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Dynamics of saccade target selection: Race model analysis of double step and search step saccade production in human and macaque

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Abstract

We investigated how saccade target selection by humans and macaque monkeys reacts to unexpected changes of the image. This was explored using double step and search step tasks in which a target, presented alone or as a singleton in a visual search array, steps to a different location on infrequent, random trials. We report that human and macaque monkey performance are qualitatively indistinguishable. Performance is stochastic with the probability of producing a compensated saccade to the final target location decreasing with the delay of the step. Compensated saccades to the final target location are produced with latencies relative to the step that are comparable to or less than the average latency of saccades on trials with no target step. Noncompensated errors to the initial target location are produced with latencies less than the average latency of saccades on trials with no target step. Noncompensated saccades to the initial target location are followed by corrective saccades to the final target location following an intersaccade interval that decreases with the interval between the target step and the initiation of the noncompensated saccade. We show that this pattern of results cannot be accounted for by a race between two stochastically independent processes producing the saccade to the initial target location and another process producing the saccade to the final target location. However, performance can be accounted for by a race between three stochastically independent processes – a GO process producing the saccade to the initial target location, a STOP process interrupting that GO process, and another GO process producing the saccade to the final target location. Furthermore, if the STOP process and second GO process start at the same time, then the model can account for the incidence and latency of mid-flight corrections and rapid corrective saccades. This model provides a computational account of saccade production when the image changes unexpectedly.

Keywords

saccade; race model; latency; double step; search step; decision making

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1. Introduction

The double step task has been used to investigate how targets for saccades are selected and how saccade initiation is controlled by stepping the target to a new location while a saccade to the initial location is prepared but not yet executed (Aslin and Shea, 1987;Becker and Jürgens, 1979;Komoda, Festinger, Phillips, Duckman and Young, 1973;Lisberger, Fuchs, King and Evinger, 1975;Ottes, Van Gisbergen and Eggermont, 1984;Van Gisbergen, Van Opstal and Roebroek; 1987). Many studies have found that performance is stochastic and that the probability of compensating for the target step by directing gaze to the final target location decreases with the delay of the step, presumably because of the advancing commitment to shift gaze to the initial target location. Studies have also found that corrective saccades are commonly produced after errors and that the latencies of these corrective saccades are short enough to require explanation in terms of preparing the corrective saccade before the consequences of the errant saccade can be registered.

We have employed a search step variant of the double step task to investigate the neural basis of saccade target selection in macaque monkeys. In the search step task the target is presented with distractors, and the step consists of an isoluminant color change such that the initial target becomes a distractor and one of the distractors becomes the target. We have found that visually responsive neurons in the frontal eye field select the location of the stepped target even if monkeys fail to compensate and direct gaze errantly to the initial target location (Murthy, Thompson and Schall, 2001). We have also found that movement-related activity in frontal eye field producing the corrective saccade begins before the consequences of the errant saccade to the initial target location could be registered (Murthy, Ray, Shorter-Jacobi, Priddy, Schall and Thompson, 2007).

The present study had three purposes. First, we investigated how performance of the search step task differs from performance of the double step task. This was necessary because the delay of saccade latency to a target in a search array as compared to single target may change performance (Findlay and Walker, 1999;Schiller, Sandell and Maunsell, 1987). It was also necessary to determine how the well-known effects of array size and similarity between the target and distractors affect responses to the target step (Wolfe, 1998). Second, we investigated whether humans and macaque monkeys perform differently in the double step and search step tasks. This was necessary because an earlier report indicated that macaque performance was different from human (Baizer and Bender, 1989). Third, we investigated whether performance could be fit by a race model because earlier reports had suggested that this was the case but had not tested it formally (Becker and Jürgens, 1979). We found that search step and double step performance are only quantitatively different, that human and macaque monkey performance are qualitatively indistinguishable and that performance can be accounted for by a race between a GO process producing the saccade to the initial target location, a STOP process interrupting that GO process and another, ongoing GO process producing the saccade to the final target location. These results provide new insights into the computations underlying saccade target selection and the control of saccade initiation.

2. Methods

2.1. Double step and search step tasks

The double step and search step tasks were run in blocks consisting of two randomly interleaved trial types: no-step and target-step trials (Figure 1). On *no-step trials* the target remained at the location it first appeared until it was fixated through a gaze shift. On *target-step trials* the target jumped to a different location before the gaze shift to the initial location was initiated. The no-step trials were necessary to prevent monkeys and humans from waiting excessively long for the target step. The target-step trials were necessary to investigate how the visual and saccade system respond to unexpected changes of the image during saccade preparation.

More specifically, in double step blocks the colored target appeared alone, and in search step blocks the target appeared among distractors of a uniformly different color from the target. On *no-step trials* the target appeared and remained in the same location until the saccade was made and the target was fixated for at least 400 ms. On *target-step trials*, the target stepped from its original location to a new location in the array after a variable delay, called *target step delay* (TSD). In the double step task, the target disappeared from its original location and reappeared at one of seven possible new locations. In the search step task, through an isoluminant color change the target became a distractor, and one of the distractors became a target. It is important to note that unlike other recent investigations of the effects of unexpected image changes on attention allocation and saccade production, no new stimuli appeared (e.g. van Zoest, Donk and Theeuwes, 2004).

Saccades to the final target location were referred to as *compensated saccades* (referred to by some other authors as final angle responses: Aslin and Shea, 1987;Becker and Jürgens, 1979) and were rewarded. Saccades to the initial target location were referred to as *noncompensated saccades* (referred to by some other authors as initial angle responses: Aslin and Shea, 1987;Becker and Jürgens, 1979). These were never rewarded. Noncompensated saccades were often followed by *corrective saccades* that directed gaze from the errant landing spot to the final target location. These too were never rewarded.

Target step delay was varied in a staircase fashion so that on average subjects produced an equal number of noncompensated and compensated saccades in step trials. Following compensated trials the TSD was increased. Following noncompensated trials the TSD was decreased. With each step of the staircase, TSD was increased or decreased by 47 ms for humans and 17 ms for macaques (TSDs were time-locked to a screen refresh and there were small differences in monitor refresh rates in the systems used to test humans and macaques). Accordingly, the shortest and longest TSDs did not yield as much data and so resulted in noisier data. Thus, step delays that did not amount to at least 2.5% of the total number step trials were not analyzed, leaving 4–5 step delays with sufficient data for each subject. Trials with anticipatory saccades with saccade latencies less than 50 ms were excluded from analyses.

2.2. Experimental design - humans

Three human subjects took part in 24 one-hour sessions (4 double step and 20 search step). Two of the subjects were familiar with the purpose of the experiment and one subject was naïve. The naïve subject was compensated for his time. All subjects had normal or corrected-to-normal vision. Informed consent was obtained before the experiment began and the experimental procedure was approved by the Vanderbilt University Institutional Review Board.

Each session consisted of five blocks of 96 trials, of which 40% were target-step trials. Task type (double step or search step) and target color (four possible colors) were blocked within a session. Within a search step session, the target could appear among 1, 3, or 7 distractors, yielding set sizes of 2, 4, and 8, respectively. The color similarity of the target to the distractors was also manipulated. Set size and similarity manipulations were interleaved within search step blocks. Stimuli were 1.5º squares at 9.5º eccentricity presented on a gray background (43.7 cd/m^2). Four isoluminant (11.0 cd/m^2) colors were used for these stimuli: green (CIE × = 291, Y = 600), gray-green (CIE × = 355 Y = 550), red (CIE × = 605 Y = 358) and gray-red (CIE × = 554, Y = 399). Humans first fixated on a black 0.5° cross which stayed on for the duration of the trial. Regardless of set size, targets were arranged with equal spacing and eccentricity about the fixation point, and orientation of the array varied between trials. On double-step blocks, the target disappeared from one location and immediately reappeared at a new location. On search-step blocks, the target changed through an isoluminant color change to a distractor at the initial location and a distractor changed to the target at the final location. The target step was always at least 90°, so in trials with set size eight, the target never stepped to an adjacent distractor position.

Eye position was recorded with an EyeLink II tracker (SR Research) at 250 Hz temporal resolution and a stated spatial resolution of 0.01°. An eye movement was classified as a saccade if velocity exceeded 35°/s. Correct no-step and compensated trials were rewarded with a tone.

2.3. Experimental design - monkeys

Data were also collected from three adult monkeys (2 *Macaca mulatta* and 1 *M. radiata*) weighing 7–12 kg. The animals were cared for in accordance with the National Institute of Health's Guide for the Care and Use of Laboratory Animals and the guidelines of the Vanderbilt Animal Care and Use Committee. Data acquisition methods have been described elsewhere (Hanes and Schall, 1995). Monkeys were tested in 5–15 sessions of approximately 500–2000 trials each, of which 50% were step trials. Task type and target color were blocked within a session. No set size or target-distractor similarity manipulations were used. The search step task used homogeneous distractors and a chromatically dissimilar target in a set size of 8. Stimuli were 1° square stimuli at 10° eccentricity, presented on a gray background (2.0 cd/m^2). Two isoluminant (10 cd/m^2) colors were used for these stimuli: red (CIE × = 632, Y = 340) and green (CIE × = 279, Y = 615). Target and distractor color were alternated across sessions. The monkeys first fixated a 0.5° white square that disappeared at target onset. Stimuli could be located at any of the vertices of an octagon centered around the fixation point. On no-step trials the target remained at its original location until it was fixated through a gaze shift. Since the behavioral data was recorded during single-unit recordings in the frontal eye field, a restricted set of targets steps was used to increase the yield of data during the neurophysiological sessions (see Murthy et al, 2007 for further detail). Targets could step to and from the three array positions centered around and the three array positions opposite to a neuron's response field, yielding 2*3*3 = 18 possible combinations of initial and final target positions. Thus, targets stepped into or out of response fields but never stepped within a response field. Target steps were randomized and were interleaved with no-steps trials in which target position was randomized and equiprobable across all locations.

Eye position was recorded with a scleral search coil. Experiments were under computer control using TEMPO/VIDEOSYNC software (Reflective Computing) that displayed visual stimuli, delivered juice, and sampled eye position at 250 Hz. An eye movement was classified as a saccade if velocity exceeded 30º /s. Correct no-step and compensated trials were rewarded with juice.

Examples of the eye movements that were produced in these tasks are shown in Figure 2. For both humans and monkeys, trials were classified as follows: On no-step trials, saccades with endpoints within 1.5º of the target were classified as correct (Figure 2A). On target-step trials, saccades with endpoints within 1.5º of the final target location were classified as compensated (Figure 2B). Those with endpoints within 1.5º of the initial target location were classified as noncompensated; these were often followed by unrewarded, corrective saccades to the final target location (Figure 2C). Infrequently, noncompensated saccades were interrupted in flight and replaced with a corrective gaze shift to the final target location (Figure 2D), or saccades were curved in the direction of the initial location (Figure 2E), these are referred to as partially compensated saccades. When a corrective saccade is present, the time between the noncompensated and corrective saccade is defined to be the *intersaccade interval* (ISI) (Figure 2C,D). *Reprocessing time* (RPT), the time available to process the target step before a noncompensated saccade is executed, is defined to be the time between the target step and the initiation the noncompensated saccade.

2.4. Race model logic

Becker and Jürgens (1979) proposed that double step saccade performance could be understood as the outcome of a race between the processes producing saccades to the initial and final target locations. To our knowledge this has not been tested quantitatively. However, a race model has been used extensively and successfully to describe behavior in the stop signal (countermanding) task (Logan, 1994;Logan and Cowan, 1984; see also Boucher, Palmeri, Logan, and Schall, 2007) as well as in tasks requiring stopping one response and producing another (e.g., DeJong et al. 1995). To determine whether a formal race model could account for performance of the saccade double step and search step tasks, we adapted the race model originally formulated to describe performance in the stop-signal task. Performance of the stop signal task is accounted for by a race between a stochastic process producing the saccade to the target and a process that interrupts that motor plan. Here, we investigated whether performance of double step and search step tasks can be accounted for by a race between a process producing the saccade to the initial target location and another process producing the saccade to the final target location. Alternatively, it is possible that an intervening stop process must interrupt the first saccade plan before the second saccade can be produced.

Each stochastic process is described by a unique distribution of finish times that satisfy two assumptions. First, the finish times of the respective processes are stochastically independent of one another. Second, they are contextually independent; the finish times of one process are not affected by the presence of another process. Thus, the distribution of finish times of the first process is equivalent to the distribution of no-step saccade latencies (Figure 3A and B).

This race model makes at least two specific predictions about performance in the double step and search step tasks. First, it predicts that stepping performance is a function of TSD. The compensation function plots the probability of failing to respond to the new target position (noncompensated saccade) as a function of TSD. When the target steps earlier (shorter TSD), the probability of making a noncompensated saccade is low. With increasing TSD the probability increases that subjects make an error through noncompensated saccades to the initial target location. Since an increasing proportion of the no-step distribution escape reprogramming, the longer TSD becomes, a larger proportion of noncompensated saccades will be executed at longer TSDs. Therefore the race model predicts a compensation function that increases monotonically from 0.0 when TSD is very short to approach 1.0 when TSD is very long. Examination of a subject's compensation function provides an important check on performance; a bias or lack of sensitivity to the target step will result in a flat compensation function (Logan and Cowan, 1984).

Second, as TSDs get longer, an increasing proportion of the no-step distribution escapes reprogramming. This leads to distributions of noncompensated saccade latencies that incorporate an increasing fraction of the distribution of no-step saccade latencies. Thus, the race model predicts that with increasing TSD the distribution of noncompensated saccade latencies will progressively approach the distribution of no-step trial saccade latencies. Violations of stochastic independence of the finish times in the race model are revealed by departures from this prediction (e.g., Band, van der Molen and Logan, 2003;Logan, Cowan and Davis, 1984;Osman et al. 1986). In particular, if the racing processes inhibit each other, then noncompensated saccade latencies would be longer than no-step saccade latencies. This is observed very rarely (but see Hanes and Carpenter, 1999;Colonius, Özyurt and Arndt, 2001;Özyurt, Colonius and Arndt 2003).

Accounting for double-step saccade performance in terms of a race between GO and STOP processes affords a theoretical bridge to the well-known race model applied to stop signal task performance (Logan and Cowan, 1984;Logan 1994). The race model of countermanding performance provides a measure of the duration of the inhibition process referred to as *stop signal reaction time*. Conceptually and mathematically, TSRT corresponds to stop signal reaction time. Therefore, the methods used to estimate stop signal reaction time can be used as well to measure TSRT (Logan and Cowan, 1984;Logan, 1994;Hanes and Schall, 1995).

According to the race model applied to the double step saccade task, performance on a target-step trial is determined by the outcome of a race between the process producing the saccade to the original target location and the process(es) interrupting that saccade and producing the saccade to the final target location. Two aspects of the behavioral performance data were used to estimate TSRT. The first is the distribution of saccade latencies collected on no step trials; this is the distribution of finish times of the first GO process (figure 3). The second is the fraction of noncompensated trials for each target step delay. Referred to as the compensation function, this is the fraction of trials in which the first GO process finished before the STOP process finished. We used two methods to estimate TSRT for each session. First and most simply, according to Logan and Cowan (1984), mean TSRT equals the difference between the mean saccade latency during no step trials and the mean of the compensation function. The mean of the compensation function is determined by treating the compensation function as a cumulative distribution and converting it to a probability density distribution. The mean of the compensation function is simply the mean of this probability density distribution.

The second method provides an estimate of the TSRT at each stop-signal delay. By this method TSRT is estimated by integrating the distribution of latencies on no step trials, beginning at the time of target presentation, until the integral equals the proportion of noncompensated saccades observed at that target step delay. The saccade latency at the integrated value yielding the appropriate fraction of noncompensated trials measures the finish time of the race, i.e., the longest saccade latency in which the GO process could finish before the deadline imposed by the STOP process for that stop-signal delay. Thus, the time between the appearance of the target step and this deadline represents the TSRT at this target step delay. In practice, TSRT is determined by first rank ordering the no step trial saccade latencies. The i^{th} saccade latency is then chosen, where i is determined by multiplying the probability of a noncompensated trial at a given target step delay multiplied by the total number of no step trials. The TSRT is the difference between the i^{th} saccade latency and the target step delay.

The TSRT estimated using the mean of the compensation function and by integrating the no step trial saccade latency distribution can vary somewhat. Further, the TSRT estimated with data from early or late target step delays can be unreliable (Hanes and Schall 1995). Therefore, we believe the most reliable overall estimate of TSRT for a session is the average of the TSRT derived from both methods.

We analyzed the patterns of behavior from both search and double step tasks to determine whether performance could be explained in terms of an independent race model.

3. Results

3.1. Effects of search and target-distractor similarity on saccade latency

Before evaluating whether performance conforms to the predictions of the race model and testing alternative race model architectures, we must first describe the effects of the experimental manipulations. We compared the latencies of saccades produced in blocks of double step trials in which the target appeared alone to the latencies of saccades produced in blocks of search step trials in which the target appeared with distractors. Human subjects were also tested with different search array set sizes with distractors that were more or less similar to the singleton target. Figure 4 compares for each human and monkey subject the mean latencies of no-step trial saccades, noncompensated saccades, and compensated saccades in blocks of double step and search step trials. As compensated saccades are made in response to the target step, the latencies of compensated saccades were measured relative to TSD. The latencies were submitted to a 2 (species - macaque or human) × 2 (task type - double step or search step) × 3 (type of trial - no step, compensated or noncompensated) mixed design (between- and within-subject effects) repeated measures univariate ANOVA; for this and all subsequent tests, statistical significance was determined using an alpha level of $p < .05$. Several trends were significant. First, there was a within-subject main effect of the presence of distractors on saccade latency ($F(1, 4) = 9.804$, MSE = 10167). We also found a significant interaction of distractor presence and species ($F(1,4) = 10.164$, MSE = 10540); in other words, it appeared the monkeys and humans exhibited different patterns of saccade latencies when the target was presented alone or with distractors, but we believe this is incidental. All human subjects and two of the three monkeys exhibited saccade latencies during search step that were systematically longer than those in double step. Second, overall human and macaque performance was not significantly different; there was no significant between-subject main effect of species ($F(1, 4) = 1.642$, $p = 0.269$, MSE = 9557). Third, individual differences were evident in the monkeys' performance. One monkey (F) exhibited no difference in saccade latencies in double step and search step blocks (2 (task type) × 3 (response type) mixed design (between- and within-session effects) repeated measures univariate ANOVA F(1,40 = 0.096, MSE = 224630, $p = 0.75$), and another monkey (L) exhibited significantly longer saccade latencies during double step as compared to search step blocks (F(1,40 = 77.6, MSE = 112124). The monkeys probably delayed saccade initiation when the target appeared without distractors because, unlike humans, they had been trained to perform memory-guided saccades to a target presented alone. Fourth, there was a within-subject main effect of the type of trial ($F(2, 8) = 9.804$ MSE = 10874). Specifically, the latencies of noncompensated saccades were less than the latencies of saccades in no-step trials, and the latencies of compensated saccades measured relative to the target step were less than the latencies of saccades on no-step trials.

Figure 5 compares for each human subject the mean latencies of no-step trial saccades, noncompensated saccades and compensated saccades as a function of set size (2, 4, 8) and target-distractor similarity. The latencies were submitted to a 2 (similarity) × 3 (set size) × 3 (type of trial - no step, compensated or noncompensated) between-subject repeated measures univariate ANOVA. Several results were evident. First, saccade latencies were elevated when the target and distractors were more similar in color (2 (similarity) × 3 (set size) × 3 (response type) repeated measures univariate ANOVA subject CC: $F(1,19) = 39.9$, MSE = 61490; subject LB: $F(1,19) = 17.6$, MSE = 37587; subject SS: $F(1,19) = 26.5$, MSE = 163527). Second, though, there was not a significant overall effect of set size ($F(2,4) = 0.87$, MSE = 710, $p = 0.918$), target-distractor similarity ($F(2,4) = 5.701$, MSE = 4431, $p = 0.140$) nor a significant interaction of set size and target-distractor similarity ($F(2,4) = 1.769$, MSE = 595, $p = 0.282$). One of the three subjects exhibited a significant elevation of saccade latency with set size when the target was similar to distractors but not when they were dissimilar (subject CC: $F(2,19) = 16.8$, MSE = 25965). Third, there was a significant main effect of response type ($F(2,4) = 9.719$, MSE = 2922); saccade latencies in compensated and noncompensated trials were significantly shorter than those in no-step trials. This was the case for all three subjects (subject CC: $F(2,19) = 22.0$, MSE = 34023; subject LB: $F(2,19) = 28.7$, MSE = 61448; subject SS: $F(2,19) = 33.8$, MSE = 209253). Thus, saccade latencies were elevated when the target and distractors were more similar in color, but no consistent effect of set size on reaction time was present

3.2. Target step performance: comparison to race model predictions

The race model applies to data of a particular form; in other words, it entails certain requirements about the quality of performance. In particular, the race model predicts a monotonically increasing compensation function as a function of TSD. Also, the independence of the racing processes predicts that the latencies of noncompensated saccades must not exceed the latencies of no-step trials saccades. This section will demonstrate that the performance of humans and monkeys performing both double step and search step conforms to these predictions. Performance of a representative human subject 'SS' will be used for illustration, and the results for all subjects and conditions are detailed in Table 1.

Figure 6 shows the compensation function for this subject's double step performance. As expected, the probability of not compensating for the target step increased monotonically from close to 0.0 at the shortest TSD toward 1.0 at the longest TSD.

To compare the distributions of noncompensated saccade latencies with the predictions of the race model, Figure 7A plots the cumulative distributions of noncompensated saccade latencies produced following four TSDs along with the cumulative distribution of saccade latencies in no-step trials for this representative subject. Two trends are characteristic of the data from all subjects, both human and monkey. First, the latencies of noncompensated saccades are shorter than the latencies of no-step trial saccades. Second, noncompensated saccades produced at shorter TSDs had shorter latencies than those produced at longer TSDs.

A fundamental motivation of the description of these data in terms of an independent race between the process producing the saccade to the initial target location and a process interrupting that saccade plan is the observation that noncompensated saccade latencies rarely if ever exceed no-step saccade latencies. If noncompensated saccade latencies routinely exceeded no-step saccade latencies, this would be evidence that the processes responding to the target step slowed the process producing the initial saccade. Such an interaction would violate the fundamental assumption of stochastic independence of the finish times of the racing processes (Colonius et al., 2001). To carry out the most sensitive test possible for such violations, we performed a Kolmorogoff-Smirnoff test to assess whether the noncompensated saccade latency distribution was significantly different from the no-step saccade latency distribution. Figure 7B illustrates the results of this analysis for all 27 double step and search step sessions of both monkeys and humans. Each point plots the difference between the no-step and noncompensated latency cumulative distributions at each TSD. To evaluate the difference between the distributions, the measure was defined to be the mean difference of the values at their respective quintiles. In a given session, there is one noncompensated distribution per TSD, and lines between the points connect data from the same session. These points are filled if the noncompensated distribution was significantly different from the no-step distribution according to a Kolmorogoff-Smirnoff test, and are not filled otherwise.

Out of 101 target step delays, in only three delays across three different sessions were the latencies of noncompensated saccades significantly longer than those in no-step trials; this occurred in three different subjects. The fact that the overwhelming majority of noncompensated saccade latencies do not exceed no-step saccade latencies provides convincing evidence of stochastic independence, establishing the basis for applying a race model analysis of the data. As further evidence of the independence of these processes, the few violations occur only at the longest TSD. If the processes interacted, one would expect greater delays for noncompensated saccade latencies at the shortest TSD, because the processes have the longest time to interact. Instead, these few noncompensated delays occurred only at the longest step delays, which is not consistent with interacting processes. Thus, the latencies of noncompensated error saccades correspond to what is predicted if they are the outcome of a race between processes producing the alternative saccades.

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3.3. Target step reaction time

As previously discussed, application of the race model to stepping performance affords a measurement of the time taken to cancel the first saccade in order to produce the compensated saccade. This perspective on these data and analysis are motivated by the application of the race model to characterize performance in stop signal tasks by *stop signal reaction time* (Logan and Cowan 1984). In parallel, we define the time to interrupt the incomplete motor program in response to the target step as *target step reaction time* (TSRT). This quantity is determined as described in Methods. We now analyze whether TSRT was different in double step as opposed to search step blocks and whether TSRT is affected by search array set size or target-distractor similarity. Figure 8A plots mean TSRT for double step and search step performance for monkeys and humans. TSRT was ~40 ms longer during search step blocks as compared to double step blocks for both humans and monkeys. A 2 (task type) × 2 (species) repeated measures mixed design (within- and between-subject effects) ANOVA demonstrated a significant within-subject effect of the presence of distractors ($F(1,2) = 30.544$, $MSE = 4236$). However, TSRT did not differ between humans and macaques ($F(1,4) = 0.498$, $MSE = 61$, $p = 0.519$). Figure 8B shows mean TSRT for humans performing search step with different set sizes and target-distractor similarity. TSRT was significantly longer in trials with similar target and distractors than in trials with dissimilar target and distractors ($F(1,2) = 1057.917$, $MSE = 22400$), but TSRT did not change with set size ($F(2,4) = 0.545$, $MSE = 112$, $p = 0.617$).

We found that TSRT measured by the method of integration decreased with TSD (data not shown). This is observed commonly in measurement of stop signal reaction time. While it may be an indication that the independence premise of the race model is violated, it is most likely due to the sampling from the no-step trial saccade latency distribution (Logan and Cowan, 1984;Band et al. 2003).

3.4. Compensated saccade latencies

Earlier research reported a ~30 ms delay of compensated saccade latencies on step trials measured relative to the target step, as compared to the latencies of saccades on no-step trials (Aslin and Shea, 1987;Becker and Jürgens, 1979). This difference was interpreted as evidence for a cost entailed by canceling the saccade to the initial target location before the saccade to the final target location could be prepared. Figure 9A compares the distributions of latencies of compensated saccades at four TSDs with those observed in no-step trials measured from the time of initial array presentation. Because compensated saccades are responses to the target step, their latencies measured relative to target presentation increase with TSD. However, because the compensated saccades are made in response to the target step, one can compare their latencies with no-step saccade latencies by subtracting TSD from the compensated latencies (Figure 9B). For this subject, compensated saccades to the final target location occur with latencies markedly less than those of no-step saccades.

To see if this trend is consistent across subjects, Figure 9C shows results of a comparison of compensated saccade latencies (with TSD subtracted) and no-step saccade latencies for each TSD from all human and monkey double step and search step sessions. Again, each point plots the difference between the latency of no-step trial saccades and the latency of compensated trial saccades relative to the target step, measured as the mean difference at their quintiles as a function of TSD. Lines connect points from the same subject and condition. For this analysis, we are interested in a delay measured as a difference of the central tendencies (means) of the distributions, so a t-test was used to determine if the means were significantly different from each other. Solid points indicate a significant difference and empty points indicate a non-significant difference. Points less than zero indicate a delay of the compensated saccades relative to no-step saccades, while points above zero indicate compensated saccade latencies that are faster than no-step saccade latencies.

Out of 101 delays, only four TSDs over four different sessions yielded data in which compensated saccades were produced with latencies significantly greater than the no-step distribution; these occurred across three different subjects, reducing further the sense of any trend. In general, then, compensated saccades when measured from the time of the step, had latencies significantly shorter than those observed in no-step trials. This absence of a delay, consistently seen across task types and species, suggests that there may be insufficient time for an explicit stopping process to occur before beginning the preparation of the second saccade.

3.5. Corrective saccades

Another feature of saccade production in the double step and search step tasks is the occurrence of corrective saccades after noncompensated errors (e.g., Becker and Jürgens, 1979). In fact, many investigators use double step target presentation to investigate how the visuomotor system performs coordinate transformations to accomplish these corrective saccades (e.g., Colby and Goldberg, 1999;Andersen and Buneo, 2002). We were more interested in determining the incidence, timecourse, and latencies of these corrective saccades. Becker and Jürgens (1979) showed that the interval between error and corrective saccades in a double step task varied with the latency of the first saccade relative to the target step. In this interval the visual system could update its representation of the image to identify the new target location, but once the first saccade was initiated, visual processing could not continue. The longer this interval (that is, the longer the latency of the error saccade to the initial target location), the more time was available to locate the new target. Accordingly, if an error was made, then the more time available to process the target step, the earlier the error could be corrected. In fact, this is just what has been observed. The time between the initial noncompensated saccade and the corrective saccade will be referred to as the *intersaccade interval* (ISI). Previous work has demonstrated that ISI is a function of the interval between the initiation of the noncompensated saccade and the target step (Becker and Jürgens, 1979). We refer to the interval between the initiation of the noncompensated saccade and the target step as *reprocessing time* because it is the period of time available for a target that stepped to the new location to be reprocessed (Becker and Jürgens, 1979).

Figure 10 plots the intersaccade interval between the noncompensated saccades and subsequent corrective saccades as a function of reprocessing time for a representative subject. Most of the noncompensated saccades terminated at the initial target location and were followed by corrective saccades that were produced earlier with respect to the start of the noncompensated saccade the later the noncompensated saccade was initiated after the target step. In other words, ISI decreases as noncompensated saccade latency increases. The few noncompensated trials that did not culminate in a corrective saccade were from the human hard search condition in which the subject simply failed to locate the target. A few of the noncompensated saccades, called partial compensated saccades, were interrupted mid-flight and had amplitudes less than the distance to the initial target location (Figure 10B); these may have curved trajectories. These tended to be observed at the longest reprocessing time and were always followed by corrective saccades to the final target location and these were initiated an unusually short time after the noncompensated saccade. A significant negative correlation between ISI and RPT was observed in nearly all sessions for noncompensated saccades for both human and monkey, for double step and search step regardless of set size or target-distractor similarity (Table 2). These observations indicate that the corrective saccade was prepared in parallel with the noncompensated saccade or at least that the corrective saccades can be produced in much less time than typical saccade latencies (Murthy et al., 2007).

3.6.1 Fitting race models to data—So far, we have shown that human and macaque production of saccades in double step and search step tasks is consistent with the predictions of an independent race model. In fact, the data obtained from monkeys and humans performing double step and search step saccades replicates in major respects what has been collected in earlier studies of human performance. It has been suggested that such data can be described as the outcome of a race between competing processes (Becker and Jürgens, 1979), but this has not been tested formally. Also, the nature of this reprogramming process is still unclear. On the one hand, the race has been conceived of as occurring between the two processes producing the alternative saccades to the initial and final target location. On the other hand, a delay of compensated saccades relative to no-step saccade latencies has been taken as evidence for a stopping process (Aslin and Shea, 1987;Becker and Jürgens, 1979). Yet, in our data no such delay was observed. In fact, we observed for most humans and macaques systematically shorter latencies of compensated saccades relative to the step. Therefore, through quantitative model fitting we have tested whether double step and search step performance can be accounted for by a race between independent processes, and what processes must participate in that race.

Figure 11 diagrams the three alternative architectures we analyzed. The tips of the arrows in figure 11 represent the finish times of the processes. The first architecture is simply a race between the process producing the saccade to the initial target location (GO1) and the process producing the saccade to the final target location (GO2), so this will be referred to as the *GO-GO* architecture. GO1 starts when the target appears, and GO2 starts when the target steps. It is well-known that an architecture like this will result in latencies in step trials that are shorter than those in no-step trials (Townsend and Ashby, 1983). The fact that both noncompensated and compensated saccades had latencies less than the no-step saccade latencies suggests that this architecture may be sufficient to account for the observed data.

Alternatively, the previous evidence for a cost associated with producing compensated saccades (Aslin and Shea, 1987;Becker and Jürgens, 1979) suggests that a STOP process must be included that interrupts the GO1 process and delays initiation of the second saccade. We investigated two architectures that included a STOP process. In the first, STOP must interrupt the GO1 process before the GO2 process can begin; this will be referred to as the *GO-STOP-GO* architecture. In the second architecture, the GO2 process began synchronously with the STOP process; this will be referred to as the *GO-GO+STOP* architecture.

To evaluate these three architectures, we quantitatively fitted Monte Carlo simulations of these architectures to the data collected from the individual monkeys and humans. First, the finish times of each racing process were drawn from independent Weibull distributions. These finish times were taken as the saccade latency which would include all afferent and efferent delays. The Weibull distribution was chosen because it is easily parameterized and provides a good account of observed saccade latency distributions (Becker, 1989;Van Zandt, 2000). The Weibull distributions were defined by three parameters according to the following equation:

$$f(x) = \frac{\alpha}{\beta} * \left(\frac{x-\mu}{\beta}\right)^{\alpha-1} * e^{-\left(\frac{x-\mu}{\beta}\right)^{\alpha}}$$

The shape parameter (α) affects the shape of the distribution of finish times, ranging from exponential for $\alpha < 1$ to nearly Gaussian with increasing magnitude of α. The scale parameter (β) largely affects the variability of the distribution of finish times. The positive location parameter (μ) shifts the lower bound of the distribution away from zero. For modeling data from each human and monkey, we allowed the GO1, GO2, and STOP Weibull distributions to have different shape, scale, and location parameter values.

We modeled the no-step condition and each of the target-step conditions using a Monte Carlo simulation with 50,000 trials per condition. On each simulated trial, finish times were sampled from the GO1 Weibull distribution, the GO2 Weibull distribution, and the STOP Weibull distribution (for the two architectures that assumed a STOP process). We denote a particular finish time sampled from the GO1 Weibull distribution as *go1*, from GO2 as *go2*, and from

STOP as *stop*. From these sampled finish times, the predicted response (compensated or noncompensated) and saccade latency on that trial were generated for different architectures using the rules described in the next paragraph. For all architectures, the distribution of latencies in no-step trials was simply the finish times of the GO1 process alone, consistent with the race model assumption of contextual independence.

In the GO-GO architecture, noncompensated saccades were produced when *GO1* was less than *TSD + GO2*, and compensated saccades were produced when *TSD + GO2* was less than *GO1*. In the GO-STOP-GO architecture, noncompensated saccades were produced when *GO1* was less than *TSD + STOP* and compensated saccades were produced when *TSD + STOP* was less than *GO1*. In the GO-STOP-GO architecture, the saccade latency on a compensated saccade was equal to *TSD + STOP + GO2*. For the GO-GO+STOP architecture, noncompensated saccades were produced when *GO1* was less than *TSD + STOP* and was also less than *TSD + GO2* . Compensated saccades were produced when *TSD + STOP* was less than *GO1* or *TSD + GO2* was less than *GO1*. For the GO-GO+STEP architecture, the saccade latency on a compensated saccade was equal to *TSD + GO2*.

Collating all of the individual trials from these Monte Carlo simulations produced a predicted saccade latency distribution for the no-step condition and predicted saccade latency distributions for compensated and noncompensated saccades in each target step condition (as well as a predicted compensation function relating the proportion of compensated and noncompensated saccades at each TSD). Our aim was to find Weibull parameters for GO1, GO2, and STOP that minimized the difference between predicted and observed saccade latency distributions. These distributions contained both the latencies, and frequencies of saccades, so this process also fits the compensation function.

We followed an approach to fitting models to saccade latency data recommended by Ratcliff and Tuerlinckx (2002). Specifically, we searched for parameters that minimized the lack of fit between model predictions and observed data as measured by a Pearson chi-square statistic (χ^2), defined by:

$$\chi^2 = \sum_i \sum_j \frac{\left(obs_{ij} - prd_{ij}\right)^2}{prd_{ij}}$$

The first summation over *i* indexes over the conditions in the experiment (i.e., no-step condition and the various target step conditions corresponding to the different values of TSD). In keeping with the standard use of a χ^2 statistic, within each condition a particular observed (*obs*) or predicted (*prd*) trial can have one of a discrete number of possible outcomes indexed over *j*. The χ^2 statistic compares the predicted frequency of each possible outcome (obs_{ij}) with the observed frequency of each possible outcome (prd_{ij}). On no-step trials, an observation could fall into one of six latency bins defined by the 10th, 30th, 50th, 70th, and 90th percentiles, and a model prediction could also fall into one of those six defined latency bins. Similarly, on target-step trials, an observation could fall into one of six latency bins defined by the cumulative latency distribution for compensated saccades or into one of six latency bins for noncompensated saccades; a model prediction could also fall into one of those defined latency bins depending on whether the predicted trial was compensated or noncompensated. For model predictions, the 50,000 simulated trials were used to generate the predicted *proportion* of trials falling into each latency bin and then these were converted into a predicted *frequency* of trials falling into each latency bin for each condition (see Tuerlinckx, 2004) for additional details on this procedure). Note that the compensation function is not fitted explicitly because the proportion of compensated versus noncompensated trials at each TSD is given by the distributions of finish times directly.

We independently fit predicted responses from each of the three model architectures to data from each subject and task condition. Best-fitting parameters were found by minimizing the χ^2 fit statistic using the subplex gradient descent optimization routine (Bogacz and Cohen, 2004;Rowan, 1990). This is an extension of the well-known simplex method (Nelder and Mead, 1965) that is well-suited for searching parameter spaces of stochastic models. Each parameter search was started from at least 40 randomly generated starting positions in order to avoid the possibility of settling into a local minimum in parameter space. All parameter searches were run on a parallel computer cluster consisting of several hundred dual-processor Linux systems supported by the Vanderbilt Advanced Computing Center for Research and Education.

3.6.2 Race model fits to primary saccade—Figure 12 compares the best-fitting performance of each model architecture in accounting for the data obtained in double step trials from one representative human subject. The figure displays the Weibull distributions for the component processes of the model architecture, observed and predicted compensation function, and observed and predicted cumulative latency distributions for noncompensated and compensated trials along with the no-step cumulative latency distributions. It is clear that the simplest model consisting of a race between two GO processes, the GO-GO architecture, did not fit the data very well for this subject. In contrast, the GO-STOP-GO and the GO-GO+STOP architectures fit the saccade latency distributions and reproduced the compensation function very well for this subject. Note that the GO2 distribution is earlier in the GO-STOP-GO architecture (Figure 12). Both architectures produce equivalent predictions because in the GO-STOP-GO architecture, the GO2 process is required to start later, after the STOP process finishes.

This pattern of best fitting architectures was obtained for all subjects performing both double step and search step tasks under all conditions (Table 3). In all cases, the GO-GO architecture produced fits that were substantially worse than both the GO-STOP-GO and GO-STOP+GO architectures as assessed by Akaike's Information Criterion (AIC) statistic (Akaike, 1973). Figure 13 shows scatterplots of predicted versus observed mean saccade latencies in no-step, noncompensated, and compensated trials, averaged across TSD to show how these alternative architectures accounted for each of the 27 data sets (6 double step and 21 search step across all subjects). The GO-GO architecture systematically overestimated the latencies of saccades in no-step and noncompensated trials. In contrast, both architectures with the STOP process produced excellent predictions of mean saccade latency in each kind of trial.

3.6.3 Race model account of target step reaction time—By instantiating a particular implementation of a stopping process, the GO-STOP-GO and GO-STOP+GO models can provide insights into what is measured by TSRT. Recall that TSRT measures the time needed to interrupt the planning of the first saccade. We calculated TSRT from the latency distributions and compensation functions produced by the model fit to each data set; this predicted TSRT was compared to the TSRT measured from the observed data (Figure 14). It is clear that the TSRT predicted by the models that included a STOP process agrees very well with the observed TSRT (Figure 14A,B). This is really just a reflection of the fact that the GO-STOP-GO and GO-GO+STOP architectures fit the saccade latencies and probability of saccade production so well.

The quality of this agreement permits us to explore in more mechanistic terms what TSRT measures. In general, if TSRT measures the time needed to interrupt the preparation of the first saccade, then TSRT should correspond to some measure of the finish time of the STOP process. On the one hand, TSRT could measure the mean of the distribution of all finish times of the STOP process (i.e., the expected value of STOP, E(STOP)). However, this would entail that STOP processes that outlast GO1 could influence TSRT which is logically impossible. Therefore, alternatively, TSRT could measure the mean of only those finish times for which the STOP process finished before GO1 (i.e., E(STOP | STOP < GO1)). Figure 14 illustrates scatterplots of these two measures of STOP finish time as a function of TSRT derived from the model fits to each data set. This plot supports several conclusions. First, although TSRT varies with distractor presence and similarity to the target (Figure 8), there was generally very good agreement between the two measures of STOP finish time and TSRT. Second, for both architectures E(STOP) slightly overestimated the TSRT derived from the simulated data TSRT, and E(STOP | STOP < GO1) slightly underestimated TSRT. These deviations were significant as determined by t-tests testing whether the distribution of the differences between respective distributions were significantly different from 0 for the GO-STOP-GO architecture ($t(26) = 3.61$; $t(26) = -6.19$, for E(STOP) and E(STOP | *stop* < *go1*) respectively), and the GO-GO+STOP architecture ($t(26) = 3.47$; $t(26) = -6.47$, respectively). At the same time, these deviations were very small in absolute value, owing most likely to the small variability of STOP process finish times. Therefore, we conclude that TSRT provides a useful measure of the finish time of the STOP process, but the precise value depends on statistical sampling.

3.6.4 Race model fits to corrective saccade—According to the fits to the production of the primary saccade, whether it is a correct compensated saccade or an errant noncompensated saccade, the GO-STOP-GO and GO-GO+STOP architectures mimic one another. However, we found that another line of evidence can distinguish between them. The latency of corrective saccades can be derived from the model by assuming that the finish time of the GO2 sample following the GO1 sample is the initiation time of a corrective saccade to the final target location. Moreover, partial compensated saccades could occur if GO1 finishes before GO2 both of which finishing before STOP; in other words, the stop process is too slow to interrupt the saccade produced by GO1 but GO2 finishes early enough to affect the execution of the saccade in flight.

Figure 15 shows the predicted interval between noncompensated and corrective saccades as a function of the delay from the step until the noncompensated saccade is initiated (reprocessing time) for both the GO-STOP-GO and the GO-GO+STOP architectures with parameters from a representative subject. The general form of these plots resembles the observed data (Figure 10); however, on closer inspection diagnostic differences are evident. First, the GO-STOP-GO architecture by design cannot produce corrective saccades with latencies less than the finish time of the earliest STOP process because GO2 cannot start before STOP has finished. Therefore, intersaccade intervals less than the duration of the STOP process cannot occur. Second, the GO-STOP-GO architecture by design cannot produce partial responses with mid-flight corrections because GO2 cannot start before STOP is finished. In contrast, GO1 and GO2 can finish before STOP, albeit infrequently, in the GO-GO+STOP architecture (Figure 15C). Thus, the GO-GO+STOP but not the GO-STOP-GO architecture can account for the observations of intersaccade intervals less than ~60 ms as well as mid-flight corrections.

In the data collected from humans, mid-flight corrections were observed in 5.0 ± 1.8 (min = 2.6, max = 10.3) percent of trials. Assuming that mid-flight corrections occur when GO1 finishes 0 to 50 ms (assuming a 50 ms saccade duration) before GO2 with both finishing before STOP, then the GO-STOP-GO architecture predicted no mid-flight corrections because GO2 could not start until GO1 was stopped. However, across the range of best-fit parameters the GO-GO+STOP architecture predicted mid-flight corrections in 2.2 ± 2.7 (min = 0.0, max = 9.1) percent of trials. In the model fits, the range of predicted mid-flight corrections could be accounted for by the delay of STOP relative to the delay of GO1; in other words, if the best-fit STOP process happened to be slow, then this permitted more time for GO1 and GO2 to finish first. Although the model accounted for the overall percentage of mid-flight corrections, the variability in incidence observed across subjects and conditions could not be accounted for entirely by the model. Nevertheless, the close quantitative agreement between observed and predicted incidence of mid-flight corrections is further evidence that the GO-GO+STOP architecture provides the best account of saccade production when the target can step to new locations.

4. Discussion

We investigated saccade target selection in humans and macaque monkeys in tasks in which a target stepped to a different location on random trials. Most testing was done with visual search displays in which the target step amounted to an isoluminant color change. However, to relate these data to the existing literature, testing was also done with a conventional double step procedure in which the target step was the disappearance of the target at its original location and simultaneous appearance at another location. In these double and search step trials, we found that macaque monkey performance is not qualitatively different from human performance of these tasks. We found that performance was stochastic and followed characteristic regularities. First, the probability of producing a compensated saccade to the final target location decreased with the delay of the step. Second, compensated saccades in response to the step were produced with latencies that tended to be shorter than the average latency of saccades on trials with no target step. Third, noncompensated saccades to the initial target location were produced with latencies less than the average latency of saccades on trials with no target step. Fourth, noncompensated errors to the initial target location were routinely followed by corrective saccades to the final target location with an intersaccade interval that tended to decrease with the latency of the noncompensated saccade relative to the target step (*reprocessing time*).

We also tested formally whether this pattern of results could be accounted for by different race model architectures. We found that the performance could not be accounted for by a race between just two stochastically independent GO processes producing the saccades to the initial or final target location. However, performance was accounted for by a race between three processes – a GO process producing the saccade to the initial target location, a STOP process interrupting that GO process, and a GO process producing the saccade to the final target location. Furthermore, if the STOP process and second GO process start at the same time then the model can account for the incidence and latency of mid-flight corrections and rapid corrective saccades. These results provide new information about the dynamics of saccade target selection and validate a particular computational account of saccade production.

4.1 Comparison of macaque and human performance

Contrary to previous accounts that report monkeys were unable to perform double step tasks (Baizer and Bender, 1989), we found that humans and monkeys demonstrated qualitatively similar performance on these tasks. The differences between the two studies may be due to an innate difference in species used in the two studies; the previous experiment used *Macaca fasicularis* and this study used *M. mulatta* and *M. radiata*. In the previous study it is unclear that the monkeys were sensitive to the stimulus contingencies because they also did not exhibit the well known fixation-target gap effect on saccade latency.

In our study, monkey and human performance was qualitatively indistinguishable in both double step and search step conditions. Although the set size and distractor similarity manipulations were not applied to monkeys in this study, previous work demonstrates that monkeys exhibit the same sensitivity to target target-distractor similarity as humans (e.g., Bichot and Schall, 1999;Sato and Schall, 2001;Sato, Watanabe, Thompson and Schall, 2003;Shen and Pare, 2006).

4.2 Comparison of search step with double step performance

The latencies of saccades to targets are elevated if the target is presented with distractors (Findlay, 1987;Schiller et al., 1987). We replicated this with human and monkeys, but the slowing of saccade latency by the presence of distractors was less pronounced in monkeys than in humans. We believe this difference is because the monkeys (but not the humans) were also trained to perform a memory-guided saccade task with the target presented alone. Thus, the monkeys did not initiate saccades as quickly as they might when the target appeared alone because they had more experience waiting for the fixation spot to disappear.

One of the major findings of this study is that, in spite of this difference, the overall pattern of performance in target step trials was not qualitatively different if the target appeared and stepped with or without distractors (see also Sheliga et al. 2002). In other words, subjects could respond to a target that unexpectedly changed location through a strong luminance decrement at the old location and an increment at the new location as well as to a target that changed location through an isoluminant color change at the old and new locations. Previous studies have investigated attention allocation and target selection when new stimuli are added to a search array (e.g., Godijn and Theeuwes, 2002;Theeuwes, 1991;Theeuwes, Kramer, Hahn and Irwin, 1998). Our results indicate that more subtle changes of the image can guide attention and gaze as well.

To investigate the sensitivity of target selection to the isoluminant color change, we manipulated target-distractor similarity in humans. Unfortunately, the manipulation was only marginally successful because the distractors were not similar enough to increase the display size effect for every subject. Further work is needed with more complex visual search arrays, such as targets defined by spatial configuration.

Another major finding of this study was the longer latency to react to the step in search step as compared to double step trials, as measured by TSRT. TSRT was even longer when the target and distractors were similar in color. At least two explanations can be conceived for these effects on TSRT. First, it is possible that the independence premise of the race model formulation is violated; TSRT could have been longer in the more difficult search trials because the stop process competed for resources with the go process. An alternative interpretation is that the stepped target was not as salient when presented in a search array as when presented alone and was even less salient when the target and distractor were more similar. This would introduce a longer delay in the sensory processing preceding the stop process.

The estimation of TSRT depends on the validity of the race model formulation. Some reports have provided evidence that the independence premise of the race model can be violated (e.g., Hanes and Carpenter, 1999;Özyurt, Colonius and Arndt, 2003). To examine this, we determined on a per-session basis whether noncompensated saccades were produced with latencies longer than the latencies of no step trials saccades. Because we found such violations in only three sessions and in only three target step delays of those sessions we conclude that the performance in this task is consistent with what is expected of a race.

Previous research has interpreted a delay in the saccade latencies of compensated saccades relative to no-step saccade latencies as evidence that an intervening cancellation of the first saccade must occur before a saccade to the final target location can be initiated (Becker and Jürgens, 1979). However, we have seen little evidence of this delay in both human and macaque performance in these tasks, indicating that there might not be enough time for an explicit STOP process to intervene. This difference could be due to differences in the experimental design between the two experiments. For example, in the present experiment, the target either remained at its initial location or stepped to another location at an equivalent eccentricity from the fixation point. In Becker and Jürgens' experiment the target stepped in more ways in amplitude and direction along the horizontal meridian, away from the central point, toward the central point and across the midline. Given the executive control that can be exerted in double step saccade performance (Ray et al. 2004) it is possible that the diversity of target steps used by Becker and Jürgens resulted in a general slowing of performance.

4.3 What does target step reaction time measure?

One of the utilities of the modeling results was the ability to measure explicitly certain previously unobservable intervals, such as TSRT, the time taken to interrupt the first planned saccade. Though not explicitly fit, TSRT corresponds remarkably well with the average latency of the STOP process. The challenge of measuring the duration of stochastic processes leaves an open question whether TSRT is a measure of the overall average latency of the STOP process or is a measure of the average latency of just those STOP process instances that actually interrupted the first GO process. This distinction is difficult to make because of the low variability inherent in the distributions of the STOP process and while of theoretical interest may not be of much practical value.

4.4 Race models of double step saccade performance

Becker and Jürgens (1979) suggested that double step saccade production could be explained as the outcome of a race between processes producing the alternative saccades; however, this has never been tested formally until now. We analyzed these data according to the same logical framework as has been applied to stop signal data (Logan and Cowan, 1984). The compensation function corresponds to the inhibition function. Noncompensated saccades correspond to signal-respond (also known as non-canceled) saccades. Finally, compensated saccades correspond to signal-inhibit (also known as canceled) trials. The countermanding race model has been successfully applied to stop signal and change signal task performance (e.g., Colonius et al., 2001;De Jong, Coles, Logan and Gratton, 1990;Logan and Burkell, 1986).

A recent paper by Ludwig, Mildinhall and Gilchrist (2006) describes a stochastic accumulator model of double-step saccade performance. This model included the following characteristics: saccade direction is coded by pools of units with broad movement fields; the presentation of a target results in increased activation of the unit centered on the target location with progressively less activation in neighbouring units; the activation of each unit corresponds to evidence in favor of the target being in its response field; the activation of each unit is subject to leakage such that if the target steps out of the movement field, activation passively decays; a saccade is generated to the location coded by the unit with activation that reaches a specific threshold; the latency of the saccade is determined by the time that the threshold is reached plus a constant efferent delay; the rate of accumulation varies randomly across target onsets and within a trial; the within-trial noise is independent across units. This model could account for major features of the data including the production of averaging saccades. While this model is probably correct in many respects, it has the following shortcomings. First, the model parameters were not optimized to individual data sets. Second, the model was not shown to fit the range of error and correct saccade latencies. Third, the reduction of activation exclusively through leakage is not sufficient to account for the latency of saccades and pattern of neural modulation if double-step performance is accomplished by the same circuitry that accomplishes saccade countermanding (Boucher et al. 2007). Finally, evidence in support of one model architecture was provided, but alternative architectures were not excluded.

A major goal of this study was to evaluate different architectures of the race model and in particular to gain an insight into the nature of the stopping process. For every data set examined, the best-fitting model included a STOP process that interrupted preparation of the first saccade. We also explored how this STOP process related to the second GO process that produced the saccade to the final target location. One logical possibility is that the second GO process (GO2) begins only after STOP finishes by interrupting GO1; we refer to this as the GO-STOP-GO architecture. Another logical possibility is that GO2 starts at the same time as STOP; we refer to this as the GO-GO+STOP architecture.

Both of these architectures fit the distributions of latencies of no step, noncompensated and compensated saccades and replicated the compensation function. However, the two architectures make different predictions about the distributions of finish times of the processes that prepare the first (GO1) and second saccade (GO2). In the GO-STOP-GO model the latencies of GO2 are much shorter than those of GO1. In fact, the GO2 latencies are so short as to be physiologically implausible. On the view that GO1 and GO2 are just different manifestations of the same process, this marked difference suggests that the sequential processing inherent in the GO-STOP-GO architecture may not be a viable alternative. However, the GO-GO+STOP architecture fit to the data sets also produced GO2 latencies that were systematically shorter than those of GO1. This was necessary to fit the compensated saccade latencies that were shorter than the no step trial saccade latencies for most subjects. Evidently, under the conditions used in our study there was a facilitation of saccade programming on target step trials.

The GO-STOP-GO and GO-GO+STOP architectures could be distinguished quite clearly when examining the incidence and latency of corrective saccades produced after noncompensated saccades. Noncompensated saccades were produced if GO1 finished first. In such trials we could sample a GO2 finish time, and we found that the interval between GO2 (corrective) and GO1 (noncompensated) tended to decrease with the latency of GO1 relative to the step (reprocessing time) (Figure 15). However, due to its sequential design the GO-STOP-GO architecture could not produce intersaccade intervals less than the duration of the STOP process. In contrast, due to the parallel activation of GO2 and STOP in the GO-GO +STOP architecture, it was possible to produce very short intersaccade intervals. In fact, it was possible for the GO-GO+STOP architecture to produce some trials in which GO1 finishes before GO2 that both finish before STOP. Such rare occurrences may be seen as mid-flight corrections in which the second saccade command follows on the heels of the first without any period of fixation.

A number of investigators have described saccades with curved trajectories when multiple targets are presented (e.g., McPeek, Han and Keller, 2003;Minken, Van Opstal and Van Gisbergen, 1993;Port and Wurtz, 2003). All studies agree that such curved saccade mid-flight corrections are rare. Models have been developed to account for the curvature of mid-flight corrections (e.g., Quaia, Lefevre and Optican 1999;Arai and Keller, 2005;Walton, Sparks and Gandhi, 2005;Goossens and Van Opstal, 2006). Our model provides an account of the premotor mechanisms that explain the frequency and latency of such movements.

Therefore, we believe that the GO-GO+STOP architecture is the most plausible account of how the primate brain produces saccades. This conclusion has two implications. First, it demonstrates how concurrent saccade preparation can occur in a controlled fashion. Second, the fact that GO2 and STOP occur at the same time suggests that they may in fact be the same process.

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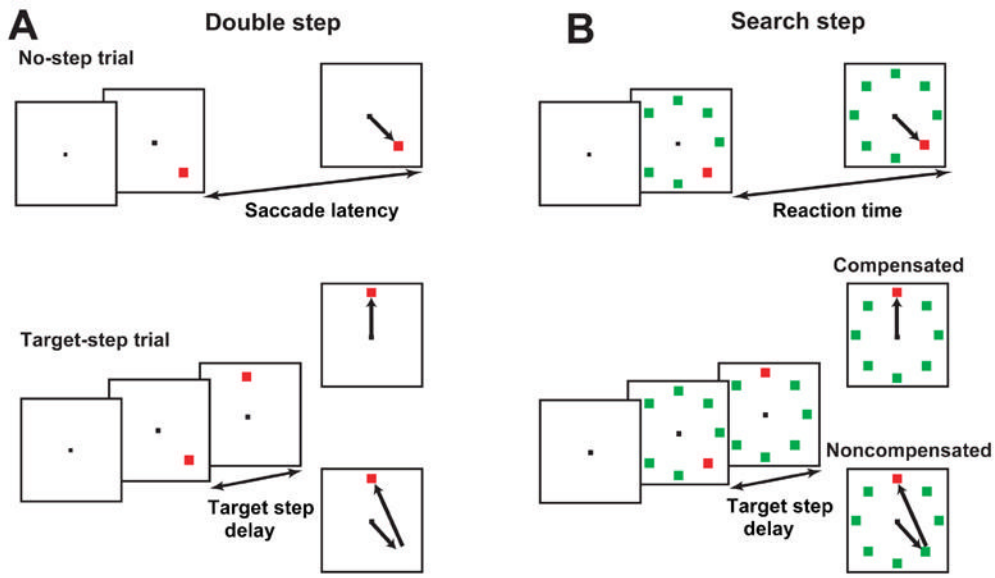

Figure 1.

Double step (A) and search step (B) tasks. All trials began after fixation of the central spot with presentation of the colored target at one of 2, 4 or 8 locations without (A) or with (B) differently colored distractors. No-step trials conclude after gaze shifted to the target for a specified interval. In target-step trials, after a delay (*TSD*) the target stepped to another of the 2, 4 or 8 positions. Two responses were possible, indicated by arrows. *Compensated saccades* were gaze shifts to the final target location. *Noncompensated saccades* were gaze shifts to the initial target location. Noncompensated saccades were commonly followed by a *corrective saccade* to the new target position.

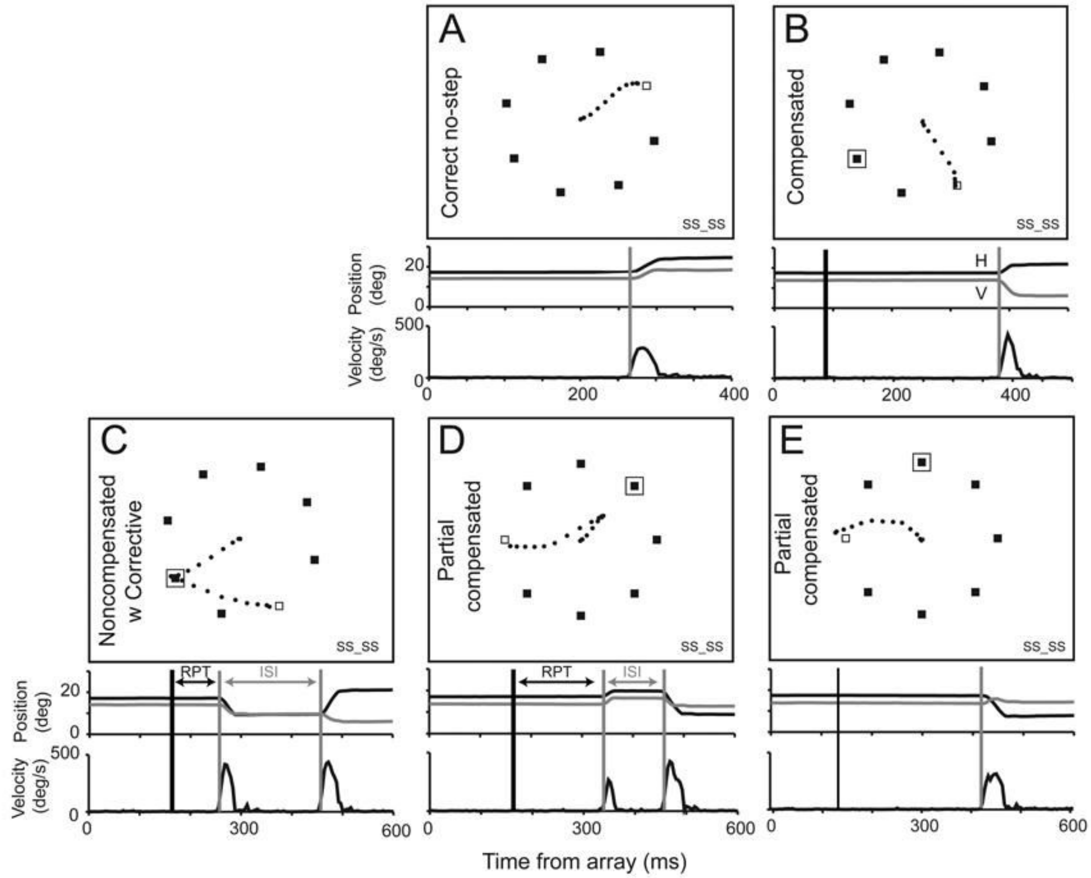

Figure 2.

Responses on representative trials from a human search step session. Open boxes indicate target location in no-step trials and final target location in step trials. Filled boxes are distractors. A box around a distractor marks the initial target location. Horizontal (black) and vertical (gray) eye velocity (upper) and vectorial eye velocity (lower) are plotted relative to target presentation time on the graphs beneath the sample displays. Vertical gray lines mark the times of saccade initiation. Vertical black lines mark target step time. Reprocessing time interval (RPT) and intersaccade interval (ISI) between noncompensated and corrective saccades are indicated. **A.** Example correct no-step saccade. **B.** Example compensated saccade. **C.** Example noncompensated saccade followed by a corrective saccade. **D.** Example partial noncompensated saccade interrupted by a corrective saccade. **E.** Example midflight correction of noncompensated saccade.

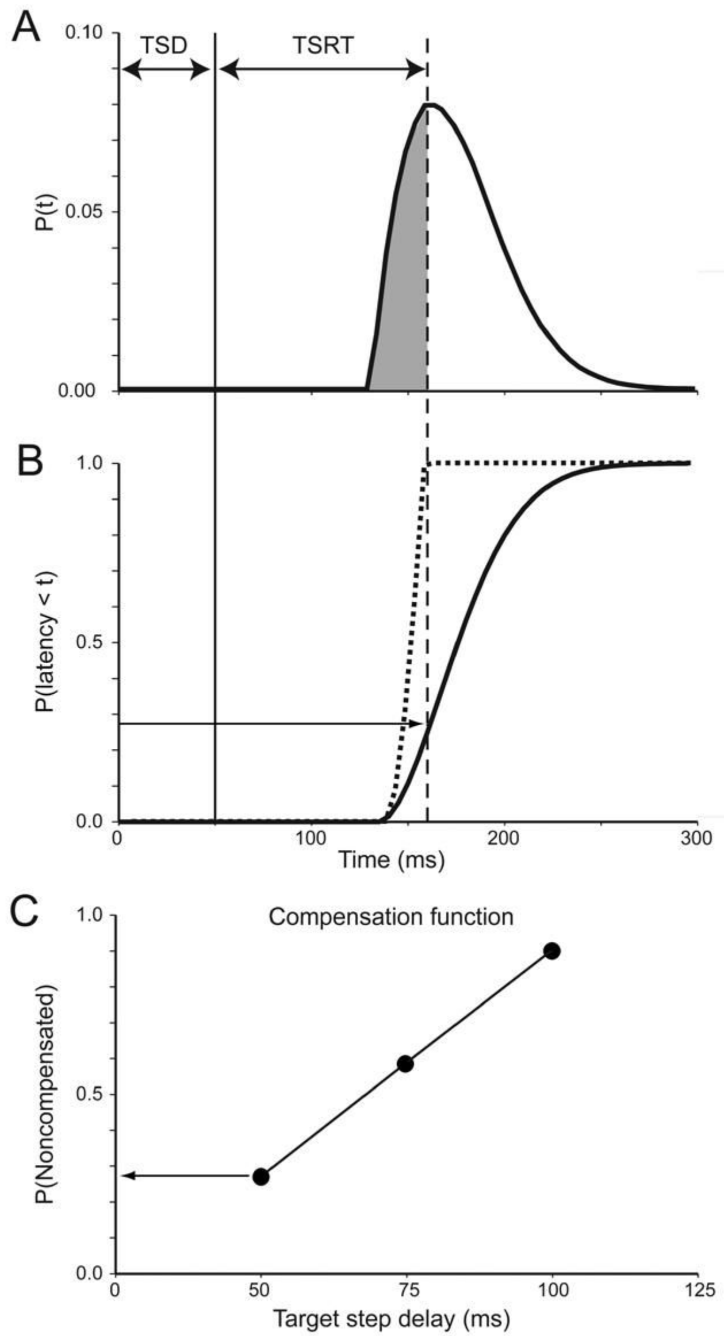

Figure 3.

Relationship between saccade latency and probability of compensating for target step. A. Probability density distribution of latencies of saccades in no-step trials. B. Cumulative distribution of latencies of correct saccades in no-step trials (solid) and of errant noncompensated saccades (dashed). C. Inhibition function plots probability of not compensating for the target step as a function of target step delay. At the earliest target step delay (50 ms, solid vertical line in A, B), the subject failed to compensate for the target step on almost 30% of trials (horizontal arrows in B, C). The key observation motivating the race model is that these errors are produced with the shortest saccade latencies (dashed plot in B). In other words, noncompensated errors are those saccades produced with latencies shorter than the latency of a process that would interrupt the process producing the saccade to the initial target location. The duration of the interruption process can be estimated by determining the latency less than which the fraction of saccade latencies corresponds to the probability of noncompensated saccades at each target step delay. This interval is the target step reaction time (TSRT) (dashed vertical line in A, B).

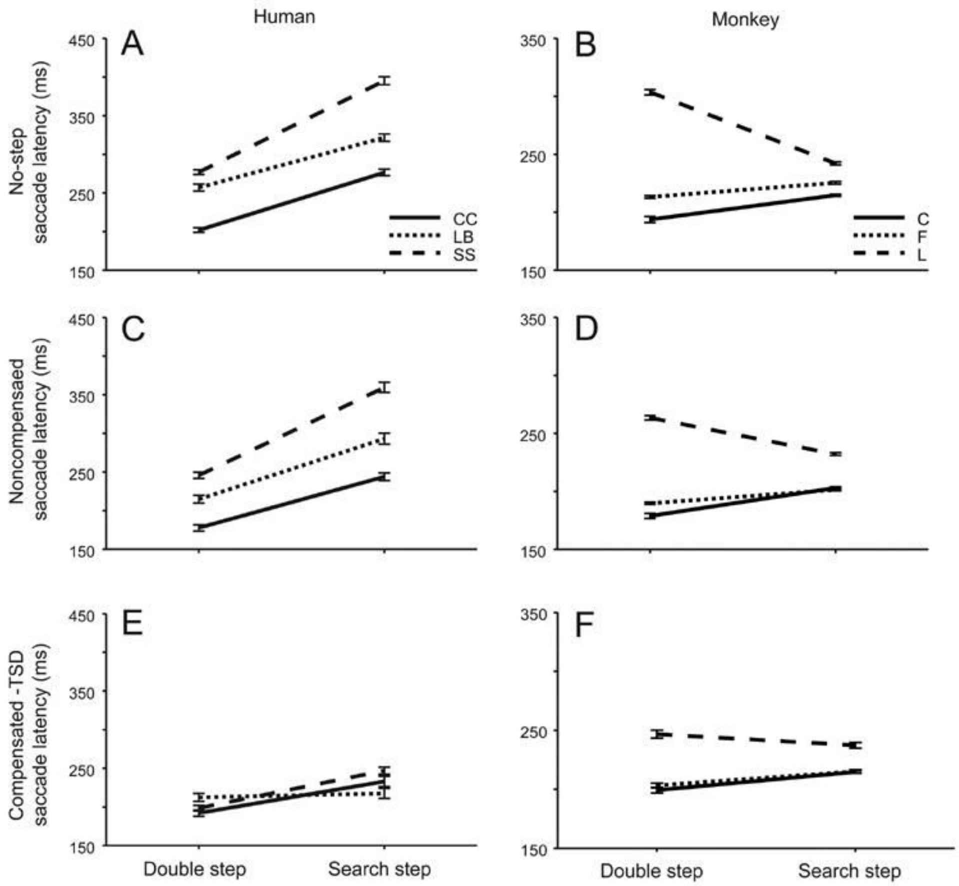

Figure 4.

Mean latencies of no-step (A, B), noncompensated (C, D), and compensated (E, F) saccades for individual human and macaque subjects as a function of double step or search step blocks. Compensated saccade latencies are measured relative to the target step. Line types for each subject indicated in legend. Error bars are within-subject 95% confidence intervals.

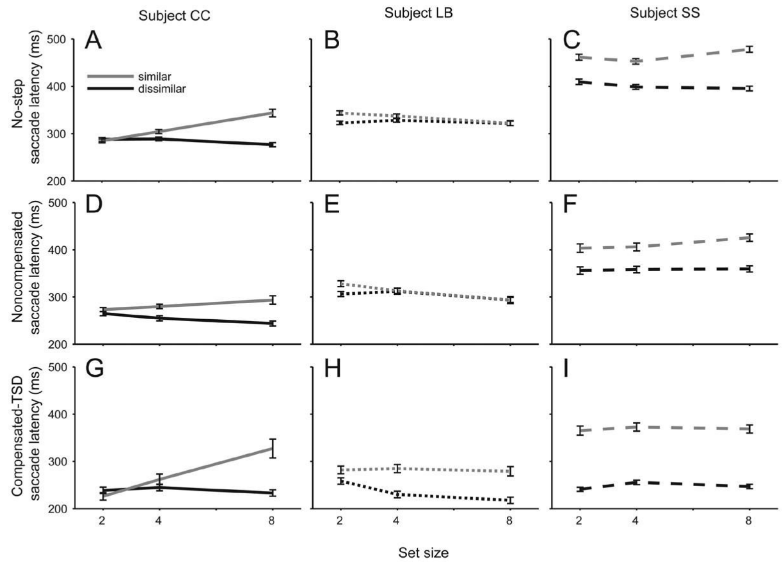

Figure 5.

Mean latency of no-step (A–C), noncompensated (D–F), and compensated (G–I) saccades as a function of set size (x axis) and target-distractor similarity (individual lines). Black lines indicate less similar target distractor colors; gray lines indicate similar distractor colors. Line types for subjects are the same as Figure 4. Error bars are within-subject 95% confidence intervals.

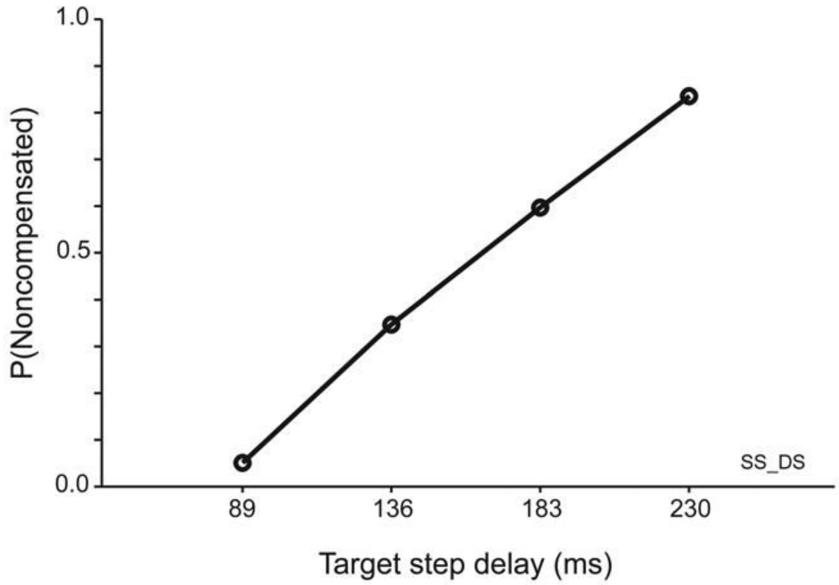

Figure 6.
Compensation function for a representative human subject performing the double step task.

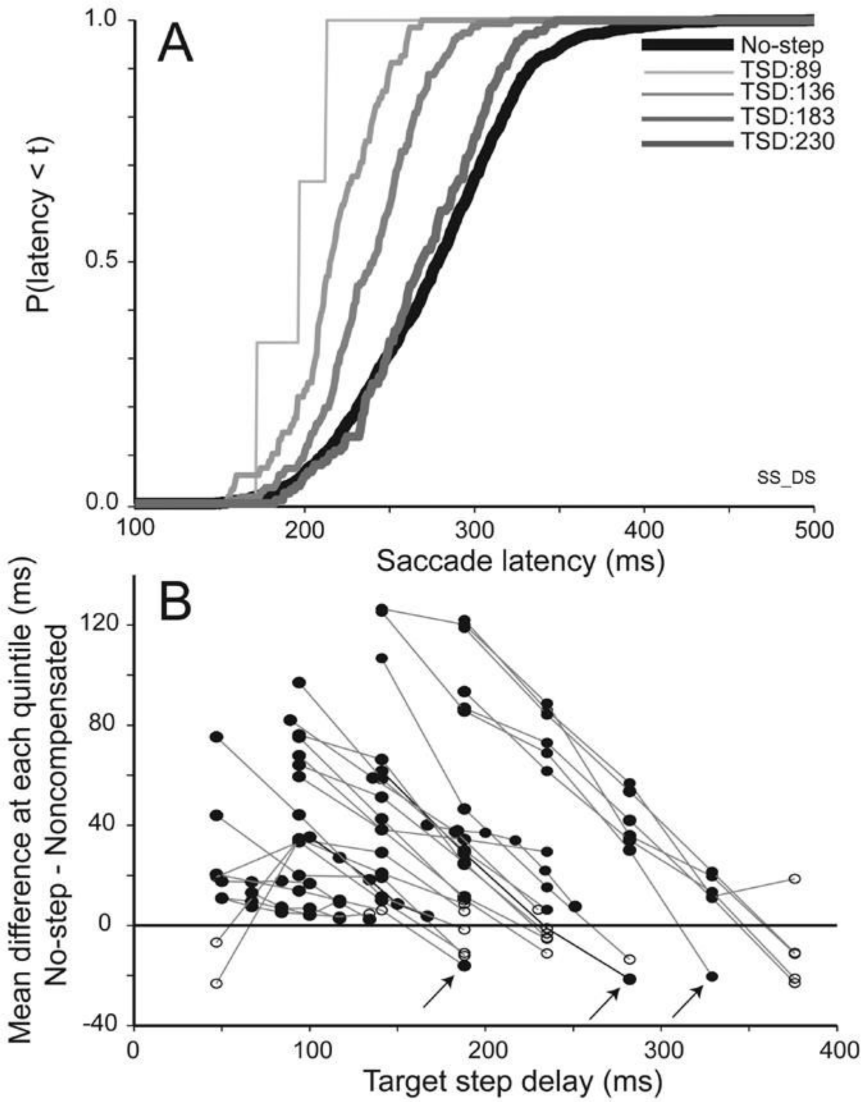

Figure 7.
Analysis of noncompensated saccade latencies. A. Comparison of cumulative distributions of latencies of no-step (black) and noncompensated saccades (gray) produced following successively longer TSDs for a representative human subject performing the double step task. Noncompensated saccade latencies are as short as the shortest no-step latencies and increase progressively with TSD. B. The race model predicts that the latencies of all noncompensated saccades will be less than the latencies of no-step trial saccades. Mean quintile difference between no-step and noncompensated saccade latency distributions plotted as a function of TSD for all data sets collected from both macaques and humans. Positive values indicate sessions in which the noncompensated saccade latencies were faster than no-step saccade latencies. Lines connect TSDs for the same session, where solid lines indicate human and dotted indicate monkey data. Solid circles indicate a difference that was significant according to a Kolomorogov-Smirnoff test ($p < 0.05$); empty circles indicate non-significant differences. Only three noncompensated saccade latency distributions were faster than the no-step saccade latency distributions (highlighted by the arrows); these all occur at the longest TSDs sampled in a session

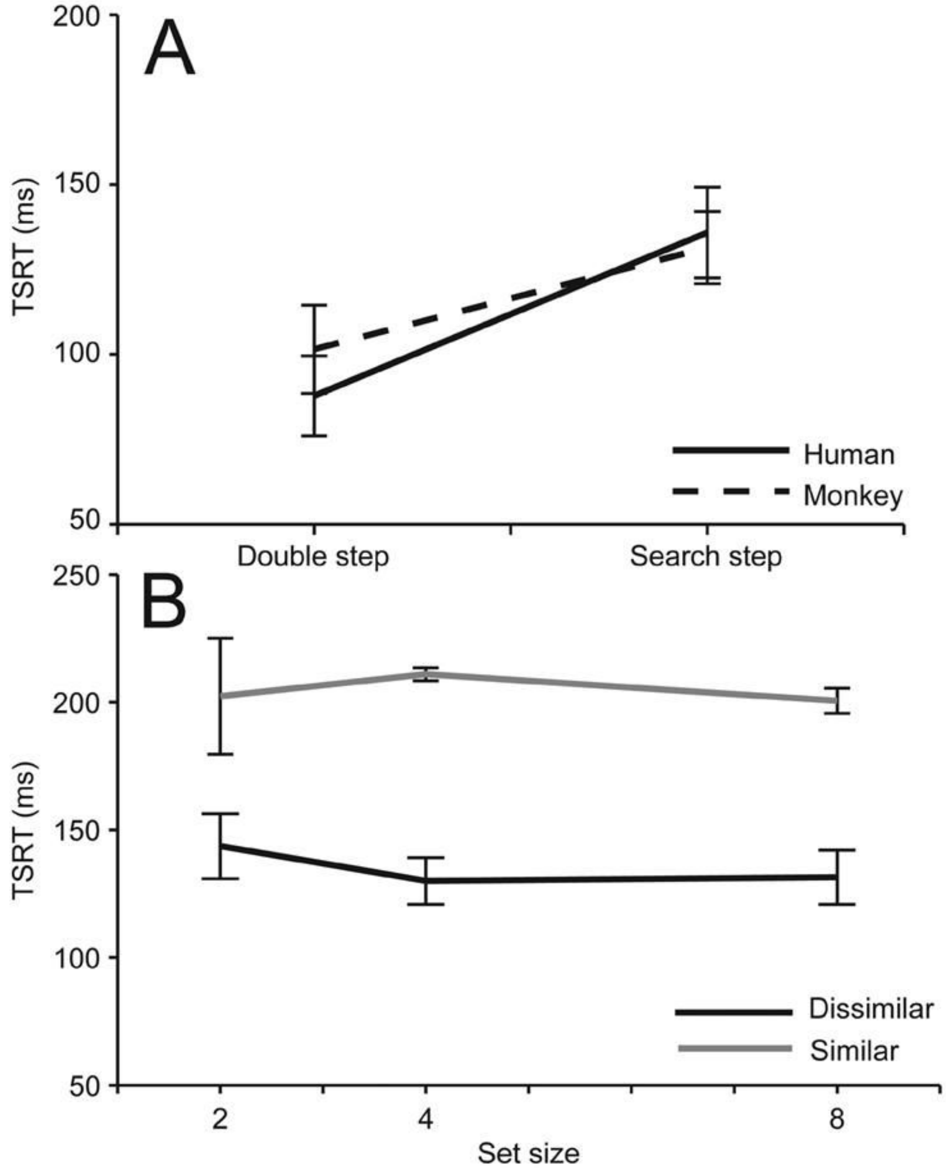

Figure 8.
Effects of manipulations on TSRT. A. TSRT for humans and monkeys as a function of presence of distractors in search step compared to double step. B. TSRT for humans as a function of search array size and target-distractor similarity. Error bars are average within-subject 95% confidence intervals. TSRT is longer when distractors are present and longer still when they resemble the target.

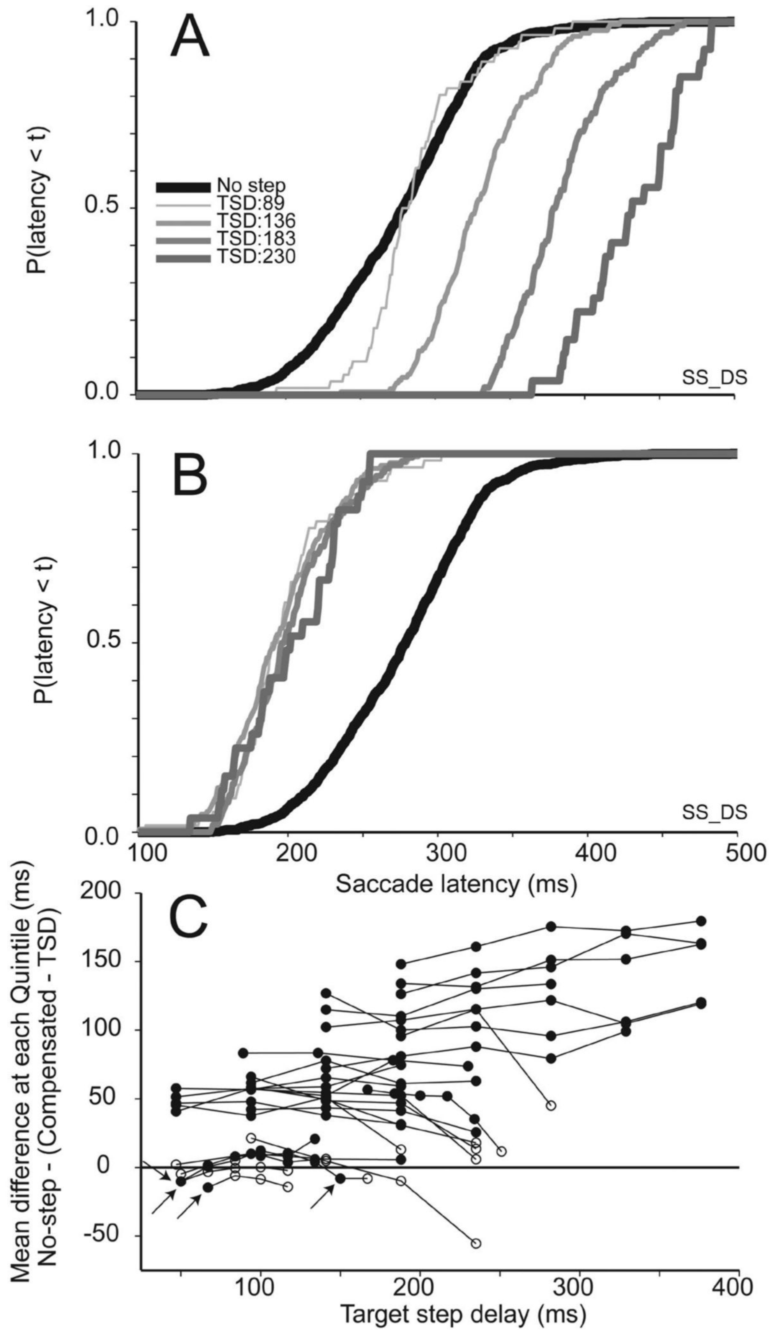

Figure 9.

Analysis of compensated saccade latencies. A. Comparison of cumulative distributions of latencies of no-step (black) and compensated saccades (gray) produced following successively longer TSDs for a representative human subject performing the double step task. The top panel plots compensated saccade latencies relative to initial presentation of the target. B. Cumulative distributions of compensated saccade latencies measured relative to the target step. Relative to the initial presentation of the target, compensated saccade latencies increase progressively with TSD. Relative to the target step, compensated saccade latencies have a common distribution that for this subject is shorter than that of no-step saccades. C. Mean quintile difference between distributions of no-step saccade latencies and distributions of compensated saccade latencies relative to the target step as a function of TSD for all data sets collected with both macaques and humans. Positive values indicate sessions in which the compensated saccade latencies relative to the target step were faster than no-step saccade latencies. Lines connect TSDs for the same session,where solid lines indicate human and dotted indicate monkey data. . Solid circles indicate a difference that was significant according to a t-test; empty circles indicate non-significant differences. Only four compensated saccade latency distributions were slower than the no-step saccade latency distributions (highlighted by the arrows); these tend to occur at the shortest TSDs sampled in a session.

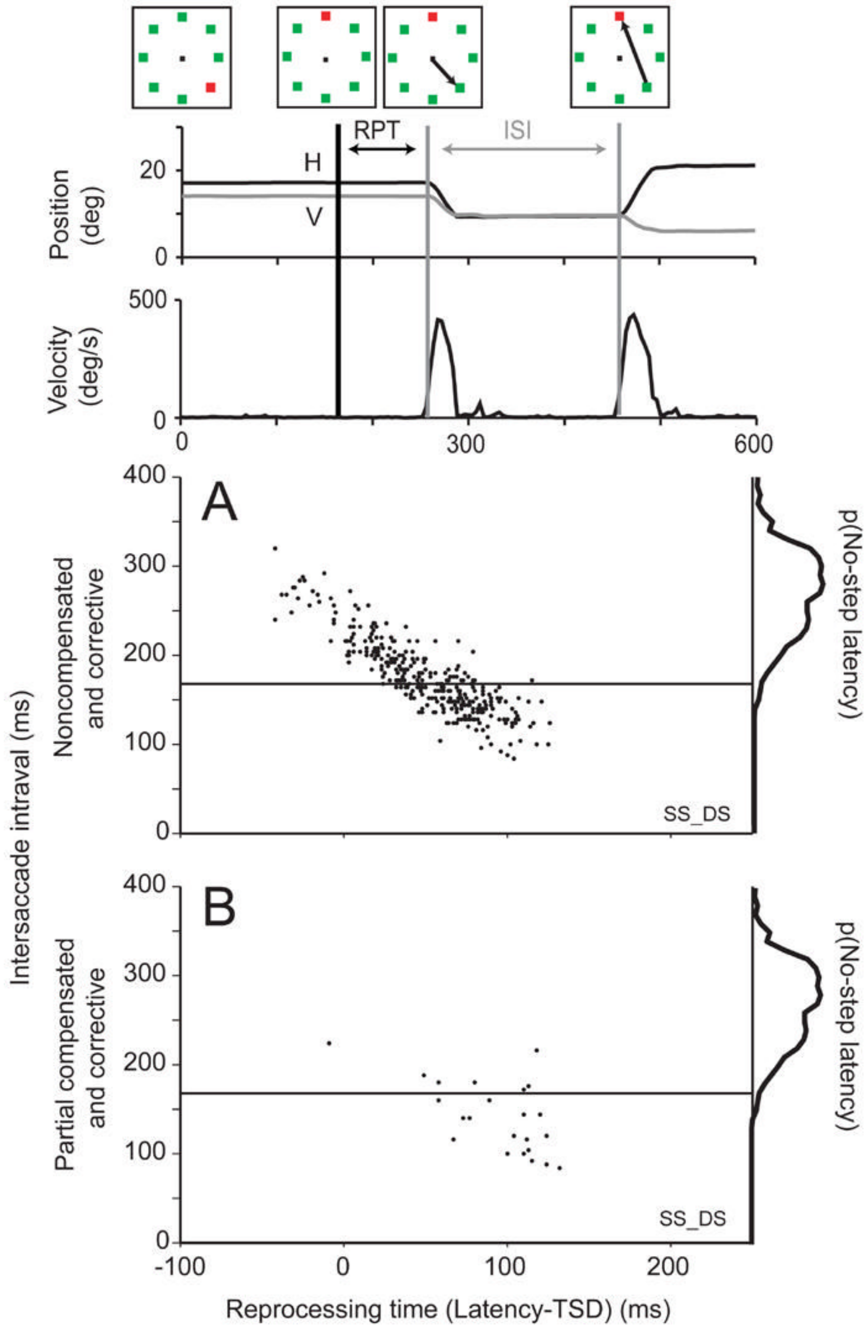

Figure 10.

Analysis of corrective saccade latencies. Top diagram illustrates sequence of events in a representative noncompensated trial. The interval between noncompensated saccades and subsequent corrective saccade (referred to as *intersaccade interval: ISI*) is plotted as a function of the interval from target step until initiation of the noncompensated saccade (referred to as *reprocessing time: RPT*) for complete (A) and partial (B) noncompensated saccades. For reference, marginal distribution shows density of no-step saccade latencies. Horizontal line shows the first percentile of no-step responses.

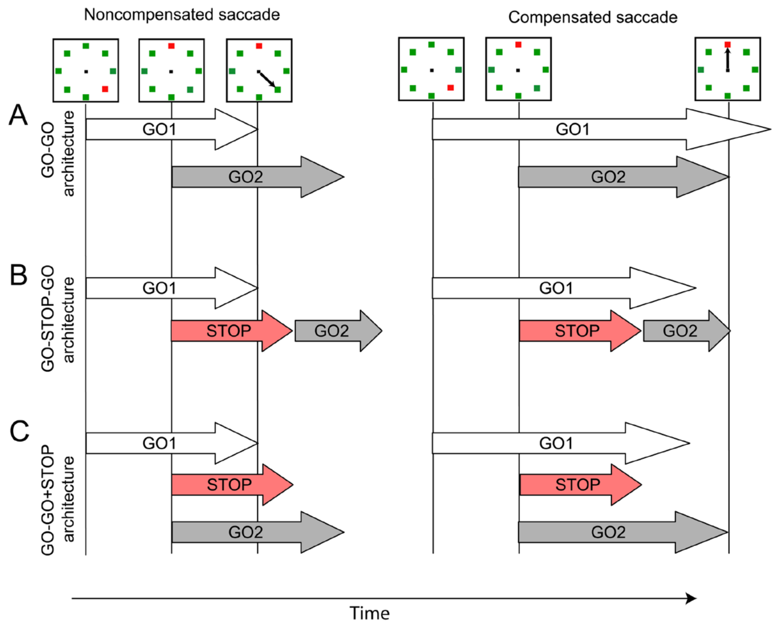

Figure 11.

Alternative race architectures producing noncompensated (left) and compensated (right) saccades. The arrows are representative finish times of stochastic processes as labeled. **A.** GO-GO architecture. Performance is the outcome of a race between the GO process producing the saccade to the initial target location (GO1) and the GO process producing the saccade to the final target location (GO2). **B.** GO-STOP-GO architecture. Compensated saccades are produced only if a STOP process finishes before the GO process producing the saccade to the initial target location (GO1) whereupon the GO process producing the saccade to the final target location (GO2) begins. **C.** GO-GO-STOP architecture. Compensated saccades are produced only if a STOP process finishes before the GO process producing the saccade to the initial target location (GO1), but the GO process producing the saccade to the final target location (GO2) begins at the same time as the STOP process. This creates the possibility of GO2 finishing after GO 1 but before STOP.

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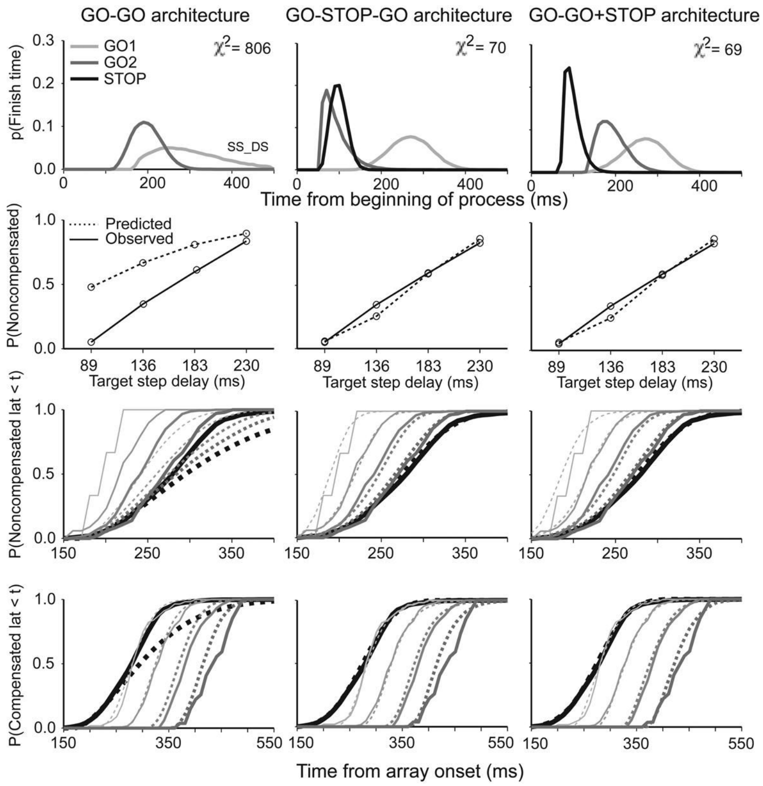

Figure 12.

Fits to representative data of the GO-GO architecture (left column), GO-STOP-GO architecture (middle column) and GO-GO+STOP architecture (right column). Top panels illustrate density distributions if finish times of the model processes as indicated by the legend. Second panels compare observed (solid) and predicted (dotted) compensation functions. Third panels compare observed and predicted cumulative distributions of no-step trial and noncompensated saccade latencies. Fourth panels compare observed and predicted cumulative distributions of no-step trial and compensated saccade latencies. For this data set only architectures including a STOP process fit the data.

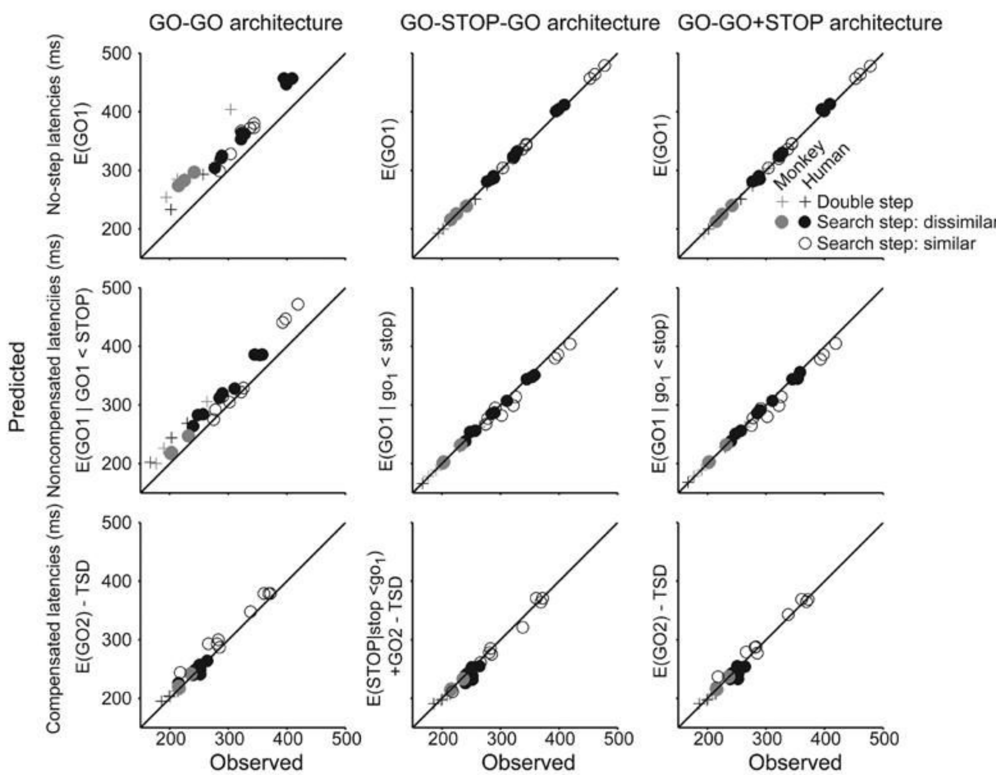

Figure 13.

Summary of fits to mean latency of no-step saccades (top row), noncompensated saccades (middle row) and compensated saccades (bottom row) of predicted means for the GO-GO architecture (left column), GO-STOP-GO architecture (middle column) and GO-GO+STOP architecture (right column). For all data sets only architectures including a STOP process fit the data. Gray symbols show data from monkeys; black, from humans. Crosses show data from double step sessions. Filled circles show data from search step with dissimilar target and distractor; open circles, search step with similar target and distractor.

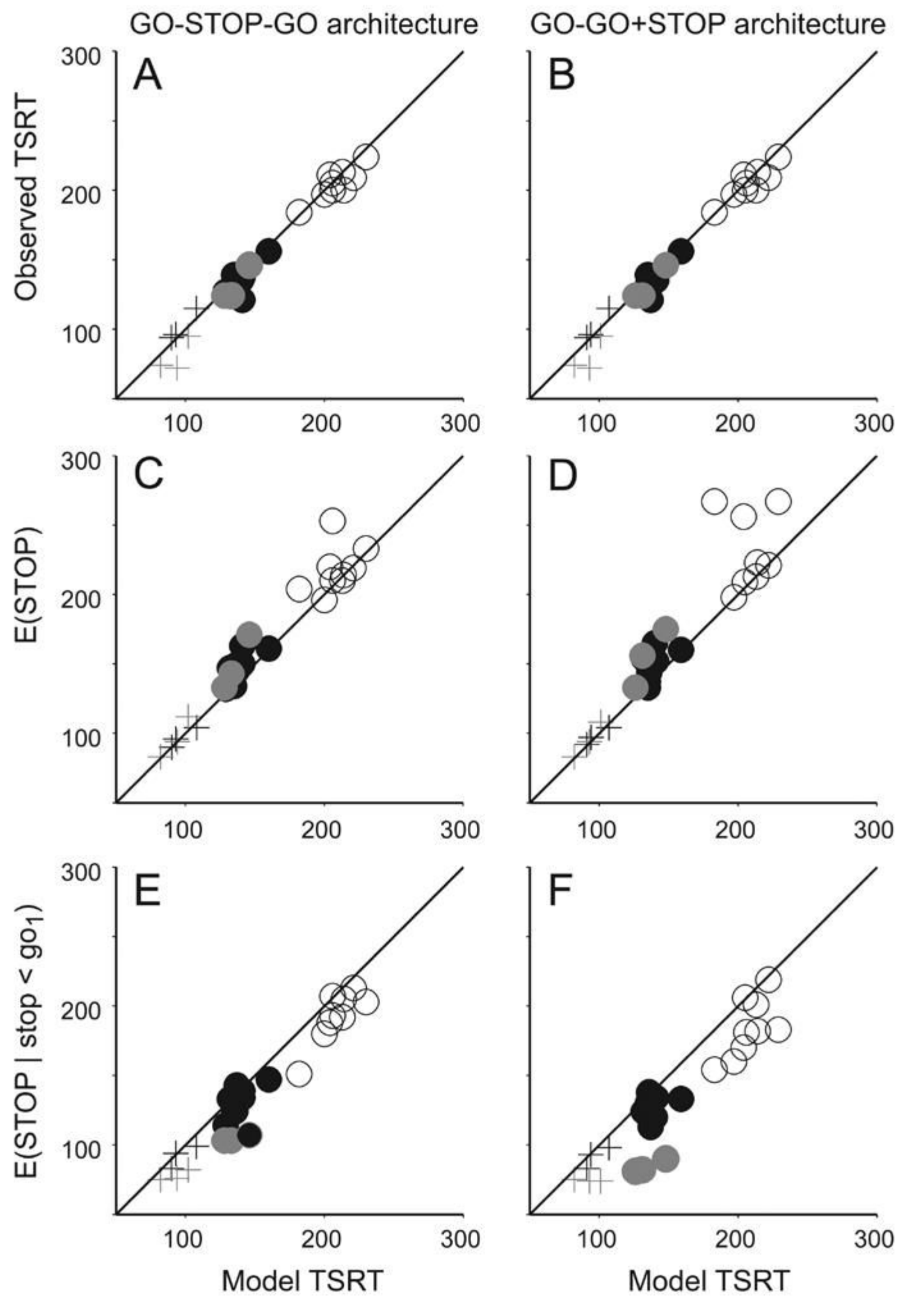

Figure 14.

Target step reaction time. A,B. Comparison of observed TSRT to model TSRT for GO-STOP-GO (left) and GO-GO+STOP (right) architectures. C,D. Comparison of average finish times of the STOP process on all trials (E(STOP)) to model TSRT. E,F Comparison of average finish times of those STOP processes that finished before the first GO process (E(STOP | stop < go_1)). Conventions as in Figure 13.

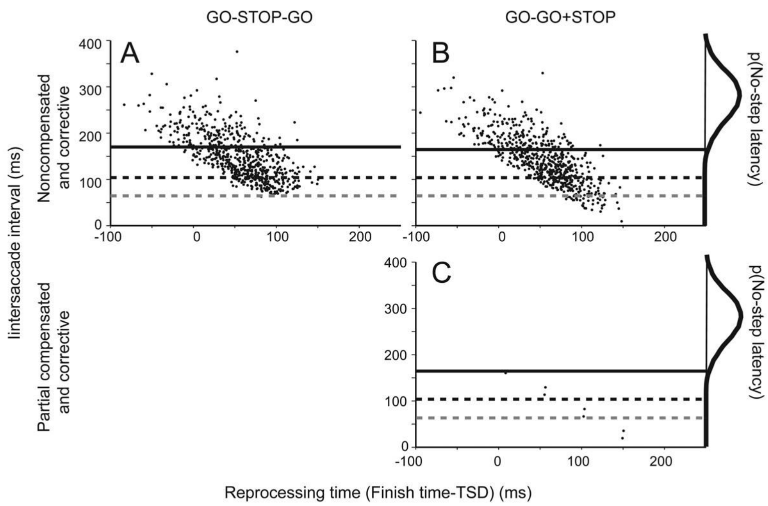

Figure 15.

Relation of interval between noncompensated and corrective saccades to reprocessing time in data simulated from the sequential (A) and simultaneous (B–C) architectures. Marginal distribution plots latencies of saccades on no-step trials. The sequential architecture does not permit the second GO process to finish after the first but before the STOP process, but this can occur for the simultaneous architecture. The simulated partial noncompensated saccades (because GO1 finished) are rare but are followed very rapidly by corrective saccades (because GO2 finished). Solid horizontal line denotes the first percentile of no-step responses. Black dashed horizontal line is TSRT. Gray dashed horizontal line is the fastest finish time of the STOP processes occurring in the simulation.

Table 1

Measures of observed and predicted behavior for all subjects and conditions. Rows list each task by species, subject and search condition, further divided by step delay. Columns from left to right are chi-squared model fit values for the three competing architectures, step delay, observed and predicted values of the compensation function, observed and predicted average latencies (measured from the time of array presentation) for no step, noncompensated and compensated saccades, and observed and predicted TSRT, with finish times of the process interrupting the first GO process for each architecture.

Table 1

					χ2				% Noncompensated				No-step latency				Noncompensated lat.				Compensated lat.				TSRT	GO-GO			GO-STOP-GO			GO-GO+STOP		
Task type	Species	Subject	Search type	Set size	GO-GO	GO-STOP-GO	GO-GO+STOP	TSD	Observed	GO-GO	GO-STOP-GO	GO-GO+STOP	Observed	GO-GO	GO-STOP-GO	GO-GO+STOP	Observed	GO-GO	GO-STOP-GO	GO-GO+STOP	Observed	GO-GO	GO-STOP-GO	GO-GO+STOP	Observed	TSRT	E(STOP)	E(STOP | STOP < GO)	TSRT	E(STOP)	E(STOP | STOP < GO)	TSRT	E(STOP)	E(STOP | STOP < GO)
Double step	Monkey	ch	n/a	n/a	1564	225	215	67	0.19	0.66	0.35	0.35	194	254	193	192	171	192	176	175	271	263	271	266	95	182	598	196	102	112	82	101	108	74
								84	0.34	0.71	0.47	0.47					179	197	177	178	280	280	284	283										
								100	0.46	0.75	0.60	0.58					182	202	178	179	299	296	297	299										
								117	0.64	0.78	0.72	0.70					178	207	181	181	323	313	312	316										
		fc	n/a	n/a	7993	498	471	100	0.19	0.68	0.24	0.24	213	285	213	212	176	216	177	177	301	300	308	306	74	181	594	199	82	83	75	82	83	75
								117	0.28	0.72	0.40	0.40					183	221	183	183	314	317	324	323										
								134	0.41	0.75	0.56	0.57					189	226	189	189	340	333	340	340										
								150	0.54	0.78	0.70	0.71					198	230	195	195	373	349	355	356										
								167	0.55	0.81	0.81	0.82					205	235	201	201	387	366	370	373										
		ly	n/a	n/a	3458	453	441	167	0.33	0.65	0.28	0.28	304	404	304	303	256	294	252	252	399	407	422	417	72	223	851	240	94	94	76	93	94	74
								184	0.33	0.68	0.38	0.38					256	299	255	255	426	424	437	434										
								200	0.33	0.71	0.47	0.48					258	303	260	260	448	440	452	450										
								217	0.35	0.73	0.57	0.57					260	308	265	265	457	457	468	467										
								234	0.41	0.75	0.65	0.65					272	313	270	270	498	474	484	484										
								251	0.56	0.77	0.72	0.73					284	317	276	275	540	491	500	501										
	Human	CC	n/a	n/a	690	65	67	47	0.20	0.60	0.12	0.12	202	233	200	200	127	181	128	133	244	236	239	238	96	187	515	187	93	96	94	94	97	93
								94	0.46	0.77	0.43	0.44					154	198	158	160	285	282	286	285										
								141	0.78	0.88	0.78	0.78					185	211	182	182	333	328	331	332										
								188	0.93	0.94	0.96	0.95					201	220	195	195	351	374	377	380										
		LB	n/a	n/a	668	74	76	94	0.32	0.62	0.17	0.18	257	293	251	251	163	221	167	171	300	297	305	302	94	201	168	202	90	90	83	91	92	83
								141	0.42	0.74	0.41	0.41					192	238	193	195	351	343	349	349										
								188	0.70	0.83	0.66	0.67					217	252	216	216	402	389	394	397										
								235	0.77	0.89	0.85	0.86					240	263	233	234	462	435	438	443										
		SS	n/a	n/a	806	70	69	89	0.05	0.48	0.06	0.06	277	310	275	274	194	245	190	187	287	283	290	286	115	181	2357	191	108	104	99	107	104	98
								136	0.35	0.67	0.26	0.25					217	263	218	216	331	328	335	333										
								183	0.60	0.81	0.59	0.59					239	279	245	244	385	373	379	380										
								230	0.84	0.90	0.87	0.87					269	290	264	263	433	418	422	428										

Table 1, continued

					χ2				% Noncompensated				No-step latency				Noncompensated lat.				Compensated lat.				TSRT	GO-GO			GO-STOP-GO			GO-GO+STOP		
Task type	Species	Subject	Search type	Set size	GO-GO	GO-STOP-GO	GO-GO+STOP	TSD	Observed	GO-GO	GO-STOP-GO	GO-GO+STOP	Observed	GO-GO	GO-STOP-GO	GO-GO+STOP	Observed	GO-GO	GO-STOP-GO	GO-GO+STOP	Observed	GO-GO	GO-STOP-GO	GO-GO+STOP	Observed	TSRT	E(STOP)	E(STOP | STOP < GO)	TSRT	E(STOP)	E(STOP | STOP < GO)	TSRT	E(STOP)	E(STOP | STOP < GO)
Search step	Monkey	ch	disimilar	8	7766	772	500	50	0.20	0.60	0.25	0.30	215	274	216	213	196	207	199	199	271	261	274	265	124	204	843	211	128	133	103	126	133	81
								67	0.30	0.66	0.34	0.38					199	212	200	201	283	278	287	282										
								84	0.38	0.71	0.46	0.47					203	218	200	202	297	295	299	299										
								100	0.45	0.74	0.58	0.56					203	222	202	203	313	310	312	315										
								117	0.53	0.78	0.70	0.65					207	226	204	204	333	327	326	332										
		fc	disimilar	8	5287	873	811	50	0.31	0.58	0.33	0.34	225	283	226	225	197	207	198	197	275	257	275	264	124	205	15934	208	133	143	103	131	156	82
								67	0.37	0.63	0.41	0.42					197	212	200	200	285	275	287	281										
								84	0.40	0.68	0.50	0.50					199	217	202	203	296	292	299	298										
								100	0.45	0.72	0.59	0.57					200	221	204	205	309	308	311	314										
								117	0.48	0.75	0.67	0.65					208	226	206	207	332	325	325	332										
								134	0.52	0.78	0.75	0.72					216	230	208	209	345	341	339	349										
		ly	disimilar	8	3869	256	275	50	0.27	0.60	0.34	0.34	242	297	239	240	226	237	232	228	300	276	297	283	146	223	101	226	146	171	107	148	175	90
								67	0.38	0.66	0.41	0.42					230	241	232	230	305	293	309	301										
								84	0.42	0.71	0.48	0.49					232	245	232	232	325	311	320	319										
								100	0.46	0.75	0.56	0.56					233	249	232	233	330	327	330	336										
								117	0.50	0.79	0.65	0.63					234	253	232	234	349	344	342	353										
								134	0.61	0.82	0.75	0.70					233	257	233	235	356	361	354	371										
	Human	CC	disimilar	2	436	45	44	94	0.31	0.61	0.24	0.25	288	321	290	290	224	263	229	229	329	322	331	327	135	228	947	226	140	149	136	141	152	134
								141	0.54	0.76	0.51	0.52					244	279	248	249	376	367	375	374										
								188	0.72	0.86	0.76	0.76					272	292	267	267	423	413	418	421										
								235	0.89	0.92	0.92	0.91					287	302	280	280	537	459	462	468										
				4	481	110	98	94	0.43	0.62	0.28	0.28	289	325	287	285	214	262	232	224	323	329	341	334	132	234	554	232	136	149	124	135	150	121
								141	0.54	0.75	0.51	0.51					225	278	246	244	386	374	382	382										
								188	0.68	0.84	0.73	0.74					264	292	262	261	439	419	423	429										
								235	0.88	0.90	0.88	0.90					289	302	274	274	517	465	465	476										
				8	529	235	234	94	0.42	0.68	0.35	0.34	277	304	281	281	208	247	210	211	317	318	327	327	134	219	990	223	137	145	143	136	144	138
								141	0.60	0.79	0.60	0.59					223	260	231	232	367	364	374	374										
								188	0.72	0.86	0.78	0.77					251	271	249	249	438	411	421	422										
								235	0.90	0.91	0.89	0.89					278	279	261	261	493	458	467	468										

Table 1, continued

Task type	Species	Subject	Search type	Set size	χ2 GO-GO	χ2 GO-STOP-GO	χ2 GO-GO+STOP	TSD	% Noncompensated Observed	% Noncompensated GO-GO	% Noncompensated GO-STOP-GO	% Noncompensated GO-GO+STOP	No-step latency Observed	No-step latency GO-GO	No-step latency GO-STOP-GO	No-step latency GO-GO+STOP	Noncompensated lat. Observed	Noncompensated lat. GO-GO	Noncompensated lat. GO-STOP-GO	Noncompensated lat. GO-GO+STOP	Compensated lat. Observed	Compensated lat. GO-GO	Compensated lat. GO-STOP-GO	Compensated lat. GO-GO+STOP	TSRT Observed	GO-GO TSRT	GO-GO E(STOP)	GO-GO E(STOP | STOP < GO)	GO-STOP-GO TSRT	GO-STOP-GO E(STOP)	GO-STOP-GO E(STOP | STOP < GO)	GO-GO+STOP TSRT	GO-GO+STOP E(STOP)	GO-GO+STOP E(STOP | STOP < GO)
Search step	Human	CC	similar	2	219	82	93	47	0.34	0.51	0.35	0.32	285	299	285	285	264	260	256	253	286	262	281	271	184	213	217	202	182	204	151	183	267	154
								94	0.63	0.71	0.58	0.56					266	271	264	261	311	298	312	312										
								141	0.75	0.84	0.77	0.79					274	281	271	270	362	338	343	356										
								188	0.86	0.92	0.91	0.92					298	288	277	277	384	379	377	399										
				4	273	64	66	47	0.19	0.57	0.34	0.35	304	328	304	304	251	280	261	264	309	290	320	311	211	246	468	242	204	220	188	204	256	170
								94	0.66	0.72	0.58	0.59					276	287	272	274	356	336	357	357										
								141	0.81	0.83	0.78	0.78					277	296	282	284	390	382	398	405										
								188	0.81	0.89	0.90	0.90					309	304	291	292	481	429	442	452										
				8	151	47	48	94	0.53	0.69	0.53	0.51	344	380	343	346	261	302	284	280	406	372	418	417	205	296	476	280	206	253	193	206	305	181
								141	0.67	0.77	0.68	0.66					299	311	290	289	468	420	464	465										
								188	0.75	0.82	0.78	0.77					307	320	299	299	525	468	510	513										
								235	0.82	0.86	0.85	0.84					297	327	308	309	610	516	557	560										
		LB	disimilar	2	749	109	94	94	0.19	0.52	0.13	0.14	323	364	323	324	248	296	256	263	357	343	358	348	156	234	344	246	160	161	147	159	160	133
								141	0.37	0.68	0.36	0.35					274	313	278	284	389	388	400	395										
								188	0.61	0.80	0.66	0.64					308	328	298	301	450	432	440	442										
								235	0.81	0.88	0.88	0.86					331	340	313	314	516	478	480	490										
				4	567	120	124	141	0.27	0.61	0.33	0.34	328	362	332	330	268	308	286	285	375	360	378	374	137	197	555	216	141	163	134	140	165	120
								188	0.59	0.76	0.59	0.59					296	323	301	302	414	405	418	421										
								235	0.80	0.86	0.81	0.81					327	336	316	315	455	449	458	469										
								282	0.90	0.92	0.95	0.94					353	345	326	324	561	495	499	517										
				8	605	182	231	141	0.32	0.57	0.32	0.33	322	353	324	325	223	288	251	256	360	346	363	357	125	184	808	200	132	147	133	132	154	124
								188	0.50	0.71	0.55	0.55					278	306	277	278	409	389	406	404										
								235	0.73	0.83	0.77	0.76					307	321	298	298	444	433	448	452										
								282	0.89	0.90	0.91	0.90					333	332	313	312	493	477	489	499										
			similar	2	275	55	54	47	0.24	0.42	0.20	0.21	344	373	345	345	321	311	299	298	333	317	339	327	224	274	811	263	230	233	203	229	267	183
								94	0.44	0.60	0.42	0.42					307	323	309	309	377	358	375	372										
								141	0.58	0.75	0.65	0.64					326	336	319	320	419	401	413	419										
								188	0.81	0.85	0.83	0.82					352	347	330	330	465	445	453	467										
				4	481	61	63	47	0.06	0.45	0.13	0.13	337	372	336	336	357	303	282	280	343	320	341	332	213	276	740	268	213	210	192	214	223	182
								94	0.30	0.62	0.32	0.33					298	316	290	291	375	363	381	379										
								141	0.59	0.75	0.59	0.59					305	329	304	305	428	408	423	426										
								188	0.87	0.84	0.81	0.80					329	341	318	318	455	453	465	475										
				8	411	64	65	47	0.07	0.46	0.13	0.14	322	367	321	320	334	288	269	263	322	306	329	322	197	267	836	258	200	196	180	197	198	160
								94	0.30	0.62	0.35	0.34					277	299	273	274	364	352	371	369										
								141	0.63	0.73	0.62	0.59					292	311	286	286	427	398	415	416										
								188	0.78	0.82	0.82	0.78					305	322	300	297	495	444	460	464										

Table 1, continued

Task type	Species	Subject	Search type	Set size	χ2 GO-GO	χ2 GO-STOP-GO	χ2 GO-GO+STOP	TSD	% Noncompensated Observed	% Noncompensated GO-GO	% Noncompensated GO-STOP-GO	% Noncompensated GO-GO+STOP	No-step latency Observed	No-step latency GO-GO	No-step latency GO-STOP-GO	No-step latency GO-GO+STOP	Noncompensated lat. Observed	Noncompensated lat. GO-GO	Noncompensated lat. GO-STOP-GO	Noncompensated lat. GO-GO+STOP	Compensated lat. Observed	Compensated lat. GO-GO	Compensated lat. GO-STOP-GO	Compensated lat. GO-GO+STOP	TSRT Observed	GO-GO TSRT	GO-GO E(STOP)	GO-GO E(STOP | STOP < GO)	GO-STOP-GO TSRT	GO-STOP-GO E(STOP)	GO-STOP-GO E(STOP | STOP < GO)	GO-GO+STOP TSRT	GO-GO+STOP E(STOP)	GO-GO+STOP E(STOP | STOP < GO)
Search step	Human	SS	disimilar	2	413	96	109	188	0.31	0.51	0.18	0.18	409	457	412	413	284	352	296	300	445	427	431	429	139	216	401	237	135	134	125	135	133	121
								235	0.46	0.63	0.35	0.36					319	371	323	324	483	473	476	476										
								282	0.53	0.73	0.54	0.55					349	388	347	347	514	519	521	523										
								329	0.65	0.81	0.71	0.71					388	403	367	367	563	565	565	570										
								376	0.66	0.86	0.84	0.83					387	415	384	384	604	612	609	617										
				4	395	95	93	188	0.45	0.58	0.26	0.28	399	447	404	401	311	355	309	325	448	438	446	443	121	218	373	249	141	150	139	137	157	113
								235	0.46	0.69	0.45	0.45					322	373	333	341	504	485	490	490										
								282	0.58	0.78	0.64	0.63					354	389	354	358	528	531	535	537										
								329	0.74	0.85	0.79	0.78					381	402	372	372	575	577	579	584										
								376	0.80	0.89	0.90	0.89					422	413	385	384	610	624	623	631										
				8	474	105	125	188	0.26	0.53	0.20	0.19	395	457	401	404	296	354	311	301	453	426	440	431	127	217	368	237	129	132	114	135	137	130
								235	0.53	0.65	0.39	0.40					330	371	331	326	486	473	482	478										
								282	0.54	0.74	0.58	0.60					356	387	350	349	527	519	525	526										
								329	0.64	0.81	0.75	0.77					377	401	367	368	553	565	567	573										
								376	0.77	0.86	0.87	0.88					410	412	380	383	605	611	609	619										
			similar	2	542	95	98	141	0.36	0.54	0.17	0.16	461	533	464	464	348	409	327	326	483	496	517	510	200	330	921	352	214	214	205	213	213	201
								188	0.44	0.63	0.31	0.30					344	425	353	352	561	542	563	557										
								235	0.42	0.71	0.47	0.47					375	441	379	378	602	587	608	604										
								282	0.58	0.77	0.63	0.63					419	456	401	401	656	633	653	652										
								329	0.71	0.83	0.76	0.76					438	469	421	421	701	678	699	699										
								376	0.67	0.87	0.86	0.86					463	481	437	437	715	724	743	746										
				4	614	111	114	141	0.37	0.56	0.16	0.16	453	524	457	457	339	410	326	320	517	502	515	510	209	337	425	358	221	219	213	222	221	219
								188	0.43	0.66	0.32	0.32					363	427	356	353	574	547	561	557										
								235	0.46	0.73	0.50	0.50					378	443	384	383	601	593	607	604										
								282	0.62	0.80	0.68	0.68					416	457	408	408	658	639	652	652										
								329	0.70	0.85	0.82	0.83					467	469	427	429	685	685	697	699										
				8	645	100	102	188	0.36	0.60	0.22	0.22	478	541	479	478	368	440	348	349	571	547	554	553	200	321	623	354	206	210	207	205	209	206
								235	0.43	0.69	0.38	0.38					384	458	380	381	602	591	601	600										
								282	0.56	0.77	0.55	0.56					421	475	408	409	642	636	647	647										
								329	0.65	0.83	0.72	0.72					444	489	432	432	705	680	693	695										
								376	0.76	0.88	0.85	0.85					480	501	452	452	733	725	739	741										

Table 2

Correlation between intersaccade interval (ISI) and reprocessing time (RPT) for all subjects and conditions. The left column indicates correlations for noncompensated saccades and right column indicates correlations for partially compensated saccades. Note prevalence of negative correlations indicating parallel processing of saccades. Starred correlation values indicate significance at p < 0.05 level.

	Subject	Simiarity	Set size	Noncompensated	Partially compensated
Double step	**CC**	**n/a**	**n/a**	−0.78*	−0.42
	LB	**n/a**	**n/a**	−0.69*	−0.46*
	SS	**n/a**	**n/a**	−0.87*	−0.60*
Search step	**CC**	**disimilar**	**2**	−0.84*	−0.76*
			4	−0.81*	−0.58*
			8	−0.86*	−0.86*
		similar	**2**	−0.47*	−0.28
			4	−0.36*	0.08
			8	−0.34*	−0.07
	LB	**disimilar**	**2**	−0.39*	−0.84*
			4	−0.07*	−0.73*
			8	−0.69*	−0.65*
		similar	**2**	−0.15*	−0.05
			4	−0.15*	−0.62*
			8	−0.29*	0.05
	SS	**disimilar**	**2**	−0.84*	−0.97*
			4	−0.85*	−0.77*
			8	−0.79*	−0.52*
		similar	**2**	−0.44*	−0.25
			4	−0.53*	0.06
			8	−0.32	−0.43

Table 3

Best fitting distribution parameters for the three competing race architectures. Rows list each task by species, subject and search condition, further divided by GO1, GO2, or STOP process. Columns indicate race architecture, chi squared fit value, and Weibull shape, scale and location parameters that describe best fitting finish time distributions of that process with the mean and variance of the finish times of each process.

Table 3

	Species	Subject	Search type	Set size	Process	GO-GO χ2	GO-GO Shape (α)	GO-GO Scale (β)	GO-GO Location (μ)	GO-GO Mean	GO-GO Variance	GO-STOP-GO χ2	GO-STOP-GO Shape (α)	GO-STOP-GO Scale (β)	GO-STOP-GO Location (μ)	GO-STOP-GO Mean	GO-STOP-GO Variance	GO-GO+STOP χ2	GO-GO+STOP Shape (α)	GO-GO+STOP Scale (β)	GO-GO+STOP Location (μ)	GO-GO+STOP Mean	GO-GO+STOP Variance
Double step	Monkey	ch	n/a	n/a	GO1	1564	1.0	119	137	256	119	225	2.3	80	122	193	33	215	2.2	77	124	192	33
					GO2		1.8	54	154	202	28		1.3	25	94	117	18		1.5	47	157	199	29
					STOP								1.1	59	55	112	52		1.6	89	29	109	51
		fc	n/a	n/a	GO1	7993	1.1	143	146	284	126	498	2.1	84	139	213	37	471	2.2	83	139	213	35
					GO2		2.0	96	127	212	44		1.6	72	66	131	41		1.8	84	131	206	43
					STOP								1.3	30	56	84	21		1.0	23	61	84	23
		ly	n/a	n/a	GO1	3458	1.0	195	207	402	195	453	1.7	120	197	304	65	441	1.7	115	200	303	62
					GO2		2.1	122	145	253	54		1.7	90	94	174	49		1.9	114	148	249	55
					STOP								1.2	56	41	94	44		1.1	52	43	93	46
	Human	CC	n/a	n/a	GO1	690	1.5	140	108	234	86	65	3.0	142	73	200	46	67	2.8	135	80	200	46
					GO2		6.8	146	59	195	24		3.4	78	27	97	23		3.3	80	119	191	24
					STOP								2.8	30	69	96	10		1.0	16	81	97	16
		LB	n/a	n/a	GO1	668	1.4	176	132	292	116	74	2.6	176	95	251	65	76	2.6	178	93	251	65
					GO2		2.4	89	132	211	35		2.4	71	61	124	28		2.4	87	131	208	34
					STOP								1.8	46	49	90	24		1.0	31	62	93	31
		SS	n/a	n/a	GO1	806	1.7	156	171	310	84	70	3.3	162	130	275	48	69	3.8	182	111	275	48
					GO2		2.5	91	123	204	35		1.2	39	61	98	31		1.8	66	138	197	34
					STOP								2.5	48	61	104	18		1.4	28	78	104	18
Search step	Monkey	ch	disimilar	8	GO1	7766	1.0	110	164	274	110	772	1.7	65	159	217	35	500	1.8	62	158	213	32
					GO2		2.1	65	160	218	29		5.8	84	35	113	16		2.0	62	160	215	29
					STOP								1.2	69	68	133	54		1.7	133	14	133	72
		fc	disimilar	8	GO1	5287	1.0	121	160	281	121	873	1.4	78	155	226	51	811	1.4	77	155	225	51
					GO2		2.3	102	130	220	42		1.6	23	91	112	13		2.2	97	130	216	41
					STOP								2.0	131	26	142	61		1.7	166	8	156	90
		ly	disimilar	8	GO1	3869	0.9	99	195	299	116	256	2.0	62	185	240	29	275	1.9	61	186	240	30
					GO2		2.5	112	143	242	43		2.8	84	51	126	29		2.5	109	140	237	41
					STOP								1.2	116	62	171	91		1.6	183	11	175	105
	Human	CC	disimilar	2	GO1	436	1.5	153	182	320	94	45	2.6	159	149	290	58	44	2.4	151	157	291	59
					GO2		1.7	76	173	241	41		1.0	35	61	96	35		1.5	62	177	233	38
					STOP								1.1	39	112	150	34		1.0	38	114	152	38
				4	GO1	481	1.6	179	165	325	103	110	2.8	183	125	288	63	98	3.4	217	91	286	63
					GO2		2.2	99	161	249	42		2.1	64	57	114	28		2.0	88	163	241	41
					STOP								1.3	70	85	150	50		1.5	80	78	150	49
				8	GO1	529	1.2	136	176	304	107	235	1.4	120	172	281	79	234	1.5	123	170	281	75
					GO2		1.6	82	167	241	47		1.1	55	37	90	48		1.1	59	176	233	52
					STOP								2.1	26	122	145	12		2.3	46	103	144	19

Table 3, continued

	Species	Subject	Search type	Set size	Process	GO-GO χ2	GO-GO Shape (α)	GO-GO Scale (β)	GO-GO Location (μ)	GO-GO Mean	GO-GO Variance	GO-STOP-GO χ2	GO-STOP-GO Shape (α)	GO-STOP-GO Scale (β)	GO-STOP-GO Location (μ)	GO-STOP-GO Mean	GO-STOP-GO Variance	GO-GO+STOP χ2	GO-GO+STOP Shape (α)	GO-GO+STOP Scale (β)	GO-GO+STOP Location (μ)	GO-GO+STOP Mean	GO-GO+STOP Variance
Search step	Human	CC	similar	2	GO1	219	1.4	103	206	300	68	82	1.8	96	200	285	49	93	1.8	98	198	285	50
					GO2		5.0	263	3	244	55		1.8	67	0	60	34		3.5	198	59	237	56
					STOP								3.1	202	23	204	64		1.4	178	105	267	117
				4	GO1	273	1.1	111	221	328	97	64	1.5	99	215	304	61	66	1.5	100	214	304	61
					GO2		1.7	156	154	293	84		0.7	43	16	70	80		1.6	134	159	279	77
					STOP								2.9	153	83	219	51		2.8	227	54	256	78
				8	GO1	151	0.9	156	218	382	183	47	1.1	132	216	343	116	48	1.1	135	216	346	119
					GO2		1.6	229	142	347	131		1.1	120	11	127	105		1.5	212	151	342	130
					STOP								1.3	151	114	253	108		1.1	189	123	305	166
		LB	disimilar	2	GO1	749	1.7	180	204	365	97	109	3.3	173	169	324	52	94	3.9	189	153	324	49
					GO2		1.6	80	192	264	46		1.1	44	66	108	39		1.4	66	194	254	44
					STOP								2.0	70	99	161	32		2.4	112	61	160	44
				4	GO1	567	1.6	166	214	363	95	120	3.4	193	159	332	56	124	3.1	173	176	331	55
					GO2		1.5	85	163	240	52		1.3	53	43	92	38		1.5	82	161	235	50
					STOP								1.2	64	103	163	50		2.0	119	60	165	55
				8	GO1	605	2.2	239	141	353	102	182	3.8	265	85	325	70	231	3.2	233	117	326	72
					GO2		1.6	96	140	226	55		0.8	37	41	83	53		1.8	97	132	218	50
					STOP								2.4	80	75	146	31		1.6	81	81	154	46
			similar	2	GO1	275	1.4	136	250	374	90	55	1.9	119	240	346	58	54	2.0	126	234	346	58
					GO2		2.9	172	139	292	57		1.2	51	26	74	40		2.1	129	173	287	57
					STOP								2.2	127	121	233	54		1.9	190	98	267	92
				4	GO1	481	1.4	158	229	373	104	61	2.3	139	214	337	57	63	2.3	138	214	336	56
					GO2		1.4	103	206	300	68		1.0	56	36	92	56		1.2	83	210	288	65
					STOP								1.3	64	152	211	46		1.2	85	143	223	67
				8	GO1	411	1.1	143	229	367	126	64	1.6	111	222	322	64	65	1.6	111	221	321	64
					GO2		1.3	103	193	288	74		1.0	62	33	95	62		1.3	91	193	277	65
					STOP								1.1	49	149	196	43		1.9	119	92	198	58
		SS	disimilar	2	GO1	413	1.4	223	255	458	147	96	2.4	234	206	413	92	109	2.1	209	228	413	93
					GO2		2.9	102	154	245	34		2.8	40	78	114	14		2.2	82	168	241	35
					STOP								2.9	96	49	135	32		2.8	91	52	133	31
				4	GO1	395	1.4	207	258	447	137	95	2.2	208	220	404	88	93	2.4	213	213	402	84
					GO2		2.8	100	168	257	34		2.4	45	74	114	18		2.3	86	179	255	35
					STOP								2.4	87	73	150	34		1.4	108	59	157	71
				8	GO1	474	1.3	206	267	457	148	105	2.1	189	234	401	84	125	2.0	186	240	405	86
					GO2		4.3	171	92	248	41		2.2	14	116	128	6		2.4	104	151	243	41
					STOP								2.9	129	16	131	43		1.8	45	97	137	23

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Table 3, continued

						GO-GO						GO-STOP-GO						GO-GO+STOP					
	Species	Subject	Search type	Set size	Process	χ^2	Shape (α)	Scale (β)	Location (μ)	Mean	Variance	χ^2	Shape (α)	Scale (β)	Location (μ)	Mean	Variance	χ^2	Shape (α)	Scale (β)	Location (μ)	Mean	Variance
Search step	Human	SS	similar	2	GO1	542	1.4	289	271	534	191	95	2.4	271	225	465	107	98	2.5	277	219	465	105
					GO2		1.6	134	258	378	77		1.2	94	78	166	74		1.4	115	264	369	76
					STOP								1.8	66	155	214	34		1.9	73	148	213	35
				4	GO1	614	1.4	263	285	525	173	111	3.0	282	206	458	92	114	3.2	302	187	457	93
					GO2		2.1	142	253	379	63		1.6	97	71	158	56		1.7	114	267	369	62
					STOP								2.7	74	153	219	26		1.8	29	195	221	15
				8	GO1	645	1.8	325	253	542	166	100	3.2	323	190	479	99	102	3.1	308	203	478	97
					GO2		3.0	195	205	379	63		2.0	124	47	157	57		2.1	135	245	365	60
					STOP								2.1	41	174	210	18		2.3	44	170	209	18