions for monkey F and H were unclear and varied. Monkey Eu and monkey X both experienced the same pattern of foreperiod distribution ranging from ~600 to ~ 2100 ms (mean ± SD range: 883.01 ± 204.23 ms, n = 29/29 sessions). This distribution was exponentially decaying, resulting in a non-ageing foreperiod (Figure 3D & E, respectively).

Comparison between early and late foreperiod for monkey H. As monkey H had two distributions of foreperiods, we compared how this variation in onset and duration effected behavior. Express saccades were more prominent in sessions with later, more variable foreperiods (16.17% ± 10.68%) than in sessions with earlier, less variable foreperiods (4.12% ± 5.60%), $t(186) = -6.11$, $p < 10\text{-}5$. Overall, saccade latencies were also faster in later foreperiod sessions (266.7 ± 52.3 ms) compared to earlier foreperiod session (385.3 ± 46.2 ms), $t(186) = 11.76$, $p < 10\text{-}5$. Saccade latencies for regular saccades only (>100ms) mirrored this, with faster latencies in later foreperiod sessions (299.3 ± 43.9 ms) compared to earlier foreperiod sessions (398.0 ± 40.6 ms), $t(186) = 11.57$, $p < 10\text{-}5$. Interestingly, saccade latencies for express saccades only (≤100ms) showed the opposite effect with slower latencies in later foreperiod sessions (84.0 ± 3.0 ms) compared to earlier foreperiod sessions (80.5 ± 8.7 ms), $t(176) = -3.79$, $p = 0.0002$.

Foreperiod & saccade latency. On a session-by-session basis, we examined the relationship between saccade latency on no-stop and non-canceled trials, and foreperiod (Figure 4A). Mean saccade latencies for all saccades, express saccades, and regular saccades for each foreperiod group are reported in Table 1. Correlation results split by trial type, restricting analysis to no-stop and non-canceled, are reported in Table 2. This section will outline findings collapsed all trial types.

For monkey F, a significant correlation between saccade latency and FP was observed in 34/84 sessions. Of these 34 sessions, 33 demonstrated a significant negative correlation, whilst 1 demonstrated a significant positive correlation. Restricting this analysis to regular saccades only, 27/84 sessions had a significant correlation between regular saccade latency and FP (Figure 4B, top). Of these 27 sessions, 26 demonstrated a significant negative correlation, whilst 1 demonstrated a significant positive correlation. Finally, restricting this analysis to express saccades only, 4/84 sessions had a significant correlation between express saccade latency and FP (Figure 4C, top). Of these 4 sessions, 3 demonstrated a significant negative correlation, whilst 1 demonstrated a significant positive correlation.

For monkey H early FP sessions, a significant correlation between saccade latency and FP was observed in 2/31 sessions. Of these 2 sessions, 1 demonstrated a significant negative correlation, whilst 1 demonstrated a significant positive correlation. Restricting this analysis to regular saccades only, 2/31

sessions had a significant correlation between regular saccade latency and FP (Figure 4B, second). Of these 2 sessions, none demonstrated a significant negative correlation, whilst 2 demonstrated a significant positive correlation. Finally, restricting this analysis to express saccades only, no sessions had a significant correlation between express saccade latency and FP (Figure 4C, second).

For monkey H later FP sessions, a significant correlation between saccade latency and FP was observed in 54/157 sessions. Of these 54 sessions, 1 demonstrated a significant negative correlation, whilst 53 demonstrated a significant positive correlation. Restricting this analysis to regular saccades only, 11/157 sessions had a significant correlation between regular saccade latency and FP (Figure 4B, third). Of these 11 sessions, 6 demonstrated a significant negative correlation, whilst 5 demonstrated a significant positive correlation. Finally, restricting this analysis to express saccades only, 7/157 sessions had a significant correlation between express saccade latency and FP (Figure 4C, third). Of these 7 sessions, 5 demonstrated a significant negative correlation, whilst 2 demonstrated a significant positive correlation.

For monkey Eu, a significant correlation between saccade latency and FP was observed in no sessions. Restricting this analysis to regular saccades only, no sessions had a significant correlation between regular saccade latency and FP (Figure 4B, fourth). Finally, restricting this analysis to express saccades only, no sessions had a significant correlation between express saccade latency and FP (Figure 4C, fourth).

For monkey X, a significant correlation between saccade latency and FP was observed in 9/17 sessions. Of these 9 sessions, all demonstrated a significant negative correlation. Restricting this analysis to regular saccades only, 10/17 sessions had a significant correlation between regular saccade latency and FP (Figure 4B, bottom). Of these 10 sessions, all demonstrated a significant negative correlation. Finally, restricting this analysis to express saccades only, no sessions had a significant correlation between express saccade latency and FP (Figure 4C, bottom).

Within foreperiod analysis. To examine how the foreperiod influenced the generation of express saccades, we split foreperiod into 100 ms bins on a session-by-session basis. For monkey F, saccade latencies significantly decreased as a function of foreperiod, $F(2, 249) = 3.65$, $p = 0.027$. There was no

variation in the proportion of express saccades produced as a function of foreperiod, $F(2, 249) = 2.11$, $p = 0.123$. For monkey H earlier foreperiod sessions, saccade latencies ($F(3, 120) = 0.49$, $p = 0.687$) and the proportion of express saccades ($F(3, 120) = 0.32$, $p = 0.811$) did not vary with foreperiod. For monkey H later foreperiod sessions, saccade latencies increased ($F(15, 2438) = 7.99$, $p < 10\text{-}5$) and the proportion of express saccades decreased ($F(15, 2438) = 14.44$, $p < 10\text{-}5$) with foreperiod bin. For monkey Eu, saccade latencies ($F(11,89) = 0.8378$, $p = 0.613$) and the proportion of express saccades ($F(11, 98) = 0.83$, $p = 0.615$) did not vary as a function of foreperiod. For monkey X, saccade latencies did not vary with foreperiod bin, $F(15, 195) = 1.51$, $p = 0.105$. However, the proportion of express saccades did decrease as a function of foreperiod bin, $F(15, 206) = 2.26$, $p = 0.006$.

Race model assumptions and express saccade production. We examined whether the prevalence of express saccades led to violation of the basic assumption of the race model that saccade latencies on non-canceled (error) trials are faster than those on no-stop trials, i.e., RT(non-canceled) < RT(no stop). The quantitative results are summarized in Table 1.

For monkey F, the RT(non-canceled) < RT(no stop) relationship was violated in 50/84 sessions (59.5 %). On no stop trials, the proportion of express saccades when RT(non-canceled) < RT(no stop) was not different from that when RT(non-canceled) > RT(no stop) (two-tail $t(82) = 1.185$, $p = 0.239$). On non-canceled trials, the proportion of express saccades when RT(non-canceled) < RT(no stop) was significantly greater than that when RT (non-canceled) > RT(no stop) ($t(82) = -2.495$, $p = 0.015$). For monkey H early FP sessions, the RT(non-canceled) < RT(no stop) relationship was violated in 14/31 sessions (45.2 %). On no stop trials, the proportion of express saccades when RT(non-canceled) < RT(no stop) was not different from that when RT(non-canceled) > RT(no stop) ($t(29) = -0.426$, $p = 0.673$). On non-canceled trials, the proportion of express saccades when RT(non-canceled) < RT(no stop) was significantly greater than that when RT (non-canceled) > RT(no stop) ($t(29) = -2.164$, $p = 0.039$). For monkey H later FP sessions, the RT(non-canceled) < RT(no stop) relationship did not hold in 83/157 sessions (52.9 %). On no-stop trials, the proportion of express saccades when RT(non-canceled) < RT(no stop) was not different from that when RT(non-canceled) > RT(no stop) ($t(155) = -1.393$, $p = 0.165$). On non-canceled trials, the proportion of express saccades when RT(non-canceled) < RT(no

stop) was significantly greater than that when RT (non-canceled) > RT(no stop) ($t(155) = -3.223$, $p = 0.002$). Hence, when monkeys F and H performed the countermanding task consistent with the race model assumption of stochastic independence, they produced more express saccades than when they performed the task in violation of the assumption.

In contrast, although monkey Eu had 3 sessions in which RT(non-canceled) > RT(no stop), the proportion of express saccades did not differ across sessions or trial types. Monkey X had no sessions in which RT(non-canceled) > RT(no stop).

Effect of trial history on express saccade production. Given that express saccades occur in predictable conditions, we examined how stimulus and response history influenced express saccade generation (Table 3). For monkey F, fewer express saccades were produced after canceled trials compared to after non-canceled trials $F(2, 248) = 5.41$, $p = 0.005$, post-hoc $p = 0.004$. There was no difference between any other conditions. For monkey H early foreperiod sessions, there was no significant effect of previous trial type on the proportion of express saccades generated, $F(2, 88) = 1.94$, $p = 0.150$. For monkey H later foreperiod sessions, there was no significant effect of previous trial type on the proportion of express saccades generated, $F(2, 464) = 0.28$, $p = 0.752$. For monkey Eu, more express saccades were produced after no-stop trials compared to after non-canceled trials (post-hoc $p = 0.004$) and canceled trials ($p = 0.056$), $F(2, 33) = 4.22$, $p = 0.023$. For monkey X, there was no significant effect of previous trial type on the proportion of express saccades generated, $F(2, 48) = 2.24$, $p = 0.118$.

We then looked at how saccade latency varied as a function of trial history. For monkey F, trial outcome significantly affected the saccade latency on the following trial, $F(2, 248) = 3.84$, $p = 0.023$. Saccade latencies on no-stop trials following canceled trials were slower than those following non-canceled (post-hoc p: 0.0301) and no-stop trials (post-hoc p: 0.066). For monkey H sessions with an earlier foreperiod, trial outcome did not affect the saccade latency on the following trial, $F(2,88) = 1.16$, $p = 0.317$. For monkey H sessions with a later foreperiod, trial outcome did not affect the saccade latency on the following trial, $F(2,464) = 0.51$, $p = 0.602$. For monkey Eu, trial outcome significantly affected the saccade latency on the following trial, $F(2, 33) = 32.58$, $p < 10^{-5}$. Saccade latencies in no-stop trials following no-stop trials were significantly faster than those following non-canceled (post-hoc $p < 10^{-5}$), and

saccade latencies in no-stop trials following non-canceled trials were significantly faster than those following canceled trials (post-hoc $p = 0.041$). For monkey X, trial outcome significantly affected the saccade latency on the following trial, $F(2, 48) = 59.98$, $p < 10^{-5}$. Saccade latencies in no-stop trials following no-stop trials (post-hoc $p < 10\text{-}5$) and non-canceled trials (post-hoc $p < 10^{-5}$) were significantly faster than those following canceled trials. There was no difference between saccade latencies on no-stop trials following no-stop trials, and those following non-canceled trials (post-hoc $p = 0.594$)

Express saccade production and simulated behavioral outcomes. To determine whether express saccade production could be advantageous, we simulated behavioral outcome measures under production of different fractions of express saccades using a linear ballistic accumulator (LBA) to instantiate the independent race underlying countermanding performance (Figure 5A). We simulated the saccade GO process with accumulators having two distributions of rates. One had slower median accumulation rates, producing longer saccade latencies. The second had faster median accumulator rates, producing express saccades. The fraction of trials governed by the faster accumulator was varied systematically.

On simulated trials with no stop-signal, reward was earned for saccades of any saccade latency. We also simulated the STOP process, corresponding to saccade inhibition. On stop-trials, if the finishing time of the STOP process preceded that of the GO process, then reward was earned for canceling the saccade. If the finishing time of the GO process preceded that of the STOP process, then no reward was earned. We did not fit the model parameters to performance measures. Instead, we explored qualitatively how reward rate varied as a function of various parameters. First, we varied the parameters of GO and STOP accumulators to generate varied proportions of express saccades (0%, 10%, 50%, 90%; Figure 5B). Second, we varied whether express saccades were rewarded or unrewarded. Third, we varied whether stop-signal delay was varied in an adaptive staircase or fixed at particular intervals. Fourth, we varied whether the trial length was fixed or varied. Finally, we varied the proportion of stop-trials in a given session. We examined how timing and experimental parameters similar to those used during data collection influenced average reward rate.

Trial rate and express saccade production. As monkey F & H both experienced trials with a fixed intertrial interval, trial length can vary as a function of response time. Under this paradigm, a faster saccade latency may lead to a shorter trial length, and thus provide the monkey with more trials per minute in order to gain reward. With 40% stop trials, simulated data demonstrated that an increase in the proportion of express saccades led to an increase in trial rate (number of trials per minute) (Figure 5C). When express saccades were elicited on 0% of trials, the average simulated trial rate was 19.23 trials per minute. When express saccades were elicited on 10% of trials, the average simulated trial rate increased to 19.42 trials per minute. With 50% express saccades, trial rate increased further to 20.37 trials per minute and with 90% express saccades, rate increased further to 22.3 trials per minute. This is only true under variable trial length conditions; when trial lengths are fixed, trial rates only slightly decrease and subjects can only initiate around 11 trials per minute.

Given that there is no penalty for making express saccades in no-stop trials, but there are time-out penalties in stop-trials, we can expect an increase in stop trial proportion will increase the error rate and trial length (due to timeouts) and lower the overall trial rate. As such, we examined if these values varied as a proportion of stop trials in a given session (Figure 5E, upper panels). Interestingly, if a session had a lower proportion of stop-trials (~10%), then producing more express saccades lead to only a small increase in the number of trials available: at 0%, subjects could experience 17.72 trials per minute, at 50% subjects could experience 18.58 trials per minute, and at 100% subjects could experience 19.65 trials per minute. However, if a session had a greater proportion of stop-trials (~70%), then producing more express saccades lead to a greater increase in the number of trials available compared to lower stop-trial proportions; at 0%, subjects could earn 17.72 rewards per minute, at 50% subjects could earn 19.29 rewards per minute, and at 100% subjects could earn 23.04 rewards per minute. This is only true for variable trial lengths. If trial lengths were fixed, then express saccades were detrimental to trial rates for all stop-signal proportions.

We then probed this relationship in our experimental data through examining the relationship between proportion of express saccades on trial rate, whilst controlling for the proportion of stop trials in the given session. For monkey F, producing a greater number of express saccades resulted in a greater number of trials per minute, in fixed SSD sessions ($r = 0.375$, $p = 0.026$). However, in staircased

sessions, there was no significant correlation between the proportion of express saccades in a session and trial rate (r = 0.1777, p = 0.234). Conversely, there was no significant correlation between the proportion of express saccades in a session and trial rate in fixed SSD sessions (r = 0.168, p = 0.368) or staircased sessions (r = -0.021, p = 0.794) for monkey H. Furthermore, there was no significant correlation between the proportion of express saccades in a session and trial rate in early foreperiod session (r = 0.243, p = 0.195) or later foreperiod sessions (r = -0.044, p = 0.588) for monkey H.

Variation of reward rate with express saccade production. When trial length varied with response time, express saccades were rewarded, and stop-signal delays adapted in a staircase procedure, we found systematic variation in reward rate with the proportion of express saccades in a session (Figure 5D).

At typical stop-trial proportions (~40%), producing a small proportion of express saccades was not detrimental to performance, and led to slightly increased reward rates. At this stop-signal proportion, when express saccades were elicited on 0% of trials, the average simulated reward rate was 15.71 rewards per minute. When express saccades were elicited on 10% of trials, average simulated reward rate increased to 15.74 rewards per minute. With 50% express saccades, reward rate decreased to 15.61 rewards per minute. With 90% express saccades, reward rate decreased further to 14.85 rewards per minute.

This relationship changed dependent on the proportion of stop-trials in a given session (Figure 5E, lower panels). If a session had a lower proportion of stop-trials (~10%), then producing more express saccades lead to greater reward: at 0%, subjects could earn 16.85 rewards per minute, at 50% subjects could earn 17.34 rewards per minute, and at 100% subjects could earn 17.69 rewards per minute. However, if a session had a greater proportion of stop-trials (~60%), then producing more express saccade was detrimental to performance; at 0%, subjects could earn 11.24 rewards per minute, at 50% subjects could earn 10.32 rewards per minute, and at 100% subjects could earn 6.95 rewards per minute. This is only true for variable trial lengths. If trial lengths were fixed, then express saccades were detrimental to reward rates for all stop-signal proportions.

Reward contingencies change express saccade production. We first examined whether express saccades were learned through changes in reward rates during the training phase. For monkey F, we tracked the progression of express saccade production from the initial training session onwards. The average proportion of express saccades significantly increased over time ($r = 0.49$, $p < 0.001$). In parallel, average reward rate within each session increased significantly with experience ($r = 0.34$, $p < 0.001$). Sessions were divided into five groups, from earliest to latest. Across groups, the proportion of express saccades increased significantly ($F(4,171) = 7.76$, $p < 0.001$, Figure 6A), and reward rate increased significantly ($F(4,171) = 11.69$, $p < 0.001$, Figure 6B).

To test the association between reward rate and express saccade production, we sampled separate blocks of sessions in which correct express saccades were rewarded (n = 13 sessions) followed by a block of sessions in which express saccades were unrewarded (n = 18 sessions). Sessions with both unrewarded and rewarded express saccades had multimodal saccade latency distributions (Figure 6C). However, when express saccades were unrewarded, saccade latency ≤ 100ms became much less common, and a new mode appeared in the saccade latency distribution in the 200 – 250 ms range. When rewarded, express saccade trials comprised 22.6% of the latency distribution. When unrewarded, the proportion of express saccade trials dropped considerably and comprised only 7.9% of the latency distribution, $\chi2\ (1, N = 10465) = 405.648$, $p < 0.001$ (Figure 6D). In contrast to the early training stages (when express saccades were rewarded), we found that the average proportion of express saccades significantly decreased with time from the reward manipulation ($r = -0.723$, $p < 0.001$, Figure 6E). Interestingly, average reward rate exhibited no trends ($r = 0.183$, $p = 0.467$, Figure 6F).

Further evidence that express saccades are produced only when rewarded was obtained by examining the saccade latency of two other monkeys who were trained with unrewarded express saccades. As described above, the saccade latency distributions were unimodal for both monkeys (Figure 2C & D). Express saccades were elicited in only 107 trials, comprising only 0.40% of all saccade latencies. Monkey Eu produced 42 (0.49%) express saccades and Monkey X produced 65 (0.36%) express saccades.

DISCUSSION

We observed multimodal distributions of saccade latencies in a saccade countermanding task. Furthermore, simulations revealed that trial and reward rate in this task can be increased by varying the proportion of express saccades made within a session, under certain conditions. We found that monkeys learnt and exploited this association over time. We then manipulated the reward contingencies for express saccade production and found when monkeys made significantly lower proportion of express saccades when no longer rewarded for them. It is important to note the incidental nature of these findings, and that the features studied were not the main focus of the investigations. As such, our interpretations of these data are limited and future experimental designs should be employed to test them more thoroughly. However, this study has demonstrated for the first time how express saccade production can be accomplished strategically under the guidance of cognitive control.

Express saccades production in atypical conditions. Consistent with classic reports of express saccades in monkeys, the earliest modes in the resulting distributions peak below 100ms and display very little variance (Boch and Fischer 1986; Boch et al. 1984; Fischer and Boch 1983; Schiller et al. 2004). However, this was unexpected given the design of the saccade countermanding task. Previous studies have outlined the typical conditions in which an express saccade is produced: the removal of fixation point before target onset, a predictable target location, or a predictable target onset time. Features of the countermanding task do not meet any of these criteria. Firstly, the fixation point distinguishes simultaneously with the presentation of a target. Secondly, the target location in our task was in one of two locations, and was randomly selected on a trial by trial basis. Thirdly, the time that the target appeared on screen varied relative to time that the monkey held gaze on the fixation spot.

Temporal predictability and saccade latency. The timing of events is an important predictor for action planning and action selection (Kolling and O'Reilly 2018; Petter et al. 2018). By monitoring temporal contingencies from the environment, predictions about when future events may occur can be generated. This temporal predictability can be measured through hazard functions - the conditional probability of an event occurring at a given time, given that it has not yet occurred (Luce 1986; Nobre et

al. 2007). The use of hazard functions is motivated by the premise that participants have a representation of the elapsed time in the current situation based on knowledge of the experienced distribution of durations. If an interval elapsing before an event is randomly sampled from a uniform distribution (also known as an aging distribution), then participants will behave as if the event becomes more likely as time progresses. For example, if you were told to definitely expect a phone-call at any point in the next hour, as time gets closer to the hour mark and you still haven't received a call, the more likely the call is to occur at the next instant. In such situations where there is a high temporal predictability of an event, if an action is required, this can be prepared ahead of time.

Thus, temporal prediction is critical in reaction time tasks in which predictive foreperiods are a major determinant of response latency. Using distributions of foreperiods selected uniformly from a range of values, i.e., aging, manual response time studies have shown as foreperiod increases, response times become faster (Drazin 1961; Klemmer 1956; Naatanen 1970; Niemi and Näätänen 1981). Consistent with the aforementioned manual response studies, this finding has been replicated focusing on saccade latencies in humans (Findlay 1981) and monkeys (Schall 1988). We replicated this finding in the current study. Monkeys can make effective, but idiosyncratic temporal predictions about the time a target may appear on screen.

Trial history influence on saccade latency. As reported previously, we also observed that trial history led to significant, systematic shifts in response times. Most monkeys produced longer saccade latencies on no stop-signal trials following correct cancelled trials. We also found most monkeys demonstrated no post-error slowing in the saccade countermanding task. Our results replicate those from previous countermanding studies. Specifically, the overall delay of saccade latencies following successful inhibition on stop-signal trials has been previously reported (Cabel et al. 2000; Kornylo et al. 2003). The absence of post-error slowing is inconsistent with previous observations, and the potential reasons for this have previously been explained (Emeric et al. 2007).

However, this task may offer new insights given the high prevalence of express saccades. We have expanded previous findings by looking at how trial history affects express saccade production. Qualitatively, we found all monkeys produced fewer express saccades after canceled trials. Given that

monkeys demonstrate significant slowing after successful inhibition of a saccade, it appears that post-stop slowing is accomplished, at least in part, by not sampling the process that produces fastest saccades.

Reward optimization. This study demonstrated that monkeys adjusted saccadic eye movement production to maximize the opportunity to gain more rewards. By including express saccades, monkeys could increase the number of trials available, and thus increase the opportunity to gain a reward. Producing express saccades was not detrimental to reward rate.

If the total time of the task is fixed, a rational subject will trade off speed and accuracy in order to try and maximize the amount of reward they can gain in the given session. If more time is spent on one trial, there will be a greater chance of a correct response; however, longer trials reduce the total amount of trials that the subject can experience, and thus lower the total amount of reward available. This ultimately gives rise to a speed-accuracy trade-off which aims to maximize gains through flexible cognitive control of behavior. Evidence from simple two-alternative choice tasks modeled through accumulator models has shown that speed-accuracy tradeoff is determined through manipulation of two parameters in the decision process: the decision threshold and the initial bias (Gold and Shadlen 2002). Bogacz et al. (2006) demonstrated that this decision threshold can be optimized in order to maximize reward rate across a range of task conditions. Behavioral evidence from human subjects has demonstrated that decision threshold can be adjusted and set at values which are close to optimal (Balci et al. 2011; Simen et al. 2009).Although this potentially offers a valuable insight into cognitive processes, it does not describe the neural processes producing the behavior. Indeed, evidence from monkey neurophysiology opposes these characterizations, suggesting adaptive adjustments in behavior occur by varying the latency at which evidence starts to accumulate (Pouget et al. 2011; Schall 2019).

Monkeys have also demonstrated near-optimal adjustments in behavior in a 2AFC task. Feng et al. (2009) developed a model allowing for the calculation of choice bias that yields the optimal harvesting of reward, given the animals' sensitivities to a visual stimulus. They found monkeys acquire over 98% of the possible maximum rewards, with shifts away from optimality erring in the direction of smaller penalties. In addition to this, monkeys have also shown to discover unexpected ways to exploit task

contingencies. Lowe and Schall (2019) demonstrated this effect in a pro-/anti-saccade visual search task where a vertical singleton cued that a pro-saccade should be made towards it, and a horizontal singleton cued an anti-saccade away from it. Close examination of the reward contingencies of the experiment found that shifting gaze towards a vertical stimulus was the correct outcome on 66% of trials. Exploiting this contingency, they found that one monkey produced more frequent and faster responses to vertical items than to any other item in the array, suggesting they adopted a strategy of searching for vertical items opposed to using the stimulus response rule provided by the singleton. Bichot et al. (1996) found a similar behavior in a color pop-out task: monkeys trained exclusively to find one color in an array persistently direct gaze to stimuli of that color, regardless of whether it is a distractor or target. These are just some of the examples of macaque monkeys creatively exploiting reward contingencies.

Conclusion. We report incidental findings that are unexpected and instructive. Given that express saccade production can be adjusted to increase the opportunities to gain reward, this suggests that the features that influence the generation of an express saccade may not be identified on a single trial but instead are sensed in the context of many trials. Information related to reward rate and action-based outcome must be integrated over the course of several trials. As such, it is likely that higher cortical areas involved in performance monitoring may contribute to the executive control of express saccade production (Donahue et al. 2013; Sajad et al. 2019; So and Stuphorn 2010; Stuphorn and Schall 2006; Stuphorn et al. 2000)

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ACKNOWLEDGEMENTS & FUNDING

The authors thank K. A. Lowe and J. A. Westerberg, and Dr.'s T. Reppert, A. Sajad, and C.R. Subraveti, for helpful discussions and comments on the manuscript. This work was supported by R01-EY019882 (SE), R01-MH55806 (JS), P30-EY08126 (JS), and by Robin and Richard Patton through the E. Bronson Ingram Chair in Neuroscience (JS). There are no reported conflicts of interest.

Figures

Figure 1: Saccade countermanding task. Monkeys initiated trials by fixating on a central point. After a variable time, the center of the fixation point was extinguished. A peripheral target was presented simultaneously at one of two possible locations. On no-stop-signal trials, monkeys were required to shift gaze to the target, whereupon after a variable period of time, fluid reward was provided. On stop-signal trials (~40% of trials), after the target appeared, the center of the fixation point was re-illuminated after a variable stop-signal delay, which instructed the monkey to cancel the saccade. After holding fixation for a period of time, the monkey received feedback and reward. In a staircase procedure, stop-signal delay was adjusted such that monkeys successfully canceled the saccade in ~50% of trials. In the remaining trials, monkeys made non-canceled errors, in which no reward was delivered. In non-staircased trials, stop-signal delays were randomly selected from a pre-determined set of stop-signal delays.

Figure 2: Distributions of saccade latencies during saccade countermanding. Histograms (left) and cumulative distribution functions (right) of saccade latencies in non-canceled (dashed lines) and no-stop trials (solid lines). **A**. Saccade latencies in example sessions for monkey's F & H. **B**. Saccade latencies collapsed across all sessions for monkey's F & H. **C**. Saccade latencies in example sessions for monkey's Eu & X. **D**. Saccade latencies collapsed across all sessions for monkey's Eu & X.

Figure 3: Distributions of foreperiods. Histograms (top), survivor distribution (middle), and hazard rate (bottom) of foreperiods used for monkey F (**A**), monkey H in sessions with earlier foreperiods (**B**), monkey H in sessions with longer foreperiods (**C**), monkey Eu (**D**), and monkey X (**E**). Monkey's F and H experienced aging foreperiods, and monkey's Eu and X experienced approximately non-aging foreperiods.

Figure 4: Relation of saccade latency and foreperiod. A. Scatter plots of saccade latency as a function of foreperiod with marginal distribution of saccade latency for representative sessions with monkey F (top), monkey H with early foreperiods (second), monkey H with later foreperiods (third), monkey Eu (fourth), and monkey X (bottom). Horizontal line indicates latency of 100 ms. The express

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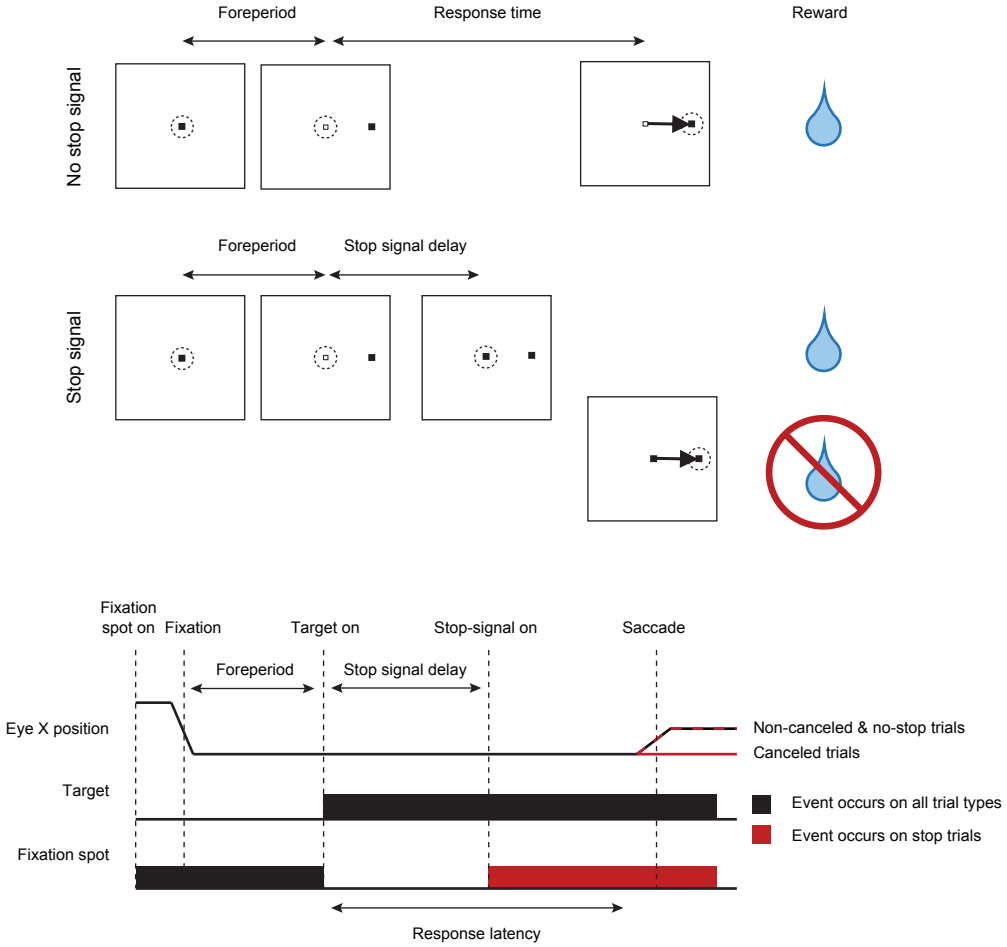
Figure 5: Simulation of reward rate earned with variable fractions of express saccades. A. Linear ballistic accumulators for GO process (left) and STOP process (right). The GO process consisted of two mean rates, one producing express saccade latencies, and the other producing regular saccade latencies. Trial outcomes were specified by the finishing time of the fastest process according to the race model (Logan and Cowan 1984). On trials with no stop-signal, reward was earned after the GO process produced either a regular or an express saccade. On trials with a stop-signal, reward was earned only if the stop process LBA finished before both the regular and the express saccade LBAs. The following combinations of trial parameters were simulated: with or without staircase adjustment of SSD, with variable or fixed trial durations, with or without rewarding express saccade latencies. **B.** Distributions of saccade latencies produced with indicated fractions of express saccades in a simulated session of 1,000 trials. **C**. Average trial length over simulated sessions with (closed) and without (open) staircasing SSD and with variable (square) or fixed (circle) trial lengths. With variable but not fixed trial lengths, trial rate increased with the fraction of express saccades because more trials could be completed. Whether or not SSD was adjusted in a staircase made negligible difference. **D.** Average reward rate over simulated sessions with (closed) and without (open) staircasing SSD and with express saccades rewarded (upright triangle) or not rewarded (inverted triangle). If express saccades were not rewarded, then reward rate decreased dramatically with increasing fraction of express saccades, whether or not SSD was adjusted in a staircase. If express saccades were rewarded, then reward rates were higher and decreased less with increasing fractions of express saccades. However, if SSD was adjusted in a staircase, then reward rate was maximal when ~10% express saccades were produced. **E.** Variation of trial rate (top) and reward rate (bottom) as a function of proportion of express saccades for fixed (left) and variable (right) trial

durations. Progressively darker points plot values with progressively higher fraction of stop-signal trials. With lower fractions of stop-signal trials, the cost of express saccades on reward rate is reduced.

Figure 6: Learning and unlearning express saccades. Variation of performance of monkey F as a function of training and task contingencies. **A.** Average reward rate earned from early to late stages of training in 18 sessions when express saccades were rewarded just like regular saccades on no stop trials. **B.** Percentage of express saccades produced across corresponding stages of training. The monkey exploited contingencies of the task to earn more reward by producing a fraction of express saccades. **C.** Distributions of saccade latencies when express saccades were rewarded (open) and in subsequent sessions when only no stop trials with regular saccade latencies were rewarded (filled). When express saccades were not rewarded, the monkey produced more regular latency saccades to earn reward. **D.** Cumulative probability of express saccade production in sessions when they were rewarded (solid) and in later sessions when they were not (dashed). **E.** The percentage of express saccades decreased across sessions following changing contingency to not reward express saccades. **F.** Average reward rate did not decrease across corresponding sessions following the change of reward contingency.



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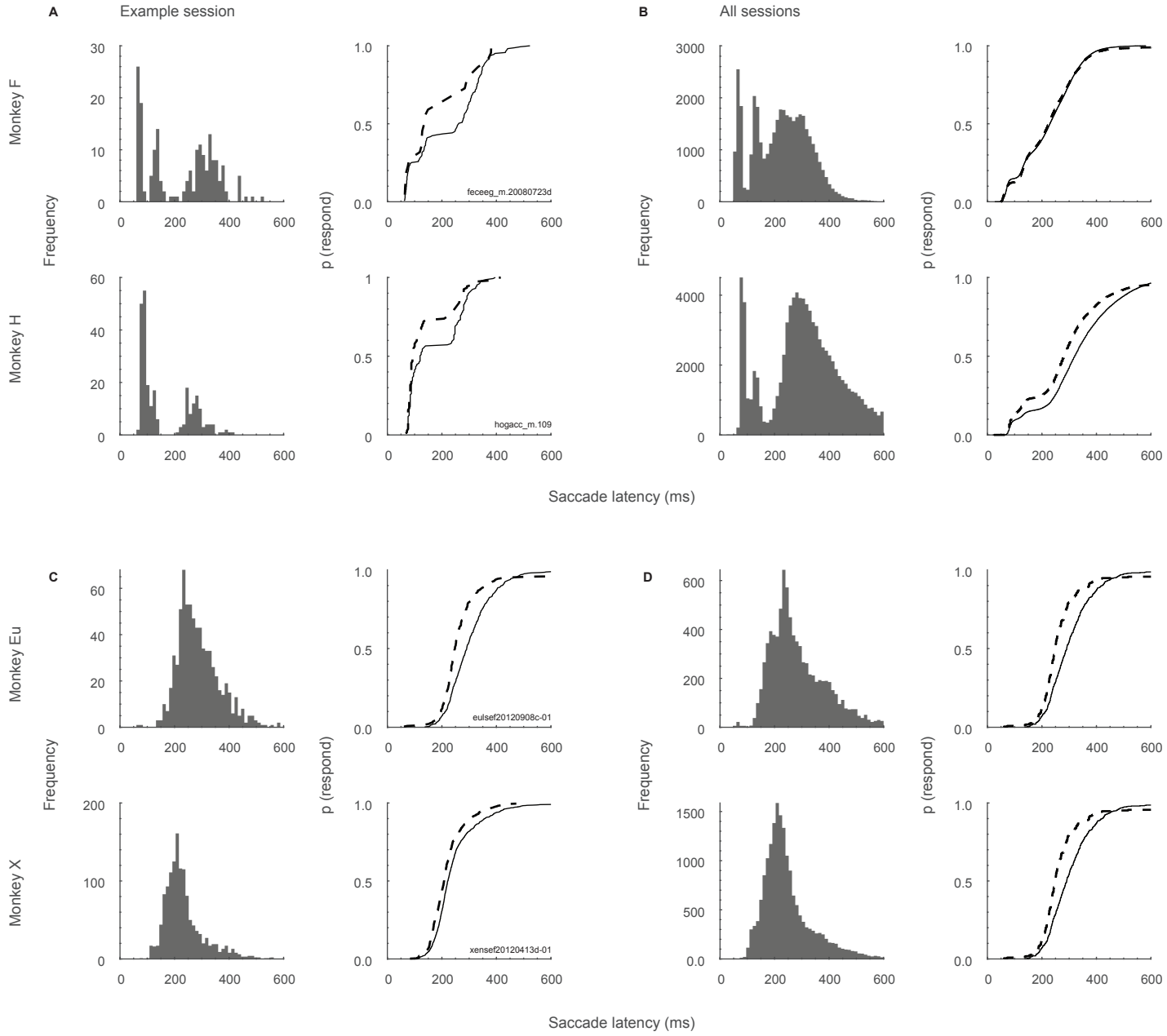

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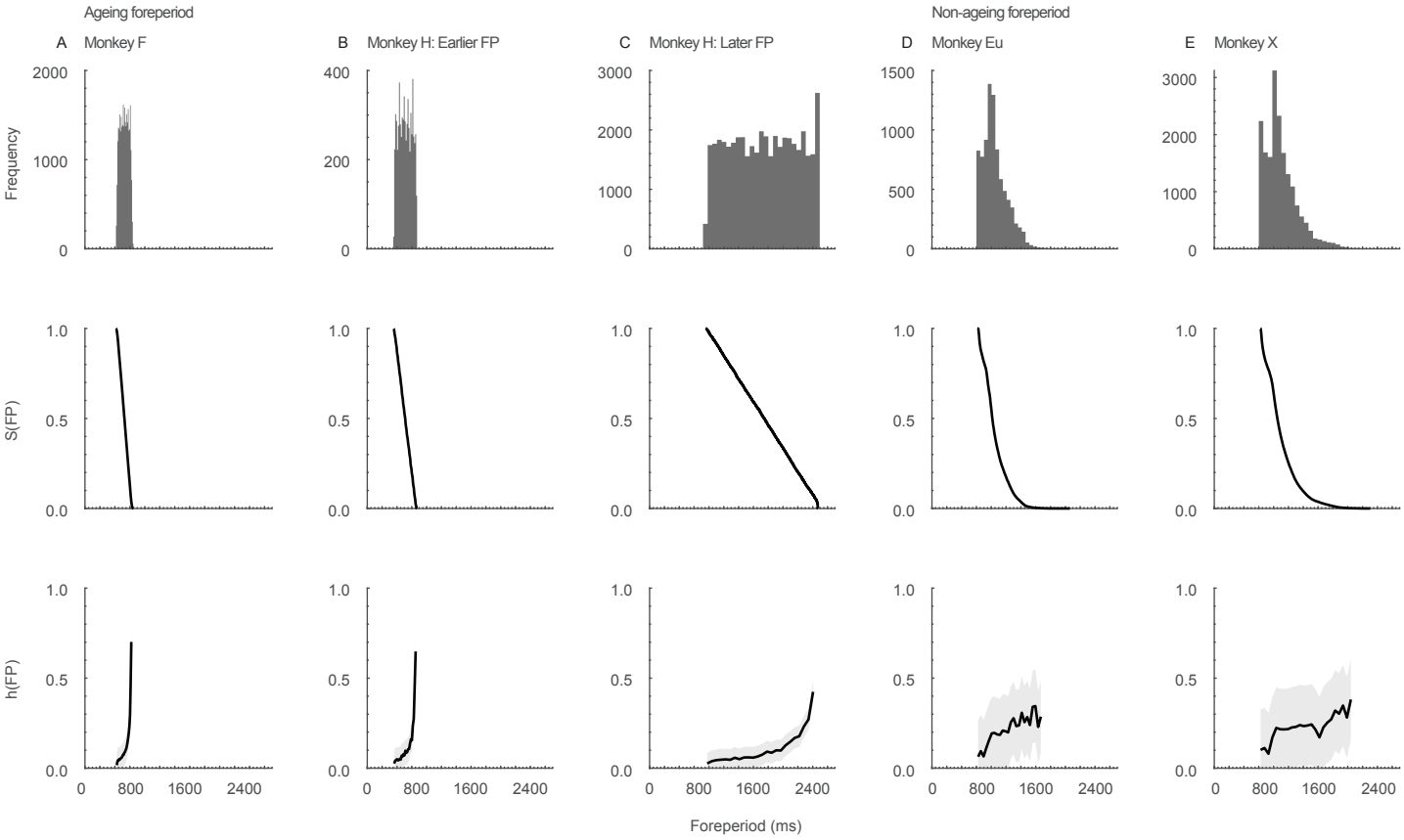

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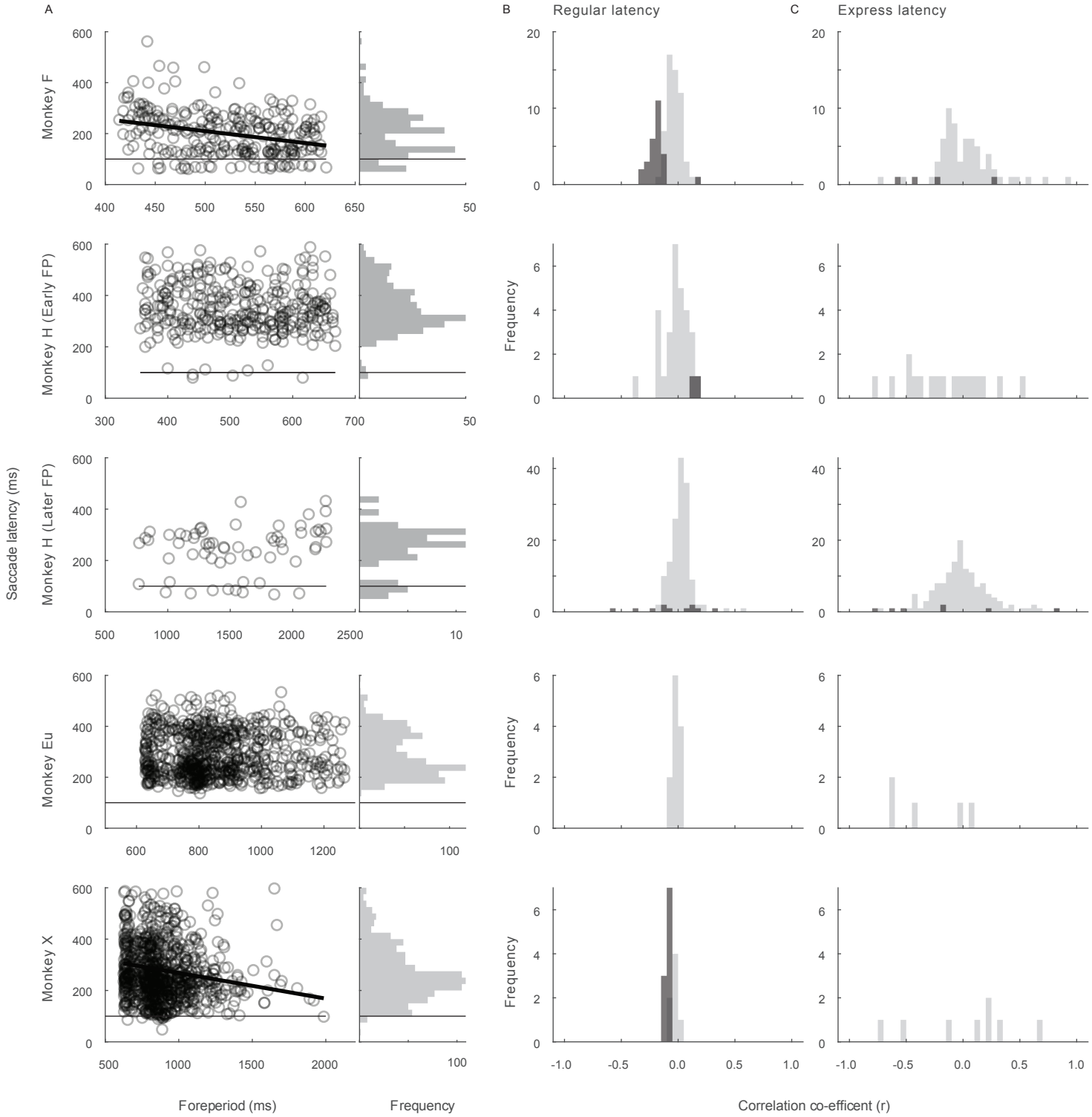

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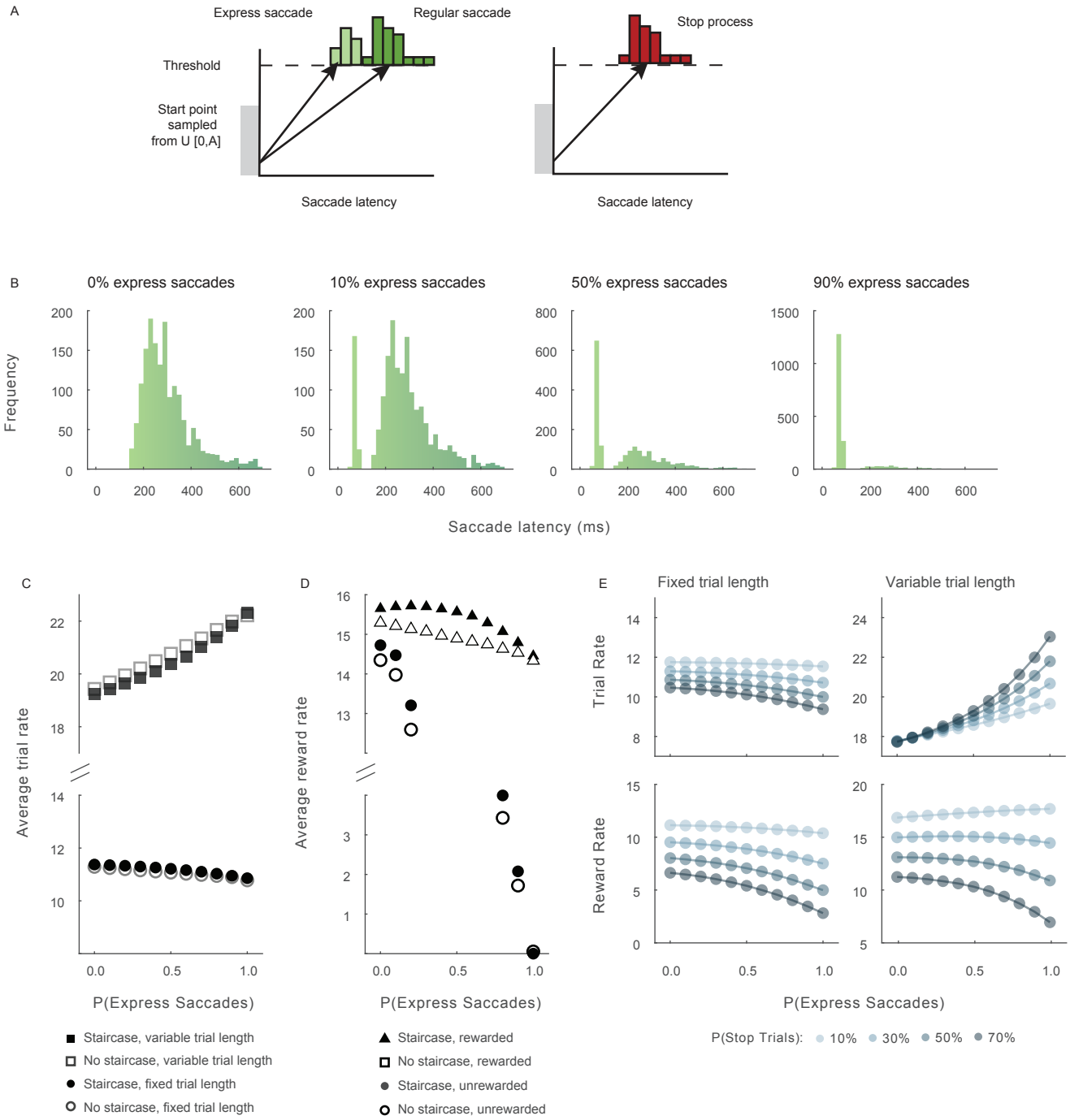

Figure 5: Simulation of reward rate earned with variable fractions of express saccades. A. Linear ballistic accumulators for GO process (left) and STOP process (right). The GO process consisted of two mean rates, one producing express saccade latencies, and the other producing regular saccade latencies. Trial outcomes were specified by the finishing time of the fastest process according to the race model (Logan and Cowan, 1984). On trials with no stop-signal, reward was earned after the GO process produced either a regular or an express saccade. On trials with a stop-signal, reward was earned only if the stop process LBA finished before both the regular and the express saccade LBAs. The following combinations of trial parameters were simulated: with or without staircase adjustment of SSD, with variable or fixed trial durations, with or without rewarding express saccade latencies. **B**. Distributions of saccade latencies produced with indicated...

... fractions of express saccades in a simulated session of 1,000 trials. **C**. Average trial length over simulated sessions with (closed) and without (open) staircasing SSD and with variable (square) or fixed (circle) trial lengths. With variable but not fixed trial lengths, trial rate increased with the fraction of... express saccades because more trials could be completed. Whether or not SSD was adjusted in a staircase made negligible difference. **D**. Average reward rate over simulated sessions with (closed) and without (open) staircasing SSD and with express saccades rewarded (upright triangle) or not rewarded (inverted triangle). If express saccades were not rewarded, then reward rate decreased dramatically with increasing fraction of express saccades, whether or not SSD was adjusted in a staircase. If express saccades were rewarded, then reward rates were higher and decreased less with increasing fractions of express saccades. However, if SSD was adjusted in a staircase, then reward rate was maximal when ~10% express saccades were produced. **E**. Variation of trial rate (top) and reward rate (bottom) as a function of proportion of express saccades for fixed (left) and variable (right) trial durations. Progressively darker points plot values with progressively higher fraction of stop-signal trials. With lower fractions of stop-signal trials, the cost of express saccades on reward rate is reduced.

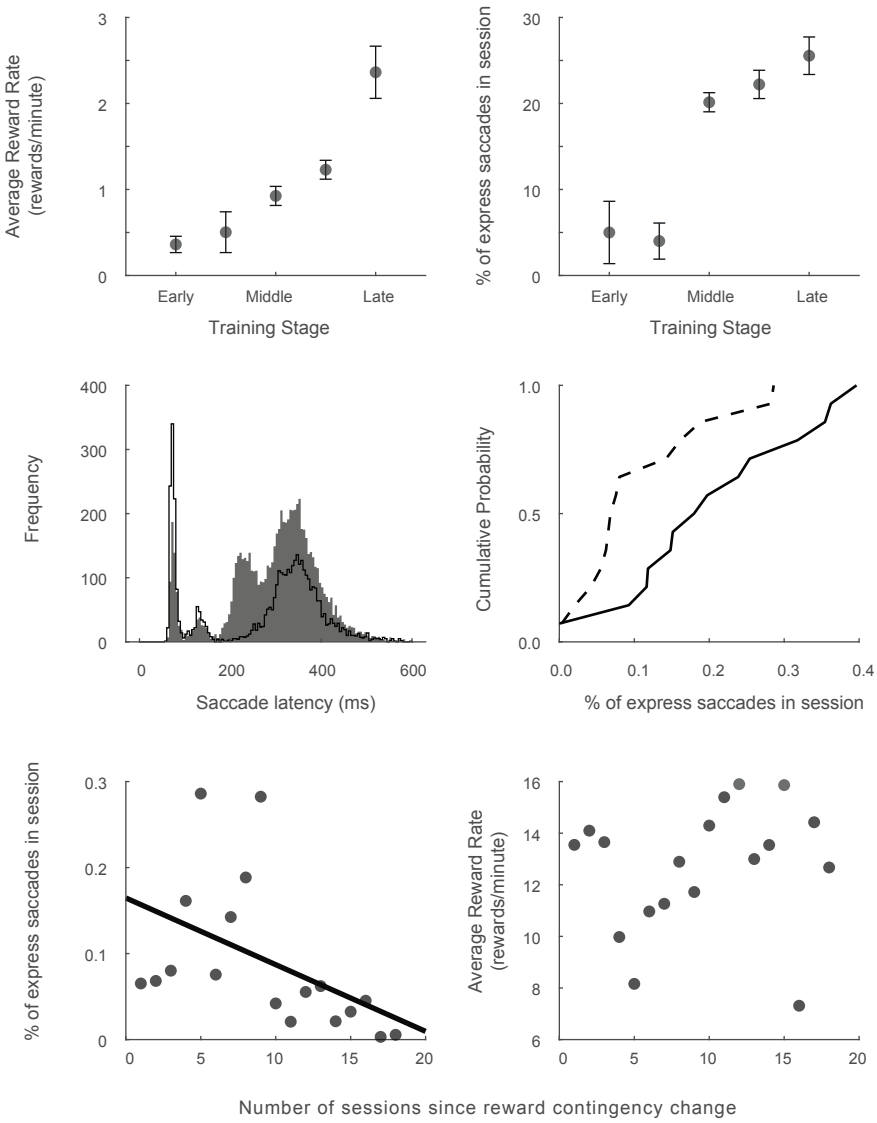

Figure 6: Learning and unlearning express saccades. Variation of performance of monkey F as a function of training and task contingencies. **A**. Average reward rate earned from early to late stages of training in 18 sessions when express saccades were rewarded just like regular saccades on no stop trials. **B**. Percentage of express saccades produced across corresponding stages of training. The monkey exploited contingencies of the task to earn more reward by producing a fraction of express saccades. **C**. Distributions of saccade latencies when express saccades were rewarded (open) and in subsequent sessions when only no stop trials with regular saccade latencies were rewarded (filled). When express saccades were not rewarded, the monkey produced more regular latency saccades to earn reward. **D**. Cumulative probability of express saccade production in sessions when they were rewarded (solid) and in later sessions when they were not (dashed). **E**. The percentage of express saccades decreased across sessions following changing contingency to not reward express saccades. **F**. Average reward rate did not decrease across corresponding sessions following the change of reward contingency.

Table 1: *Average ± SD saccade latencies and proportion of express saccades across data sets.*

		Ageing						**Non-ageing**			
		Monkey F (n = 84)		**Monkey H Early** (n = 31)		**Monkey H Later** (n = 157)		**Monkey Eu** (n = 12)		**Monkey X** (n = 17)	
RT relationship	Saccade type	RT (ms)	P(Express)	RT (ms)	P(Express)	RT (ms)	P(Express)	RT (ms)	P(Express)	RT (ms)	P(Express)
RT(Non-canceled) > RT(No stop)		n = 50 sessions		n = 14 sessions		n = 83 sessions		n = 3 sessions		n = 0 sessions	
	No-stop	225.8 ± 49.8	0.139 ± 0.119	372.5 ± 41.3	0.038 ± 0.056	261.4 ± 41.5	0.151 ± 0.084	303.7 ± 1.6	-	-	-
	Non-canceled	249.8 ± 50.3	0.042 ± 0.075	429.6 ± 74.6	0.006 ± 0.013	301.2 ± 51.9	0.110 ± 0.114	316.6 ± 17.7	0.003 ± 0.005	-	-
RT(Non-canceled) < RT(No stop)		n = 34 sessions		n = 17 sessions		n = 74 sessions		n = 9 sessions		n = 17 sessions	
	No-stop	237.8 ± 52.2	0.105 ± 0.138	391.7 ± 47.9	0.049 ± 0.075	267.0 ± 59.3	0.172 ± 0.100	314.7 ± 15.5	0.004 ± 0.004	265.8 ± 18.9	0.003 (0.003)
	Non-canceled	221.0 ± 52.4	0.112 ± 0.177	358.0 ± 48.2	0.042 ± 0.062	240.3 ± 66.7	0.195 ± 0.210	270.9 ± 15.6	0.009 ± 0.009	232.4 ± 12.9	0.006 (0.006)
Saccade type	Saccade type	RT (ms)		RT (ms)		RT (ms)		RT (ms)		RT (ms)	
All	**No-stop**	230.7 ± 50.8		383.0 ± 45.3		265.0 ± 50.6		311.9 ± 14.2		265.8 ± 18.9	
	Non-canceled	238.1 ± 52.8		390.3 ± 70.5		272.5 ± 66.5		282.3. ± 25.7		232.4 ± 12.9	
Regular	**No-stop**	252.5 ± 45.7		397.1 ± 42.2		297.8 ± 46.8		312.6. ± 14.4		266.3 ± 19.1	
	Non-canceled	249.9 ± 46.5		397.7 ± 66.1		301.8 ± 53.8		283.8. ± 25.6		233.3 ± 13.1	
Express	**No-stop**	72.1 ± 6.7		80.1 ± 8.9		84.0 ± 3.4		68.5 ± 2.5		85.5 ± 14.6	
	Non-canceled	71.0 ± 5.5		81.6 ± 4.9		84.1 ± 4.1		71.2 ± 8.4		85.3 ± 13.1	

Table 2: *Number of significant foreperiod and saccade latency correlations for each foreperiod distribution, each saccade type (all, regular, or express), and each trial type (all, no-stop, and non-canceled).*

	Foreperiod	**Ageing**			**Non-ageing**	
Saccade type	Trial type	**Monkey F**	**Monkey H Early**	**Monkey H Later**	**Monkey Eu**	**Monkey X**
All saccades	**All**	34/84 (33 negative)	2/31 (1 negative)	54/157 (1 negative)	0/12 (0 negative)	9/17 (9 negative)
	No-stop	35/84 (34 negative)	2/31 (1 negative)	51/157 (1 negative)	1/12 (0 negative)	7/17 (7 negative)
	Non-canceled	9/84 (9 negative)	1/31 (0 negative)	31/157 (4 negative)	2/12 (1 negative)	5/17 (5 negative)
Regular saccades	**All**	27/84 (26 negative)	2/31 (0 negative)	11/157 (6 negative)	0/12 (0 negative)	10/17 (10 negative)
	No-stop	30/84 (28 negative)	5/31 (2 negative)	15/157 (9 negative)	1/12 (0 negative)	6/17 (6 negative)
	Non-canceled	11/84 (10 negative)	1/31 (0 negative)	12/157 (4 negative)	2/12 (1 negative)	5/17 (5 negative)
Express saccades	**All**	4/84 (3 negative)	0/31 (0 negative)	7/157 (5 negative)	0/12 (0 negative)	0/17 (0 negative)
	No-stop	4/84 (3 negative)	0/31 (0 negative)	5/157 (3 negative)	0/12 (0 negative)	0/17 (0 negative)
	Non-canceled	1/84 (0 negative)	2/31 (0 negative)	4/157 (4 negative)	1/12 (1 negative)	1/17 (1 negative)

Table 3: *Average ± SD saccade latencies and proportion of express saccades generated as a function of previous trial outcome.*

		Ageing			Non-ageing	
	Monkey	**Monkey F**	**Monkey H (Earlier)**	**Monkey H (Later)**	**Monkey Eu**	**Monkey X**
	Previous trial	n = 84	n = 31	n = 157	n = 12	n = 17
RT	**No-stop**	232.25 ± 52.48 ms	378.31 ± 67.07 ms	266.50 ± 57.77 ms	274.80 ± 20.74 ms	247.09 ± 13.48 ms
	Canceled	250.89 ± 49.94 ms	393.22 ± 45.50 ms	272.42 ± 54.59 ms	340.02 ± 23.66 ms	329.21 ± 35.04 ms
	Non-canceled	229.63 ± 59.67 ms	401.03 ± 61.95 ms	271.87 ± 59.60 ms	319.03 ± 15.32 ms	255.17 ± 18.23 ms
P(Express)	**No-stop**	12.02 ± 13.00%	5.75 ± 12.30%	15.58 ± 11.52%	0.67 ± 0.91%	0.38 ± 0.47%
	Canceled	6.92 ± 10.57%	2.09 ± 4.15%	14.60 ± 12.24%	0.06 ± 0.19%	0.14 ± 0.39%
	Non-canceled	14.27 ± 19.50%	2.40 ± 5.03%	15.51 ± 14.63%	0.11 ± 0.37%	0.10 ± 0.40%