RESEARCH ARTICLE | Control of Coordinated Movements

Task context determines whether common or separate inhibitory signals underlie the control of eye-hand movements

Sumitash Jana and Aditya Murthy
Center for Neuroscience, Indian Institute of Science, Bangalore, Karnataka, India

Submitted 2 February 2018; accepted in final form 19 June 2018

INTRODUCTION

Flexibility of action involving the modification or suppression of planned movements when they are no longer appropri-
ate is a necessary requirement of everyday life. In our daily lives, we frequently couple our eye and hand movements (Land 2009; Land and Hayhoe 2001), posing the question whether common or separate stopping mechanisms are responsible for the control of the two effectors. Whereas the frontal eye field (Hanes et al. 1998) and supplementary eye field (Stuphorn et al. 2000) have been implicated in inhibition of saccades, hand movements are thought to be controlled by the dorsal premotor cortex (Mattia et al. 2013; Mirabella et al. 2011) and primary motor cortex (Coxon et al. 2006; Mattia et al. 2012). In contrast, the right inferior frontal gyrus (Aron et al. 2003, 2014; Konishi et al. 1999), presupplementary motor area (Cai et al. 2012a; Nachev et al. 2007; Swann et al. 2012), and the subthalamic nucleus (Aron and Poldrack 2006; Mirabella et al. 2012; Obeso et al. 2014; Wessel et al. 2016) are thought to be responsible for more general effector-independent inhibitory control (but see also Erika-Florence et al. 2014; Li et al. 2008; Mirabella et al. 2017; Swick et al. 2008). Additionally, Leung and Cai (2007) found both overlapping and nonoverlapping regions of activations in the ventrolateral prefrontal cortex during cancelling of eye and hand button presses, suggesting both common and independent nodes controlling eye-hand movements. Hence, in terms of neural representation, it is not clear whether common or separate networks are responsible for the control of concurrently produced eye and hand movements.

In the context of behavior, two studies that investigated stopping of eye and hand button presses, Logan and Irwin (2000) and Boucher et al. (2007b), observed that the stop signal reaction time or the time to inhibit an action is shorter for eye movements compared with hand movements. Whereas the former study concluded that the two effectors are controlled by separate processes, the latter study proposed that the stopping of eye and hand movements was neither completely independent nor completely common. Boucher et al. (2007b) suggested that the STOP process comprised a common central process and an effector-specific peripheral process. This idea was also supported by Gulberti et al. (2014) in a study involving saccade and reaching movements. In contrast, Gopal and Murthy (2016) have suggested that coordinated saccade and reaching movements are stopped by a common control mechanism. By incorporating a ballistic stage (de Jong et al. 1990; Mirabella et al. 2006; Osman et al. 1986) in the hand-movement planning stage, they were able to explain eye-hand control using a common control signal. Although there are notable differences between the studies [some of the previous studies used button
presses, which ostensibly are not naturalistic movements, whereas the Gopal and Murthy (2016) study looked at reaching movements, such differences in the conclusions remain unexplained.

In light of the flexibility underlying eye-hand coordination (Frens and Erkelens 1991; Jana et al. 2017; Sailer et al. 2000), we hypothesized that there may be two distinct and task-dependent mechanisms controlling eye-hand movements, a common control signal and effector-specific control mechanisms. Our rationale was that when GO processes for eye and hand are separate, so would be the STOP processes, whereas a common GO process would work in tandem with a common STOP process. We (Jana et al. 2017) have previously demonstrated the flexibility that exists in the initiation of eye-hand movements. Briefly, with the use of a stochastic accumulation-to-threshold model, which predicts a linear relation between the mean and standard deviation (SD) of reaction time (RT) distributions (Wagenmakers et al. 2005; Wagenmakers and Brown 2007), we have shown that depending on the task context, eye and hand movements may be initiated by a common or separate GO signals. Thus the signatures of a common GO process are comparable SDs of eye and hand RT distribution and high RT correlation, whereas the signatures of separate GO processes are scaling of SD of RT distribution along with its mean RT and low RT correlation. In a visual search task, where the GO cue for both of the effectors was common, the initiation of eye and hand movements was best explained by a common accumulation process. On the other hand, in the dual task, where the GO cues of the two effectors were separate, the initiation of the movements was best explained by separate accumulators for eye and hand. It then follows that common STOP signal should be observed in conjunction with high RT correlation, whereas separate STOP signals should be observed in conjunction with low RT correlation. In support of this argument, the Boucher et al. (2007b) study reported low RT correlation (suggesting separate GO processes), whereas the Gopal and Murthy (2016) study found moderate-to-high RT correlations. In this paper, we extend our previous work to test how task context affects the control of eye-hand movements by incorporating a redirect component [a modification of the double-step task (Becker and Jürgens 1979)] in the search and dual task.

METHODS

Subjects

Eye, hand, and electromyography (EMG) activity were recorded in 12 healthy subjects (11 right-handed, 6 women) while they performed the Search Step and Dual Redirect tasks on separate days. They were aged between 20 and 29 yr and had normal or corrected-to-normal vision. Before the experiments, the subjects gave their written, informed consent in compliance with the Institutional Human Ethics Committee of the Indian Institute of Science, Bangalore, which approved the protocol. Subjects were paid for their participation.

Setup of the Experiment

TEMPO/VIDEOSYNC software (Reflecting Computing, St. Louis, MO) was used to generate the stimuli and simultaneously acquire the data in real-time at a temporal resolution of ~1 ms. A head-mounted pupil tracker (ETL-200, RK-706PCI; ISCAN, Boston, MA) was used to sample eye position at 240 Hz. Hand position was sampled at 240 Hz by an electromagnetic tracking system that followed the position of a sensor placed at the tip of the pointing finger, with reference to a source (LIBERTY; Polhemus, Colchester, VT). Both tracking systems interfaced with TEMPO with a delay of 8 ± 1 ms.

A Cerubes data acquisition system (Blackrock Microsystems) was used to record the EMG activity using 10-mm gold cup electrodes (CareFusion). EMG activity was sampled at 1 kHz and stored in TEMPO.

A 24-in. Dell light-emitting diode monitor (60 Hz), placed face down on a wooden frame, was used to display the stimuli. A semitransparent mirror (25% transmission-75% reflectance) was placed at an angle below the monitor and reflected the stimuli. While images were visible on the plane of the mirror, an acrylic sheet placed parallel to and below the mirror served as the plane for the hand movements. This setup provided the notion that both of the movements were being made in the same plane, while reducing the electromagnetic interference of the monitor on the hand tracker [for more details, see Fig. 1C in Gopal et al. (2015)].

Recording Procedures

Experiments were performed in a dark room where subjects sat with their chin resting on a chin rest attached to the wooden-frame setup and looked down at the mirror. Visual feedback of finger position was provided by strapping a battery-driven light-emitting diode at the tip of the pointing finger. The subject’s head was locked at the temple to minimize head movements. The head-mounted eye camera was positioned below the eye such that it did not block the stimuli. Before each session, a calibration block was run where subjects looked at targets on the screen and the eye gains and camera positions were adjusted. EMG electrodes were placed on the belly of the anterior and posterior deltoid muscles to track muscle activity. The ground electrode was placed on the ear lobe of the subject, and the reference electrode was placed at the elbow.

Behavioral Tasks

Search Step task. Each trial began with a white fixation spot/box appearing in the center of the screen where the subject had to fixate his/her eyes and hand (Fig. 1A; see Table 1 for behavioral performance). After a fixation delay of 500–1,000 ms, an array of four targets were displayed at an eccentricity of 10°, which could contain a red target among three green distractors or a green target among three red targets. The red-among-green and green-among-red conditions were randomly presented in each trial with a probability of 0.5. Such no-step trials comprised 60% of all of the trials. In 40% of the trials, following a target step delay (TSD), the target switched to any of the other three distractor locations. There were three blocks of trials: the coordinated block, where the subjects had to make both eye and hand movements to the target (TSDs 50, 166, 283, and 400 ms); an eye-alone block, where the subject had to make only an eye movement while keeping the hand fixated at the center (TSDs 50, 166, 283, and 350 ms); and a hand-alone block, where the subject had to make only a hand movement to the target while keeping his/her eyes fixated at the center (TSDs 50, 166, 283, and 450 ms). The presentation of these blocks was counterbalanced across subjects. Each correct response was indicated by a tone (1,000 Hz, ~70 dB). Subjects were instructed to make a movement to the target as fast and as accurately as possible. Each subject performed ~300 trials of coordinated eye-hand responses and ~200 trials of eye-alone and hand-alone trials in separate blocks. The order of presentation of these blocks was counterbalanced across subjects.

Cutoff for RT. Reaction time (RT) was calculated as the difference between the target onset (2nd target for step trials) and the movement onset and corrected for the system delay. Typically, eye RT precedes hand RT by 80–100 ms (Biguer et al. 1984; Prablanc et al. 1979; Sailer et al. 2000); hence, trials in which eye onset was after hand
onset were removed from the analysis (Fischer and Rogal 1986; Jana et al. 2017). This accounted for ~8% of coordinated trials. To remove outliers, we considered only those trials for which RTs were within mean ± 3 times the standard deviation for both eye and hand RTs. In total, ~6% of eye RT and ~1% of hand RT (alone and coordinated trials combined) were removed.

The Dual Redirect task. The experiment had Eye Block and Hand Block conditions. Each trial began with a white fixation box at the center where the subject had to fixate his/her eyes and hand. In the Eye Block condition (Fig. 1B; see Table 1 for behavioral performance), after a fixation delay of 500–1,000 ms, a green target appeared at one position along the cardinal axes at an eccentricity of 10° of visual angle. These trials represented the eye-alone trials where the subject had to make an eye movement while maintaining hand fixation. In 40% of the trials (representing the coordinated trials), a tone (1,000 Hz for 100 ms, ~70 dB) was sounded along with the presentation of the target, and in these trials the subject had to make both eye and hand movements to the target. In 40% of both eye-alone and coordinated trials, a yellow target appeared in any of the other three locations with a TSD of 50, 200, 350, or 600 ms to which the subjects had to redirect their movement/s. Subjects were instructed to make a movement as fast and as accurately as possible. In other words, in the Eye Block condition, the default instruction was to make an eye movement to the green square and additionally make a hand movement to the target if a tone was presented and redirect the movement/s to the yellow target if it appeared.

The Hand Block condition (Fig. 1C; see Table 1 for behavioral performance) was almost entirely similar to the Eye Block condition, except that the default instruction was to make a hand movement to the target and also make an eye movement to the target if a tone was presented and that the initial target was red (instead of green) in color. In both the Eye Block and Hand Block conditions, correct responses were indicated by a green tick mark, whereas errors were indicated by a red cross displayed on the screen.

Each subject performed ~400 trials of Eye Block and Hand Block conditions, the order of presentation of which was counterbalanced across subjects. The same subjects performed both Search Step and Dual Redirect tasks on separate days, the order of which was also counterbalanced across subjects.

Cutoffs for reaction time. The RTs during the Eye Block and Hand Block conditions were checked for outliers separately as the mean eye and hand RT in the two blocks were different. Whereas the Eye Block had 2% trials where eye RT was greater than hand RT, in the Hand Block 39% of trials had eye RTs greater than hand RTs (outlier rejection done separately as the mean eye and hand RT were different). In the early part of the paper, we consider only the trials where the eye RT is less than hand RT (which putatively can be generated by both a common or separate accumulator/s), whereas we consider trials with eye RT greater than hand RT in a later section of the paper. Eye and hand RT within mean ± 3 times the SD was included in the analysis. This outlier cutoff removed <1% of eye RTs and hand RTs.

Criterion for Determining the Outcome of the Trials

If the direction of the first saccade (>2°) and the direction of the first hand movement when half of the movement was over were within an arc of 45° in the direction of the correct target location, the movements were deemed correct.

Detection of Eye and Hand-Movement Onsets

Onsets of eye and hand movements were decided using a velocity criterion. Saccade onset and ending were distinguished when the instantaneous velocity crossed the cutoff of 30°/s. Saccades were further verified using its acceleration-deceleration profile by validating that a peak in acceleration was followed within 100 ms by a peak in deceleration. Furthermore, the saccade beginning and ending were altered depending on when 10% of the peak velocity of the saccade was reached. Only those saccades for which amplitudes were >2° and <24° were accepted. Hand-movement beginning and end were marked using an instantaneous velocity cutoff of 10 cm/s and thereafter adjusted depending on when 10% of the peak velocity of the hand movement was reached. Furthermore, hand movements had to satisfy an amplitude criterion (>1 cm) and a duration criterion (>40 ms).

Table 1. Behavioral performance

<table>
<thead>
<tr>
<th>Type of Trial</th>
<th>Outcome</th>
<th>Search Step</th>
<th>Hand Block</th>
<th>Eye Block</th>
</tr>
</thead>
<tbody>
<tr>
<td>No-step</td>
<td>Correct, %</td>
<td>97 (3)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Step</td>
<td>Correct, %</td>
<td>45 (7)</td>
<td>54 (11)</td>
<td>32 (14)</td>
</tr>
<tr>
<td></td>
<td>Error, %</td>
<td>40 (5)</td>
<td>41 (11)</td>
<td>41 (8)</td>
</tr>
<tr>
<td></td>
<td>Dissociated, %</td>
<td>9 (4)</td>
<td>6 (4)</td>
<td>27 (10)</td>
</tr>
</tbody>
</table>

Values indicate means (SD).

J Neurophysiol  doi:10.1152/jn.00085.2018 • www.jn.org
Downloaded from www.physiology.org/journal/jn at Indian Inst of Sci (014.139.128.011) on September 25, 2019.
Analyzing EMG Signals

EMG onset times were detected using the full-wave-rectified EMG signal. This signal was first smoothed using an 8-ms uniform window, and then the threshold was determined. For each trial, the threshold was adjusted such that 70% of the EMG signal during the baseline period (i.e., from beginning of the trial to target onset) was lower than the threshold.

To capture the dips in EMG activity, the root mean square of the full-wave-rectified EMG signal was filtered using a low-pass filter with cutoff at 6 Hz. This cutoff was chosen on the basis of hand-movement duration. Hand-movement duration was ~300 ms across subjects. The EMG rose and fell during this duration and was considered to encompass the full cycle of EMG activity. Thus the frequency of EMG rise and fall was ~3 Hz. A cutoff frequency of twice this value was chosen.

Statistical Tests

The data were first checked for normality using a Lilliefors test, and, depending on its results, either a two-tailed t-test or Wilcoxon signed-rank test was used. Unless otherwise mentioned, the Pearson correlation coefficient was used. To test whether SDs of two distributions matched, an F test was used. Similarly, for multiple comparisons, a repeated-measures ANOVA or a Kruskal-Wallis test was used. Cohen d and partial $\eta^2$, which measure the effect size, have also been included in the text. Predicted percentage of trial outcomes was compared with that observed using a $\chi^2$ goodness of fit. A binomial test was used to assess whether the number of subjects with correct prediction was significantly greater than chance.

Modeling RT Distributions

A stochastic accumulation-to-threshold model was used to model the RT distributions. The activity of a GO unit was simulated in which sensory evidence is accumulated to a threshold after an afferent delay of 60 ms. On reaching the threshold, a movement is thought to be initiated. Such accumulation to threshold has been observed in many regions of the brain, including frontal eye field (Hanes and Schall 1999), lateral intraparietal area (Shadlen and Newsome 2001), superior colliculus (Horwitz and Newsome 1999), dorsal premotor cortex (Song and McPeek 2010), and basal ganglia (Ding and Gold 2010).

The level of accumulation can be expressed as:

$$a_{GO}(t) = a_{GO}(t-1) + \mu_{GO} + \epsilon_{GO},$$

where $a_{GO}$ is the level of accumulation at time $t$, $\mu_{GO}$ is the mean drift rate, and $\epsilon_{GO}$ is a Gaussian noise term with mean 0 and SD equal to that of the GO unit, which represents the noise in the input signal. The accumulation was modeled without any leak. The variability of the accumulation process at any time point $t$ across different instances of accumulation is given by the equation:

$$\sigma_{GO}(t) = k \cdot \sigma_{noise} \sqrt{t},$$

where $\sigma_{noise}$ is Gaussian noise and $k$ is scaling constant. Thus intuitively slower RT distributions should be more variable due to greater accumulation of noise as a consequence of larger number of stochastic iterations required to reach the desired threshold. Such monotonic scaling of the SD of the RT distribution with the mean RT is not only borne out experimentally, but also can be more formally derived (Wagenmakers et al. 2005; Wagenmakers and Brown 2007).

Estimation of Model Parameters

Estimation of the model parameters has been mentioned in detail in Jana et al. (2017). Briefly, for estimating $\mu_{GO}$ and $\sigma_{GO}$ RT distributions were simulated using Eq. 1. A range of values that could generate behaviorally relevant RT distributions were uniformly and “coarsely” sampled to simulate RT distributions of 2,000 trials, and those parameters that generated a RT distribution with a mean and SD within 30 ms of the mean and SD of the empirical RT distribution were fed into the fmincon function for minimization in MATLAB. A nonlinear constraint was applied whereby 70% of the simulated RT distribution had to lie within the extent of the empirical RT distribution. To fit the tails of the RT distribution, the error was calculated as the difference between inverted Gaussian-weighted cumulative distribution functions of the empirical and simulated RT distributions. The minimum error solution typically converged within <20 iterations. To obtain the best estimate of the parameter, multiple runs of minimization were simulated using the different starting points.

Models of Eye-Hand Coordination

Common accumulator model. This model simulates a single accumulator for both eye and hand [refer to Gopal et al. (2015) and Jana et al. (2017)]. When the accumulator reaches threshold, an eye movement is generated. A delay, representing the delay in activation of hand muscles leading to hand movement, is added at the periphery, which accounts for the greater hand RT compared with the eye RT. The accumulation at time $t$ can be expressed as:

$$a_{GO-Com}(t) = a_{GO-Com}(t-1) + \mu_{GO-Com} + \epsilon_{GO-Com},$$

where $a_{GO-Com}$ represents the activity of the common accumulator, $\mu_{GO-Com}$ represents the mean accumulation rate of the accumulator, and $\epsilon_{GO-Com}$ represents the Gaussian noise.

Briefly, $\mu_{GO-Com}$ and $\sigma_{GO-Com}$ were first estimated from the observed coordinated eye RT distribution, using the estimation method described above. The parameters of the hand delay were estimated using the hand RT distribution in the coordinated condition. Out of a large range of values for $\mu_{delay}$ and $\sigma_{delay}$ only those parameters that satisfied the constraints (mean and SD of the simulated hand RT was within 30 ms of the mean and SD of the observed hand RT, and 70% of the simulated hand RT distribution lay within the extent of the observed hand RT distribution) were fed into fmincon for minimization. After estimation of the best parameters, the predicted RT correlation was calculated as the correlation between the predicted eye and hand RT distributions.

Separate accumulators with interaction between accumulators. In this model, separate accumulators representing the developing motor command of the eye and hand were simulated (refer to Gopal et al. 2015; Jana et al. 2017). Each accumulator was independent and had its own $\mu_{GO}$ and $\sigma_{GO}$. The $\mu_{GO-E}$ and $\sigma_{GO-E}$ and $\mu_{GO-H}$ and $\sigma_{GO-H}$ were estimated based on the empirical eye-alone and hand-alone RT distributions, respectively. Thus $\beta_{E-H}$ and $\beta_{E-E}$ represented the strength of the interaction from the eye accumulator to the hand accumulator and the interaction from the hand accumulator to the eye accumulator, respectively.

The accumulation process at time $t$ can be represented as:

$$a_{e}(t) = a_{e}(t-1) + \mu_{GO-E} + \beta_{E-H} \cdot a_{h}(t-1) + \epsilon_{GO-E},$$

$$a_{h}(t) = a_{h}(t-1) + \mu_{GO-H} + \beta_{E-H} \cdot a_{e}(t-1) + \epsilon_{GO-H},$$

where $a_{e}$ and $a_{h}$ represent the value of accumulation of the eye and hand accumulator, respectively, at time $t$, $\mu_{GO-E}$ and $\mu_{GO-H}$ represent the mean drift rate of the eye and hand accumulator, respectively, and $\epsilon_{GO-E}$ and $\epsilon_{GO-H}$ represent the Gaussian noise term associated with the eye and hand accumulators, respectively.

The interaction parameters were estimated from the observed coordinated eye and hand RT distributions. A sufficiently large range of the interaction parameters were used as seeds, and whichever parameters satisfied the constraints (namely, simulated eye and hand means and SDs were within 30 ms of the empirical eye and hand means and SDs, respectively) were fed into fmincon for minimization. The inputs to the eye and hand accumulators were considered to be completely correlated.
**Compensation Function**

The performance of subjects in step trials was quantified using a compensation function that shows the probability of error response as a function of TSD. The compensation functions were fitted using a cumulative Weibull function, $W(t)$ (Hanes et al. 1998; Ramakrishnan et al. 2010):

$$W(t) = \gamma - (\gamma - \delta)e^{-\left(\frac{t}{\alpha}\right)^b},$$  \hspace{1cm} (6)

where $t$ is the TSD, $\alpha$ is the time at which the function reaches 64% of its full growth, $\beta$ is the slope, $\delta$ is the minimum value of the function, and $\gamma$ is maximum value of the function. The difference between $\delta$ and $\gamma$ marks range of the compensation function. In this study, this difference was always $>0.5$. The fitted $\alpha$ had $\alpha > 0.9$. The mean of the fitted compensation function (Weibull mean, WM) was calculated as:

$$WM = \frac{\sum \left[W(t) - W(t-1)\right]}{W(t_{\text{max}}) - W(t_{\text{min}})} \cdot t,$$  \hspace{1cm} (7)

where $t$ ranges from the minimum to the maximum TSD in 1-ms intervals.

**Race Model Framework**

The race model is a popular framework used to understand behavior when subjects are faced with stopping/redirection of their movements. The race model considers that there exist two processes, a GOI process and a STOP process, that race against each other to reach a decision threshold, and the outcome of this race determines the response in a step trial. If the GOI process reaches the threshold first, then a response to the initial target is initiated, resulting in an error trial. However, if the STOP process reaches the threshold first, the response to the initial target is curbed. Subsequently, a GO2 process (which starts with the initiation of the STOP process) rises to threshold, resulting in a correct response to the final target. Since the outcome of the trial is determined by GOI and STOP processes only, the GOI process will be referred to as the GO process henceforth.

**TSRT Calculation**

Target step reaction time (TSRT) is the time taken to stop a movement. It is analogous to the stop signal RT calculated in stop-signal paradigms. As stopping is not an overt process, it cannot be estimated directly from the experimental results. However, an independent race model provides a framework for its calculation (Logan and Cowan 1984; Camalier et al. 2007; Murthy et al. 2009; Ramakrishnan et al. 2010).

The TSRT was calculated in three ways by using the mean, median, and the integration method using the logic described by Logan and Cowan (1984; see also Hanes et al. 1998; Murthy et al. 2009; Ramakrishnan et al. 2010). The TSRT values calculated by these three methods were slightly different and, hence, were averaged to get a single estimate (Gopal and Murthy 2016).

**Z-Score, Relative Finishing Time**

Z-score, relative finishing time (ZRFT) was calculated to normalize each compensation function using the mean and SD of the no-step RT distribution, the TSDs, and the TSRT as:

$$\text{ZRFT} = \frac{\text{mean RT}_{\text{No-Step}} - \text{TSRT}}{\text{SD RT}_{\text{No-Step}}},$$  \hspace{1cm} (8)

The probability of error plotted against ZRFT was nonlinear and thus fitted with an inverted sigmoid function, $S(t)$ of the form:

$$S(t) = \frac{a}{1 + e^{-\frac{Wt}{b}}},$$  \hspace{1cm} (9)

where $a$ is the maximum value of the function and $b$ is the slope. These fits had a mean $r^2$ of 0.98 ± 0.03 and 0.96 ± 0.09 in the Search Step and Dual Redirect task, respectively. As ZRFT slopes can be misleading, we used the area under each fit (AUC) as a metric to quantify inhibitory control (Carter et al. 2003). The ZRFT range was chosen as the maximum and minimum value within each task condition. The difference between the eye and hand AUC in the alone and the coordinated condition were then compared.

**Parameter Estimation for Race Model**

The GO and STOP processes that determine the outcome of a step trial were modeled as noisy accumulators.

**GO process.** The level of accumulation in the GO process was determined by Eq. 1 and was simulated as mentioned previously.

**STOP process.** The STOP process represents the inhibitory process that gets initiated with the appearance of the second target and races with the GO process. The rate of accumulation of the STOP process is governed by the equation:

$$a_{\text{STOP}}(t) = a_{\text{STOP}}(t-1) + \mu_{\text{STOP}} + \epsilon_{\text{STOP}},$$  \hspace{1cm} (10)

where $a_{\text{STOP}}$ is the level of accumulation at time $t$, $\mu_{\text{STOP}}$ is the mean drift rate, and $\epsilon_{\text{STOP}}$ is the Gaussian noise term with mean 0 and SD equal to that of the STOP unit, which represents the noise.

Once the parameters of the GO process were estimated, the parameters of the STOP process were then estimated. Three thousand five hundred step trials were simulated using a range of $\mu_{\text{STOP}}$ and $\sigma_{\text{STOP}}$ values between 0.001 and 0.1, which could give rise to behaviorally observed compensation functions. Following the appearance of the second target (using the same TSDs as used in the experiment), the STOP accumulator started. The GO RT and STOP RT in a trial were determined by the time each process reached the threshold. If the GO RT was less than STOP RT, it was considered to be an error trial, whereas if the STOP RT was less than the GO RT, then it was considered to be a correct trial. This generated a compensation function based on the probability of error response at each TSD. The least-squares error was calculated between the simulated and observed compensation function, which was then minimized using the fmincon function in MATLAB. The function typically converged in <20 iterations. The $\mu_{\text{STOP}}$ and $\sigma_{\text{STOP}}$ that gave rise to the compensation function that best matched the experimental one were used to generate the STOP RT distribution.

**Ballistic Stage**

The ballistic stage refers to the stage during motor planning during which the movement cannot be influenced by any control signal and, hence, cannot be stopped (Osman et al. 1986). During motor planning after a point called the point of no return, which separates the initial controllable stage and the ballistic stage, the movement is impervious to control and is irrevocably executed. Since there is no direct method of calculating the ballistic stage from the observed data, it has to be estimated using simulations. It was hypothesized that the Eye-STOP and a ballistic stage would give rise to the hand compensation function (Fig. 2A).

The $\mu$ and $\sigma$ of the duration of the ballistic stage was estimated from the hand-coordinated compensation function (Gopal and Murthy 2016) using the following steps. First, the $\mu_{\text{STOP}}$ and $\sigma_{\text{STOP}}$ of the eye was estimated from the eye-coordinated compensation function using the procedure described above. Second, with the use of this $\mu_{\text{STOP}}$ and $\sigma_{\text{STOP}}$ of the eye and $a$ and $\sigma$ of the duration of the ballistic stage (sampled from a range between 1 and 250 ms), 3,500 step trials spanning across all of the TSDs were simulated. The error and correct
trials were calculated depending on whether the STOP accumulator lost or won the race, respectively. This allowed a compensation function to be calculated, which was then fitted using a cumulative Weibull function, and the least-squares error between the observed and predicted compensation function was calculated. The \( \mu \) and \( \sigma \) of the ballistic stage were uniformly sampled from a range of 1–250 ms, generating an array of error values. Fifty of the smallest error values were chosen and then fed into fmincon for minimization.

**Models to Explain Redirect Behavior**

The STOP process for eye and hand could be common or separate. Similarly, the GO process of the eye and hand could be common or separate. This gave rise to four models: 1) common GO and STOP process for eye and hand (1Go1Stop model; Fig. 2A). This model had eight parameters: \( \mu_{\text{GO}} \) and \( \sigma_{\text{GO}} \) for eye, \( \mu_{\text{Delay}} \) and \( \sigma_{\text{Delay}} \) for hand, \( \mu \) and \( \sigma \) of the ballistic stage, and \( \mu_{\text{STOP}} \) and \( \sigma_{\text{STOP}} \); 2) common GO process and separate STOP processes for eye and hand (1Go2Stop model; Fig. 2B). This model had eight parameters: \( \mu_{\text{GO}} \) and \( \sigma_{\text{GO}} \) for eye, \( \mu_{\text{Delay}} \) and \( \sigma_{\text{Delay}} \) for hand, \( \mu_{\text{STOP}} \) and \( \sigma_{\text{STOP}} \) for eye, and \( \mu_{\text{STOP}} \) and \( \sigma_{\text{STOP}} \) for hand; 3) separate GO processes and a common STOP process for eye and hand (2Go1Stop model; Fig. 2C). This model had six parameters: \( \mu_{\text{GO}} \) and \( \sigma_{\text{GO}} \) for eye, \( \mu_{\text{GO}} \) and \( \sigma_{\text{GO}} \) for hand, and \( \mu_{\text{STOP}} \) and \( \sigma_{\text{STOP}} \); and 4) separate GO and separate STOP processes for eye and hand (2Go2Stop model; Fig. 2D). This model had eight parameters: \( \mu_{\text{GO}} \) and \( \sigma_{\text{GO}} \) for eye, \( \mu_{\text{GO}} \) and \( \sigma_{\text{GO}} \) for hand, \( \mu_{\text{STOP}} \) and \( \sigma_{\text{STOP}} \) for eye, and \( \mu_{\text{STOP}} \) and \( \sigma_{\text{STOP}} \) for hand.

We chose the simplest models that could theoretically account for the expected trial outcomes: correct, error, and dissociated. In all but the 1Go1Stop model, the dissociated trials could be generated due to the presence of separate GO or STOP processes. Hence, only the 1Go1Stop model was incorporated with a ballistic stage, which allowed it to account for dissociated trials. All four models were simulated to check which better predicted the observed compensation functions and the observed percentages of trial outcomes.

**RESULTS**

In continuation of our previous study (Jana et al. 2017), where we showed that the task context determines whether a common or separate accumulator model is able to explain better the RTs of eye and hand movements, we tested the mechanism of redirection/control of the two effectors when they were initiated by a common vs. separate accumulators. We incorporated a redirect component in the search and dual tasks to elucidate the mechanism of control of eye and hand movements. Hence, in the Search Step task, the oddball target infrequently switched to a new location, whereas in the Dual Redirect task a new target could appear in 40% of trials. In both conditions, the subjects were instructed to make an eye and hand movement to the second target if it appeared. Our working hypothesis was that the task context that invoked a common GO process would invoke a common STOP, whereas the task context that invoked separate GOs would invoke effector-specific STOPs.

**RT Distributions in the Coordinated No-Step Trials**

We began by testing whether the different coordinated task contexts bore signatures of being initiated by a common or separate GO processes. Across the population, the mean hand RT was always greater than the mean eye RT (Fig. 3A; Table 2). However, the SD of eye and hand RT distributions were...
Fig. 3. Behavior in no-step coordinated trials. A: scatter plot showing that the mean hand reaction time (RT) is greater than the mean eye RT in all of the conditions. Each dot and cross-hair represents the mean ± SE of the RT for a subject in Search Step (green), Eye Block (violet), and Hand Block (brown). Squares and cross-hairs represent the population means ± SE. Unity line is shown as a dotted line. B: scatter plot showing that the SD of the hand RT is greater than that of the eye RT distribution only in the Eye Block condition but is comparable in the Search Step and Hand Block conditions. Filled dots represent subjects where the SDs are not comparable. C: bar plot showing the eye and hand RT correlation (Pearson r) across the population in the 3 conditions. Each dot represents a subject, and the bar represents the mean ± SE of the RT correlation across the population. Mean RT correlation was comparable between Search Step and Hand Block conditions but was significantly less in the Eye Block condition. **P < 0.01 and P ≥ 0.001; ***P < 0.001; ns, nonsignificant.

Validation of the Common and Separate Accumulator Model Using EMG

The Common Accumulator model suggests that EMG onset should be closely associated and sometimes even precede saccade onset as a consequence of the peripheral delay, whereas the Separate Accumulator model suggests that EMG onset should not be associated with saccade onset and could occur even after saccade onset. To test this, EMG onsets were aligned to the saccade onset for each subject for the top and left targets, which were in the movement field of the anterior deltoid muscle. Across the population, EMG onset was before saccade onset in 88 ± 9% trials in the Search Step and 95 ± 5% trials in the Hand Block conditions, which were both significantly greater than chance of 50% [W(11) = 0; P < 0.001 in both conditions]. However, EMG onset was before saccade onset in only 26 ± 22% trials in Eye Block condition, which was significantly less than 50% [W(11) = 5; P = 0.005]. Furthermore, eye and EMG RT were significantly correlated in 12/12 subjects in the Search Step (mean r = 0.85 ± 0.08) and in 9/12 subjects in the Hand Block (mean r = 0.63 ± 0.22) conditions but significantly correlated in only 3/12 subjects in the Eye Block condition (mean r = 0.24 ± 0.18). The eye and EMG RT correlation in the Eye Block was significantly less than the correlation in both Search Step [W(11) = 0; P < 0.001] and Hand Block [W(11) = 3; P = 0.002]. This further validates the applicability of the Common Accumulator model in the Search Step and Hand Block conditions and the Separate Accumulator model in the Eye Block condition.

Validation of the No-Step RT Results Using Simulations

To validate the behavioral results observed in the no-step trials in the three conditions, eye and hand RT distributions were simulated using the Common Accumulator and Separate Accumulator models. In the Search Step condition (see Table 3), there was no difference between the observed mean eye RT and hand RT and that predicted by both models. However, whereas there was no significant difference between the SD of observed eye and hand RT distributions and that predicted by

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Search Step</th>
<th>Hand Block</th>
<th>Eye Block</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean RT</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eye</td>
<td>449 (33)</td>
<td>455 (62)</td>
<td>335 (75)</td>
</tr>
<tr>
<td>Hand</td>
<td>528 (25)</td>
<td>511 (67)</td>
<td>561 (51)</td>
</tr>
<tr>
<td>Stats</td>
<td>t(11) = 19.3</td>
<td>t(11) = 9.1</td>
<td>W = 0</td>
</tr>
<tr>
<td></td>
<td>P &lt; 0.002</td>
<td>P &lt; 0.001</td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>d = 2.7</td>
<td>d = 0.9</td>
<td>d = 3.7</td>
</tr>
<tr>
<td>SD RT</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eye</td>
<td>78 (12)</td>
<td>91 (19)</td>
<td>81 (25)</td>
</tr>
<tr>
<td>Hand</td>
<td>75 (11)</td>
<td>86 (14)</td>
<td>115 (27)</td>
</tr>
<tr>
<td>Stats</td>
<td>t(11) = 1.8</td>
<td>t(11) = 1.2</td>
<td>t(11) = 3.2</td>
</tr>
<tr>
<td></td>
<td>P = 0.107</td>
<td>P = 0.242</td>
<td>P = 0.008</td>
</tr>
<tr>
<td></td>
<td>d = 0.3</td>
<td>d = 0.3</td>
<td>d = 1.3</td>
</tr>
</tbody>
</table>

Values indicate means (SD). Within each condition, significant difference between the values for eye and hand are indicated in boldface. d, Cohen d; RT, reaction time; Stats, statistics; W, Wilcoxon signed-rank statistic.
and that predicted by both models. There was also no significant difference between the SD of the observed eye RT distribution and that predicted by both models. However, whereas there was no significant difference between the SD of the observed hand RT distribution and that predicted by the Common Accumulator model, the Separate Accumulator model overpredicted the SD. These results corroborate the idea that a common accumulation process drives the initiation of eye and hand movements in the no-step trials in the Hand Block.

In the Eye Block condition (see Table 3), there was no difference between the observed mean eye RT and hand RT and that predicted by both models. Additionally, there was no difference between the SD of the observed eye and hand RT distribution and that predicted by both models. However, the Common Accumulator model tended to underpredict the SD of hand RT distribution. This supports the notion that the no-step eye and hand RT might stem from separate accumulators.

Taken together, the simulation results were consistent with the behavioral results. It supported the notion that a common GO process probably initiated movements in the no-step trials of the Search Step and Hand Block conditions, whereas separate GO processes initiated movements in the no-step trials of the Eye Block task. Next, the step trials were analyzed to check whether the control of eye and hand movements in the Search Step, Eye Block, and Hand Block conditions were better explained by a common or separate STOP processes.

Assessing Common vs. Separate Control: Target Step Reaction Time

It was hypothesized that a common GO process would invoke a common STOP process and separate GO processes would invoke separate STOP processes. Hence, the eye and hand TSRT should be similar in the Search Step and Hand Block conditions but different in the Eye Block condition. Contrary to this supposition, the eye TSRT was less than the hand TSRT in all of the coordinated conditions (Table 4), suggesting that the control signals for eye and hand were separate. In the Dual Redirect-Alone condition, the eye TSRT was also less than the hand TSRT. However, in the Search Step-Alone condition, the eye TSRT was not significantly

Table 3.  Mean and SD of predicted eye and hand RT distributions

<table>
<thead>
<tr>
<th>Task</th>
<th>Condition</th>
<th>Eye, ms</th>
<th>Hand, ms</th>
<th>Stats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Search Step</td>
<td>Coordinated</td>
<td>229 (31)</td>
<td>280 (25)</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Alone</td>
<td>261 (31)</td>
<td>288 (38)</td>
<td>1.6</td>
</tr>
<tr>
<td>Dual Redirect</td>
<td>Eye Block (Coordinated)</td>
<td>128 (22)</td>
<td>211 (33)</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>Hand Block (Coordinated)</td>
<td>136 (36)</td>
<td>238 (29)</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>Alone</td>
<td>151 (31)</td>
<td>197 (27)</td>
<td>3.8</td>
</tr>
</tbody>
</table>

Values indicate means (SD). d, Cohen d; TSRT, target step reaction time; Stats, statistics; W, Wilcoxon signed-rank statistic.
different from hand TSRT. This result was driven by 3/12 subjects whose difference between mean eye-alone and hand-alone RT was significantly less than the population [23 ± 23 vs. 104 ± 42 ms; t(10) = 3.1, P = 0.011, d = 2.1], suggesting that these subjects probably employed a waiting strategy in the eye-alone condition. In conclusion, eye TSRT was less than hand TSRT in most of the alone and coordinated conditions as reported by some studies (Boucher et al. 2007a; Gopal and Murthy 2016; Logan and Irwin 2000). To elucidate further the nature of the control signals of eye and hand, the compensation functions between the alone and the coordinated conditions were compared.

Assessing Common vs. Separate Control: Compensation Functions

The compensation functions were realigned to the $z$-score, relative finishing time (ZRFT; see METHODS; Logan and Cowan 1984) to account for the mean and SD of the no-step RT distributions. Then, the difference in the area under the curve between eye and hand (AUC) was compared between the alone and coordinated conditions. This comparison within each task was preferred over comparison of the coordinated conditions between tasks as the alone and coordinated conditions were conducted in the same recording session.

In the Search Step condition, for the exemplar subject, the difference in the AUC was much larger in the alone trials (0.650) compared with the coordinated trials (0.135; Fig. 4A).

Similarly, across the population, the difference in AUC in the alone trials (0.628 ± 0.393) was significantly greater than that in the coordinated trials [0.203 ± 0.123; Fig. 4D; W(11) = 76, P = 0.002, d = 1.5]. In the Hand Block condition, for the exemplar subject, the difference in the AUC was much larger in the alone trials (0.576) compared with the coordinated trials (0.162; Fig. 4B).

Similarly, across the population, the difference in AUC in the alone trials (0.770 ± 0.425) was significantly greater than that in the coordinated trials [0.233 ± 0.235; Fig. 4E; W(11) = 77, P < 0.001, d = 1.6]. In the Eye Block condition, for the exemplar subject, the difference in the AUC was similar between the alone trials (0.576) and the coordinated trials (0.529; Fig. 4C).

Similarly, across the population, the difference in AUC in the alone trials (0.770 ± 0.425) was significantly greater than that in the coordinated trials [0.622 ± 0.538; Fig. 4F; t(11) = 0.709, P = 0.493, d = 0.307]. These results suggest that in the coordinated trials, the eye and hand control are similar in the Search Step and Hand Block but not in the Eye Block condition and are consistent with the notion of common vs. separate control mechanisms.

Fig. 4. Compensation functions. A: $Z$-score, relative finishing time (ZRFT) fits for eye-alone (green), hand-alone (blue), eye-coordinated (Coord; orange), and hand-coordinated trials (red) in the Search Step condition in a representative subject. Each dot represents the probability of error at a particular ZRFT value (Eq. 8), whereas the traces represent the inverted sigmoid fit (Eq. 9). Inset: the bars denote the difference in the area under the curve between eye and hand fits in the alone (gray) and coordinated trials (green). B: same as A but for the Hand Block condition. Inset: the bars denote the absolute difference in the AUC between eye and hand fits in the alone (gray) and coordinated trials (brown). C: same as A but for the Eye Block condition. Inset: the bars denote the difference in the area under the curve between eye and hand fits in the alone (gray) and coordinated trials (violet). D: bar plot showing that the absolute difference in the AUC of eye and hand in the alone (gray) is greater than that of coordinated trials (green) across the population in the Search Step task. Each dot represents a subject, whereas the bar and cross-hair represents the mean ± SE across the population. The difference was significantly greater in the alone condition compared with the coordinated condition. E: same as D but for Hand Block condition. The difference was significantly greater in the alone condition compared with the coordinated condition. **P < 0.01 and P ≥ 0.001; ***P < 0.001; ns, nonsignificant. P( Error), probability of error response.
Assessing Common vs. Separate Control: Dissociated Trials

As mentioned in Table 1, among the three conditions, the percentage of dissociation observed was highest for Eye Block (27 ± 10%) and similar between Search Step (9 ± 4%) and Hand Block (6 ± 4%). In the dissociated trials, the error response could be made by the eye (eye landing on initial target, whereas the hand landed on the final target), the hand (eye landing on final target, whereas the hand landed on the initial target), or both (only in Search Step condition, both eye and hand landed on distractors). Eye dissociation errors were most frequent in the Search Step and Eye Block (Search Step = 81 ± 14%; Eye Block = 95 ± 6%; Hand Block = 22 ± 23%; Kruskal-Wallis: \( \chi^2 = 25.1, P < 0.001 \)), whereas hand dissociation errors were most frequent in Hand Block condition (Search Step = 16 ± 11%; Eye Block = 5 ± 6%; Hand Block = 78 ± 23%; Kruskal-Wallis: \( \chi^2 = 25.0, P < 0.001 \)), whereas both dissociation errors were present in only 3 ± 4% of trials in the Search Step condition.

One prediction of a common control signal is that there should not be any dissociated trials. Surprisingly, there was a small fraction of dissociated trials in both Search Step and Hand Block conditions that seems to be a violation of the conclusion of common STOP, which necessitated further investigation of the dissociated trials. Dissociation can result from 1) trials where eye and hand movements emanate from separate accumulators and 2) stopping of movements at the level of the muscle, where one movement has started but the other gets stopped. We tested both of these ideas in the data.

Presence of separate GO signals in a subset of trials in Search Step and Hand Block. As mentioned earlier, the presence of two STOP processes seems likely when there are separate GO signals for eye and hand movements, and these trials are likely to show dissociated behavior. Hence, the dissociated trials should show a large difference between the SDs of eye and hand RT distributions and show low RT correlations compared with trials that resulted from a common GO signal. For this analysis, the Hand Block condition was not considered as it had few dissociated trials (11/12 subjects had ≤5 dissociated trials), and, furthermore, the eye RT was often beyond the RT cutoffs in these trials.

In the Search Step condition, the RT correlation in the dissociated trials (\( r = 0.63 \pm 0.22 \)) was significantly less than that in the correct (\( r = 0.80 \pm 0.08; W(11) = 5; P = 0.005 \)) and error trials where both eye and hand went to the initial target (\( r = 0.78 \pm 0.06; W(11) = 10; P = 0.021 \)). The absolute difference between the SDs of eye and hand RT distributions was significantly greater in the dissociated trials (mean difference = 28.3 ± 21.2 ms) compared with the correct trials [mean difference = 7.1 ± 3.4 ms; \( t(11) = 3.3, P = 0.007 \)]. This suggested that the eye and hand movements in the dissociated trials in Search Step task could have originated from separate accumulators (and concomitantly had separate control signals).

In contrast to the Search Step condition, in the Eye Block condition, both the correct and dissociated trials are expected to be initiated by separate GO signals. Hence, the behavior in the dissociated trials should be comparable with the behavior in the correct and error trials. In the Eye Block condition, the RT correlation in the dissociated trials (\( r = 0.26 \pm 0.15 \)) was comparable with both correct (\( r = 0.27 \pm 0.12; W(11) = 39; P = 1 \)) and error trials (\( r = 0.27 \pm 0.20; W(11) = 39; P = 1 \)). The absolute difference between the SDs of eye and hand RT distributions was comparable between the dissociated trials (mean difference = 46.9 ± 22.6 ms) and correct trials [mean difference = 36.4 ± 34.4 ms; \( t(11) = 1.4, P = 0.179 \)].

EMG signals as a correlate of peripheral control. We hypothesized that if the common control signal reached threshold during the hand delay period, then it would not be able to stop the eye movement but should be able to stop the hand movement leading to dissociated trials. In these trials, the hand EMG activation should initially increase (as it has received the GO signal), but when the STOP signal arrives the EMG activation should decrease before increasing before the movement to the final target. Thus the EMG trace should show a dip in activation before movement onset (“Dip in EMG”), but such a dip should not occur if the control signals are separate for eye and hand.

We compared the probability of observing a dip in the low-pass-filtered EMG activity (Fig. 5, A and B) in the dissociated trials in the Search Step and Eye Block condition (we considered subjects who showed ≥5 dissociated trials; the Hand Block condition had few dissociated trials and, hence, was not considered). As EMG signals are noisy, we compared the difference or change in the probability in observing a dip in EMG \( [P(Dip \text{ in } \text{EMG})] \) between the dissociated and no-step trials (where there should not exist any control signal as redirection has not been instructed). In the Search Step condition, the change in the \( P(Dip \text{ in } \text{EMG}) \) (mean = 0.22 ± 0.09) was significantly greater than that in Eye Block condition [mean = 0.00 ± 0.08; \( W(11) = 0; P < 0.001 \)]. The change in the \( P(Dip \text{ in } \text{EMG}) \) was also significantly greater than 0 in Search Step condition \( [W(11) = 0; P < 0.001] \) but not in the Eye Block condition \( [W(11) = 31; P = 0.569] \), suggesting that the dissociated trials in the Search Step condition could also arise due to peripheral control mechanisms (Fig. 5C).

Thus it seems that the dissociated trials are not a violation of the common control signal. However, why are the compensation functions of eye and hand in the Search Step and Hand Block conditions similar despite the mean no-step hand RT being ~80 ms greater than the mean no-step eye RT? Potentially, the common control signal should be able to stop the hand more often compared with the eye due to this additional 80 ms, which should result in dissimilar compensation functions for eye and hand. Thus we postulated the presence of a ballistic stage for the hand that is not penetrable to control.

Assessing Common vs. Separate Control: Testing for a Ballistic Stage

Since the entire hand RT encompasses both the controllable and ballistic stage, there is no direct method of estimating it from the behavioral results. It can, however, be estimated from simulations, which has been mentioned in detail in Methods. Briefly, first, the STOP process was estimated from the eye-coordinated compensation function. Then, with the use of the \( \mu_{\text{STOP}} \) and \( \sigma_{\text{STOP}} \) of the eye, the mean and SD of the ballistic stage were estimated that would best fit the hand-coordinated compensation function. The prediction is that the estimated ballistic stage should relate to the difference in TSRT of eye and hand.

J Neurophysiol • doi:10.1152/jn.00085.2018 • www.jn.org

Downloaded from www.physiology.org/journal/jn at Indian Inst of Sci (014.139.128.011) on September 25, 2019.
The duration of the ballistic stage was similar to the difference between the TSRT of eye and hand in both Search Step [ballistic stage = 45 ± 26 ms, difference in TSRT = 51 ± 14 ms; \( t(11) = 1.0, P = 0.362, d = 0.1 \)] and Hand Block [ballistic stage = 95 ± 38 ms, difference in TSRT = 83 ± 37 ms; \( t(11) = 1.5, P = 0.172, d = 0.3 \)] conditions, suggesting that the difference between the TSRT of eye and hand observed in the coordinated condition might be due to the ballistic stage. These values were also similar in the Eye Block condition, but in this condition the estimated ballistic stage had unreasonable values, either being very small (< 2 ms in 6/12 subjects) or large (> 200 ms in 5/12 participants). The duration of the ballistic stage was also positively correlated with the difference between the TSRT of eye and hand in both Search Step condition \( (r = 0.65, P = 0.022) \) and Hand Block condition \( (r = 0.73, P = 0.008) \) but not in the Eye Block condition \( (r = -0.16, P = 0.620) \). This suggests that incorporation of a ballistic stage can explain dissociated trials when a common STOP is responsible for controlling both of the effectors. To validate further whether a common or separate control signals were applicable in the three task conditions, we checked how well the common and separate STOP models were able to predict the data in the three task conditions.

Validation of the Behavioral Results Using Simulations

Both the GO and the STOP processes could be either common or separate, suggesting the possibility of four competing models (1Go1Stop, 1Go2Stop, 2Go1Stop, and 2Go2Stop model; see Fig. 2, A–D). The behavioral results of the no-step and step trials suggested that the data in the Search Step and Hand Block conditions would be best explained by a common GO and common STOP (1Go1Stop) model, whereas the data in the Eye Block condition would be best predicted by separate GO and separate STOP (2Go2Stop) models. Nonetheless, all of the possible models were tested to see which model predicted the behavioral data best, in terms of the Weibull mean of the eye and hand compensation functions and the percentage of correct, error, and dissociated trials. The results of the simulations are summarized in Table 5 for the compensations functions and in Table 6 and Fig. 6 for the trial outcomes. Consistent with the data, the simulations showed that the behavior in the Search Step (Fig. 6, A–D) and Hand Block conditions (Fig. 6, E–H) could only be explained by the 1Go1Stop model as all other models failed to explain the compensation functions and/or the trial outcomes. In contrast, the Eye Block condition could only be explained by the 2Go2Stop model as the other models failed to explain the compensation functions and/or the trial outcomes (Fig. 6, I–L).

Behavior in Trials with Eye RT Greater than Hand RT in the Hand Block Condition

In the previous analyses, we only considered the trials in the Hand Block where eye RT was less than the hand RT. Now, we consider a consistent proportion of trials (39%) where the eye

Table 5. Models comparing the experimental and predicted Weibull means from the compensation function for the eye and hand

<table>
<thead>
<tr>
<th>Condition</th>
<th>Model</th>
<th>WM of Eye, ms</th>
<th>WM of Hand, ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Search Step</td>
<td>1Go1Stop</td>
<td>217 ± 24</td>
<td>239 ± 19</td>
</tr>
<tr>
<td></td>
<td>1Go2Stop</td>
<td>215 ± 25</td>
<td>236 ± 24</td>
</tr>
<tr>
<td></td>
<td>2Go1Stop</td>
<td>216 ± 23</td>
<td>246 ± 17</td>
</tr>
<tr>
<td></td>
<td>2Go2Stop</td>
<td>213 ± 24</td>
<td>239 ± 20</td>
</tr>
<tr>
<td>Eye Block</td>
<td>1Go1Stop</td>
<td>207 ± 71</td>
<td>255 ± 42</td>
</tr>
<tr>
<td></td>
<td>1Go2Stop</td>
<td>207 ± 72</td>
<td>322 ± 38</td>
</tr>
<tr>
<td></td>
<td>2Go1Stop</td>
<td>206 ± 65</td>
<td>250 ± 63</td>
</tr>
<tr>
<td></td>
<td>2Go2Stop</td>
<td>205 ± 63</td>
<td>309 ± 35</td>
</tr>
<tr>
<td>Hand Block</td>
<td>1Go1Stop</td>
<td>320 ± 59</td>
<td>289 ± 64</td>
</tr>
<tr>
<td></td>
<td>1Go2Stop</td>
<td>320 ± 59</td>
<td>314 ± 64</td>
</tr>
<tr>
<td></td>
<td>2Go1Stop</td>
<td>300 ± 53</td>
<td>292 ± 62</td>
</tr>
<tr>
<td></td>
<td>2Go2Stop</td>
<td>295 ± 55</td>
<td>310 ± 60</td>
</tr>
</tbody>
</table>

Values refer to the predicted Weibull means (WM). Models in boldface are those that survive this criterion check, whereas models in plain text are those that do not predict the experimental WM well.
and hand in this subset of trials. There were separate GO and separate STOP processes for eye movement, as suggested by Jana et al. (2017). In continuation to the previous work, there could be trial-by-trial variation such that a common or isolated eye and hand movements. We demonstrate that redirect behavior is best explained as a race between a GO and a STOP process, and not by a race between two competing GO processes, suggesting that inhibitory control mechanisms can be studied using these paradigms as well (Camalier et al. 2007; Ramakrishnan et al. 2010).

**Race Model of Redirect Behavior**

Customarily, the independent race model has been used to study the inhibition of single effector movements. The interactive race model, which is thought to be a better estimate of the neurophysiological processes controlling inhibition of movements (Verbruggen and Logan 2009), has been used in some studies to study inhibitory control/redirect behavior (Boucher et al. 2007a; Ramakrishnan et al. 2012). However, we preferred the independent race model compared with the interactive one due to a couple of reasons. First, studies have demonstrated the independence of the GO and STOP processes (Hanes and Carpenter 1999; Hanes and Schall 1996; Logan and Cowan 1984), particularly in the context of reach movements (Mirabella et al. 2006; Venkataramani et al. 2018). Second, the fanning effect was observed for eye and hand across the Search Step, Eye Block, and Hand Block conditions as predicted by the independent race model (data not shown). Third, the interactive race model possesses more parameters compared with the independent race model, making the estimation of the optimum more prone to multiple solutions. Last but not the least, the main observation was based on the empirical difference between the eye and hand compensation functions in the independent vs. coordinated condition, which did not depend on the architecture of the underlying race model per se. Nevertheless, it is not difficult to envision that an interactive race model might be able to fit the data better, albeit with the same conclusion. Future research might investigate this further.

**Control of Eye and Hand Movements Executed Concurrently**

At least four studies have investigated inhibitory control of eye and hand movements. Logan and Irwin (2000) proposed separate control signals for eye and hand, whereas Boucher et al. (2007b) proposed separate but interactive control signals, which they suggested could be a common central inhibition and separate peripheral inhibition mechanisms. This view was traditionally, studies of inhibitory control have used a variety of tasks, including the go/no-go task (Eimer 1993), the antisaccade task (Machado and Rafal 2004), and the stop-signal task (Hanes et al. 1998; Logan and Irwin 2000). Although stop-signal paradigms have dominated the study of response inhibition, stop-change paradigms (Brown and Braver 2005; Verbruggen et al. 2008) and redirect paradigms (Bhutani et al. 2013; Camalier et al. 2007; Kapoor and Murthy 2008; Ramakrishnan et al. 2010, 2012) have also been used to study inhibitory control. In both of these paradigms, subjects not only have to stop their primary response when the change/redirect signal is presented, but also have to replace the inhibited response with a new response. These paradigms are arguably more similar to the real-world scenario where we not only cancel impending movements, but also often replace them with another response. Previous studies have demonstrated that the redirect behavior is best explained as a race between a GO and a STOP process, and not by a race between two competing GO processes, suggesting that inhibitory control mechanisms can be studied using these paradigms as well (Camalier et al. 2007; Ramakrishnan et al. 2010).

**DISCUSSION**

We investigated the nature of control of concurrent and isolated eye and hand movements. We demonstrate that redirection of movements can be driven by either a common control signal or separate, effector-specific signals depending on the demands of the task. This was observed using three task conditions, Search Step, Eye Block, and Hand Block, which possibly coupled or decoupled the movement preparation stage of the eye and hand movements. These behavioral results were further validated using simulations of a race model having either a common GO and common STOP process with a ballistic stage for hand movements or effector-specific GO and STOP processes.

**Table 6. Comparison of how well each model predicted the trial outcomes**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Model</th>
<th>N</th>
<th>%Correct</th>
<th>%Error</th>
<th>%Dissociated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Search Step</td>
<td>1Go1Stop</td>
<td>10/12</td>
<td>49 ± 6</td>
<td>44 ± 5</td>
<td>8 ± 4</td>
</tr>
<tr>
<td></td>
<td>1Go2Stop</td>
<td>6/12</td>
<td>45 ± 7</td>
<td>40 ± 7</td>
<td>15 ± 5</td>
</tr>
<tr>
<td></td>
<td>2Go1Stop</td>
<td>8/12</td>
<td>45 ± 6</td>
<td>40 ± 5</td>
<td>15 ± 3</td>
</tr>
<tr>
<td></td>
<td>2Go2Stop</td>
<td>3/12</td>
<td>41 ± 5</td>
<td>39 ± 6</td>
<td>20 ± 4</td>
</tr>
<tr>
<td>Eye Block</td>
<td>1Go1Stop</td>
<td>7/12</td>
<td>28 ± 11</td>
<td>53 ± 9</td>
<td>19 ± 8</td>
</tr>
<tr>
<td></td>
<td>1Go2Stop</td>
<td>5/12</td>
<td>36 ± 13</td>
<td>42 ± 8</td>
<td>22 ± 8</td>
</tr>
<tr>
<td></td>
<td>2Go1Stop</td>
<td>10/12</td>
<td>27 ± 9</td>
<td>52 ± 9</td>
<td>21 ± 6</td>
</tr>
<tr>
<td></td>
<td>2Go2Stop</td>
<td>10/12</td>
<td>35 ± 11</td>
<td>43 ± 8</td>
<td>22 ± 7</td>
</tr>
<tr>
<td>Hand Block</td>
<td>1Go1Stop</td>
<td>9/12</td>
<td>51 ± 10</td>
<td>42 ± 10</td>
<td>7 ± 3</td>
</tr>
<tr>
<td></td>
<td>1Go2Stop</td>
<td>9/12</td>
<td>53 ± 10</td>
<td>40 ± 10</td>
<td>7 ± 3</td>
</tr>
<tr>
<td></td>
<td>2Go1Stop</td>
<td>6/12</td>
<td>49 ± 9</td>
<td>41 ± 9</td>
<td>10 ± 3</td>
</tr>
<tr>
<td></td>
<td>2Go2Stop</td>
<td>8/12</td>
<td>50 ± 9</td>
<td>40 ± 10</td>
<td>10 ± 2</td>
</tr>
</tbody>
</table>

N refers to the number of subjects where the model correctly predicted the trial outcomes as determined by a χ² goodness-of-fit test. Other columns refer to the predicted %correct, %error, and %dissociated. Models that predicted the trial outcomes significantly better than chance (P < 0.05) are indicated in boldface, whereas those that did not are in plain text.

RT (615 ± 76 ms) was greater than hand RT (495 ± 70 ms; Fig. 7A). Such behavioral response is not expected according to the Common Accumulator model, suggesting that these responses were better explained by the Separate Accumulator model. In congruence with this idea, we observed that in these trials the SD of eye RT distribution was greater than the SD of hand RT distribution in 9/12 subjects and at the population level as well [SD(Eye RT) = 114 ± 33 ms, SD(Hand RT) = 82 ± 15 ms; t(11) = 5.6, P < 0.001, d = 2.4; Fig. 7A]. In addition, the RT correlation was lower in these trials (mean r = 0.52 ± 0.23) compared with the trials where eye RT was less than hand RT (mean r = 0.84 ± 0.09; W = 1, P < 0.001, d = 1.8; Fig. 7B). This shows that even in the same block of trials there could be trial-by-trial variation such that a common or separate accumulators might be used to initiate eye and hand movement, as suggested by Jana et al. (2017). In continuation of results already discussed above, it is expected that these trials should have separate control signals for eye and hand. Consistent with this idea, the AUC for the ZRFT fits for eye and hand (0.781 ± 0.459) was not significantly different from that in the alone trials [0.704 ± 0.445; Fig. 7C; t(11) = 0.7, P = 0.734, d = 0.2]. Taken together, these results suggest that there were separate GO and separate STOP processes for eye and hand in this subset of trials.

**Using Redirect Task to Study Inhibitory Control of Movements**

Traditionally, studies of inhibitory control have used a variety of tasks, including the go/no-go task (Eimer 1993), the antisaccade task (Machado and Rafal 2004), and the stop-signal task (Hanes et al. 1998; Logan and Irwin 2000). Although stop-signal paradigms have dominated the study of response inhibition, stop-change paradigms (Brown and Braver 2005; Verbruggen et al. 2008) and redirect paradigms (Bhutani et al. 2013; Camalier et al. 2007; Kapoor and Murthy 2008; Ramakrishnan et al. 2010, 2012) have also been used to study inhibitory control. In both of these paradigms, subjects not only have to stop their primary response when the change/redirect signal is presented, but also have to replace the inhibited response with a new response. These paradigms are arguably more similar to the real-world scenario where we not only cancel impending movements, but also often replace them with another response. Previous studies have demonstrated that the redirect behavior is best explained as a race between a GO and a STOP process, and not by a race between two competing GO processes, suggesting that inhibitory control mechanisms can be studied using these paradigms as well (Camalier et al. 2007; Ramakrishnan et al. 2010).
also supported by Gulberti et al. (2014). A previous study from the laboratory by Gopal and Murthy (2016) broached the idea of a common STOP signal for both of the effectors. They suggested that the difference in their results compared with the former two studies could stem from the type of manual response used. The former tasks involved button presses and joystick movements, which were not naturalistic movements, compared with the reaching movements used by Gopal and Murthy (2016). This implied that for ethologically valid movements, the eye and hand movements may be initiated and controlled by common signals. However, they also broached the idea that if saccades and reaching movements were initiated by separate signals, they were likely to be controlled by separate inhibitory signals.

Here, we demonstrate that the eye and hand movements in the no-step trials of Search Step and Hand Block task conditions seem to be driven by a common accumulator with a peripheral hand-specific delay, whereas in the Eye Block task the movements were driven by effector-specific accumulators. The results also validated the prediction that a common GO and a common STOP signal work together and separate GO and separate STOP signals work together. These results may be extended to address questions about global and selective stopping of movements. In the Search Step condition, since both eye and hand movements seem to be under the influence of a common STOP process, it is likely that this STOP signal may be global in nature (Cai et al. 2012b; Wessel et al. 2013, 2016). In contrast, eye and hand movements in the Eye Block condition, which seem to be controlled by separate STOP signals, may indicate a selective stopping mechanism (Greenhouse et al. 2012; Majid et al. 2012). Although global and selective inhibitory controls were not directly addressed here, this study provides a starting point for future research. Furthermore, a similar computational approach could be used to study whether global or selective processes control different effectors during other coupled movements like eye and head during gaze orientation (Corneil and Elsley 2005) or different segments of the arm during reaching (Brunamonti et al. 2012).

Interestingly, we also observed that not all trials in a particular task followed one mode of initiation and control. For
example, in the Search Step condition, there was a small population of dissociated trials that agreed with the predictions of separate GO signals (discussed in a later section). In addition, a separate proportion of trials in the Hand Block condition seem to follow the predictions of common or separate GO and STOP signals. Whereas trials where eye RT was less than hand RT followed the prediction of common GO and STOP signals, trials where the eye RT was greater than the hand RT followed the prediction of separate GO and STOP signals. Such a criterion of separating trials may seem artificial, but in the absence of a single-trial neural correlate such a criterion for discriminating common vs. separate GO signals may be the best approach.

In line with Gopal and Murthy (2016), we used two metrics for comparing the models: 1) how well the models predicted the Weibull mean of the behavioral compensation functions and 2) how well the models predicted the percentage of correct, error, and dissociated trials. Thus, in essence, there were four prediction criteria for each model. Despite having the same number of parameters, the two models, 1Go1Stop and 2Go2Stop, each fared better than the other in predicting the behavior in the two different task contexts, validating the conclusion that the redirecting behavior observed was driven by either a common or separate STOP signals.

**Dissociated Trials in Context of a Common STOP Process**

A common STOP process for eye and hand predicts that there should not be any dissociated trials. However, there was a small percentage of dissociated trials in both Search Step and Hand Block conditions. This can originate due to the following reasons, which are, in themselves, not mutually exclusive hypotheses.

**Peripheral control of hand movements.** Because of the difference in the biomechanics of the eye and hand, overcoming the inertia of the hand requires greater activation of the hand muscles compared with that of the eye. This delay time at the level of the muscles is ~100 ms for the hand (Gopal et al. 2015), whereas it is ~30 ms for eye (Ron et al. 1972; Schiller and Stryker 1972). This additional 70 ms provides the STOP signal an additional time window to stop the hand movement. Such cases of peripheral stopping or covert error, where the EMG response shows a change in activity without any overt movement, has been previously reported in literature (Bonini et al. 2014; de Jong et al. 1990). In accordance with this notion, we also observed signatures of peripheral control in the anterior and posterior deltoid muscle in the Search Step condition (Cornelis et al. 2013; Goonetilleke et al. 2010, 2012). Although a potentially more informative way of conducting this analysis would have been to see whether these signatures of stopping were present when a movement was made in the movement field of the muscle, to distinguish whether stopping was a selective vs. a global process, the number of dissociated trials was few and the activity of the muscles often showed cocontraction.

**Ballistic stage in hand control.** This observation about peripheral control raises the question regarding how long into the delay period of the hand can the STOP process act? Conceivably, the STOP process can control a movement plan until a point called the point of no-return, and once this is crossed a ballistic stage ensues and movement is inevitable (de Jong et al. 1990; Osman et al. 1986). As the ballistic stage was not directly measurable from the data, it was estimated using simulations. Although conclusive evidence of a ballistic stage in manual movement has proved to be elusive (de Jong et al. 1990; McGarry et al. 2000; Mirabella et al. 2013; Osman et al. 1986), Gopal and Murthy (2016) suggested the existence of a ballistic stage in hand control in case of the redirection of coordinated eye-hand movements.

In the present study, we found that incorporation of a ballistic stage in the hand motor plan could explain the dissociated trials in the context of a common STOP process. Furthermore, such a ballistic stage in hand control made the TSRT of eye and hand in the coordinated condition comparable (as suggested by Logan and Cowan 1984). The difference between the duration of the hand delay and the ballistic stage is the time when the eye movement starts but the STOP process can act in the periphery and stop the hand movement, thereby leading to a dissociated trial. Consistent with this idea, the difference between these two durations was positively correlated with the percentage of dissociated trials.
An alternate explanation of the observed ballistic stage was suggested by Gopal and Murthy (2016). They reasoned that the observed ballistic stage could just be a manifestation of the STOP process dying out when the GO process reaches the threshold, giving rise to a “pseudoballistic stage” where the hand is not controlled because of the lack of a control signal. Although these two possibilities cannot be clearly distinguished in the present study, a comparison of the signatures of control seen in the hand muscles might provide an insight. Signatures of control were evident in the Search Step condition (common STOP) but not in the Eye Block condition (separate STOPs). It can be speculated that in the context of highly coordinated eye-hand movements (as in the Search Step task), the STOP signal can continue and inhibit the hand at the periphery until the ballistic stage starts. However, in case of separate STOP signals (as in the Eye Block condition), the hand STOP gets extinguished when the eye GO signal reaches a threshold, generating a pseudoballistic stage where no signatures of peripheral control are seen.

Typically, one would expect the duration of the ballistic stage to be smaller than the duration of the hand delay. Furthermore, one would expect this difference to be correlated with the percentage of dissociation observed, i.e., the longer this difference, the greater is the chance that the STOP signal acts on the hand muscles at the periphery and halts the impending hand movement. Although this was observed in the Search Step condition, this was not seen in the Hand Block condition. This could be the result of the Hand Block condition having a mixture of trials stemming from a common accumulator and from separate accumulators (discussed below). Although trials were divided by an artificial metric of before and after hand movement, the division is arguable. Nonetheless, the duration of the ballistic stage was highly correlated to the difference between TSRT of eye and hand, suggesting that the common STOP model with a ballistic stage was the more apt model among the rest.

Switching between a Common and Separate STOPs Modes

The task context determined whether a common or separate STOP explained the data best. However, this motor set or cognitive set may not be absolute. It is possible that in the majority of the trials, the brain chooses a common GO and common STOP for executing the movements but in a fraction of trials it might stochastically use separate GO and STOP processes as part of movement planning and these fractions of trials could lead to dissociated trials. In the dissociated trials of the Search Step task, the SDs of eye and hand were no longer comparable and the RT correlation decreased compared with the correct trials. However, this drop in correlation was not observed in the Eye Block condition where the default initiation mode was via separate GO processes. This speculation suggests the involvement of central executive processes, which choose the motor set best applicable for the task context. Consistent with this idea, we have shown that within the dual redirect task, the architecture of planning and subsequent control differs between the Eye Block and Hand Block conditions.

Furthermore, within the Hand Block condition itself there were interspersed trials that bore signatures of emanating from both a common and separate accumulators. To understand the behavior better, we divided the data into trials where the eye-movement onset was before and after hand-movement onset. In light of previous literature that has demonstrated that eye RT is usually less than hand RT, this division made logical sense, but it has two potential drawbacks: some trials where the eye-movement onset was before hand-movement onset could have emanated from separate accumulators; this reduced the number of trials, which made fitting the data more difficult. A potential proof of the first drawback can be seen as subjects shows greater hand errors compared with eye errors in the dissociated trials in Hand Block. Furthermore, as a result of this division, the data from the trials where hand onset was before eye onset could not be fit reasonably (low $r^2$) due to the low number of trials.

Conclusions

This study illustrates the flexibility underlying the control of coordinated movements, where not only can the initiation of the two movements be via common or separate accumulators, which might indicate common or separate networks, but also the inhibitory control of the movements can be via a common stopping network or via separate networks.

GRANTS

Indian Institute of Science (S. Jana and A. Murthy), Council of Scientific and Industrial Research (S. Jana), a DBT-IISc Partnership Program from Department of Biotechnology, Ministry of Science and Technology (A. Murthy), and Department of Science and Technology, Ministry of Science and Technology (A. Murthy) supported this study.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.J. and A.M. conceived and designed research; S.J. performed experiments; S.J. analyzed data; S.J. and A.M. interpreted results of experiments; S.J. prepared figures; S.J. drafted manuscript; S.J. and A.M. edited and revised manuscript; S.J. and A.M. approved final version of manuscript.

REFERENCES


Coordination of hand movements and saccades: Countermanding eye-head gaze shifts in humans.


