

A common control signal and a ballistic stage can explain the control of coordinated eye-hand movements

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Gopal A, Murthy A. A common control signal and a ballistic stage can explain the control of coordinated eye-hand movements. *J Neurophysiol* 115: 2470–2484, 2016. First published February 17, 2016; doi:10.1152/jn.00910.2015.—Voluntary control has been extensively studied in the context of eye and hand movements made in isolation, yet little is known about the nature of control during eye-hand coordination. We probed this with a redirect task. Here subjects had to make reaching/pointing movements accompanied by coordinated eye movements but had to change their plans when the target occasionally changed its position during some trials. Using a race model framework, we found that separate effector-specific mechanisms may be recruited to control eye and hand movements when executed in isolation but when the same effectors are coordinated a unitary mechanism to control coordinated eye-hand movements is employed. Specifically, we found that performance curves were distinct for the eye and hand when these movements were executed in isolation but were comparable when they were executed together. Second, the time to switch motor plans, called the target step reaction time, was different in the eye-alone and hand-alone conditions but was similar in the coordinated condition under assumption of a ballistic stage of ~40 ms, on average. Interestingly, the existence of this ballistic stage could predict the extent of eye-hand dissociations seen in individual subjects. Finally, when subjects were explicitly instructed to control specifically a single effector (eye or hand), redirecting one effector had a strong effect on the performance of the other effector. Taken together, these results suggest that a common control signal and a ballistic stage are recruited when coordinated eye-hand movement plans require alteration.

eye-hand coordination; race model; inhibitory control; ballistic stage; reaction times

THE ABILITY TO INHIBIT or change a planned movement is a critical feature that characterizes all voluntary movements. Such control is typically studied by assessing a subject's ability to stop or change his/her planned movement to an original target after presentation of a STOP/CHANGE signal delivered at successively increasing delays, producing a performance function or an inhibition/compensation function, respectively. Performance is typically modeled as an independent stochastic race between processes that initiate and inhibit the old motor plan (Hanes and Carpenter 1999; Lappin and Eriksen 1966; Logan 1982; Logan and Cowan 1984; Ramakrishnan et al. 2010). The corresponding neurophysiological basis for implementing such a race has also accumulated over the years (Hanes et al. 1998; Mattia et al. 2012; Mirabella et al. 2011; Murthy et al. 2007; Paré and Hanes 2003; Schmidt et al. 2013). This notwithstanding,

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little is known about the mechanisms that instantiate control when multiple effectors encompass an action. Is control simply given by the concatenation of control seen when these effectors are executed in isolation? Or are there dedicated mechanisms that are instantiated when coordinated effectors are controlled?

We used eye-hand movements to test the computational mechanisms underlying multieffector control. Current evidence, derived largely from the countermanding task, indicates that the ability to stop eye movements is different from the ability to stop hand movements when these movements are generated in isolation. This is inferred based on differences in the duration it takes to inhibit a movement, called the stop signal reaction time (SSRT) and derived from the race model (Logan and Cowan 1984; Verbruggen and Logan 2009). Typically it takes longer to inhibit a hand movement (200 ms; Logan 1982; Mirabella et al. 2006) than an eye movement (100 ms; Hanes and Carpenter 1999; Kapoor and Murthy 2008; Logan et al. 1984; Ramakrishnan et al. 2010). In addition, the “gap effect” that affects the reaction times (RTs) of saccade and hand movements reduces the SSRT of the eye (Stevenson et al. 2009) but increases the SSRT of the hand (Mirabella et al. 2009), further validating the duality of control of eye and hand effectors in isolation.

In contrast, much less is known about the nature of control during coordinated eye-hand movements. The existing evidence derives from just two studies and is based on the differences between the SSRTs of the eye and hand effectors and their similarity with the SSRTs obtained from measurements made during the control of eye and hand movements in isolation (Boucher et al. 2007; Logan and Irwin 2000), indicating separate signals for eye and hand control. However, the eye-hand correlation, a measure of eye-hand coordination, was low in these studies. In addition, these movements were not natural reaching movements but involved the use of button presses and joysticks instead. However, in previous work we have shown that when eye-hand RT correlation is strong, combined eye and hand movements appear to engage a common motor command, which is qualitatively distinct from planning of eye and hand movements made in isolation (Gopal et al. 2015; Gopal and Murthy 2015). Here we test whether effector-specific multiple control signals or a single control signal is recruited to control coordinated eye-hand movements. In the process we also address whether eye-hand control reflects a common dedicated mechanism qualitatively distinct from a control mechanism instantiated when the eye and hand are controlled separately.

MATERIALS AND METHODS

Subjects

We performed two experiments. In *experiment 1*, we recorded eight right-handed subjects (4 men, 4 women), between 23 and 26 yr of age, with normal or corrected to normal vision on a visually guided redirect task. In *experiment 2* we recorded six right-handed subjects (3 men, 3 women) between 21 and 28 yr of age. All subjects gave their informed consent in accordance with the protocol, which was reviewed and approved by the institutional human ethics committee. Subjects were monetarily rewarded for their participation in the study.

Experiment 1

We used a visually guided redirect task (Fig. 1), which is a modified version of a double-step paradigm with a countermmanding signal incorporated in it. This data set was also used in two earlier published papers to test the common command hypothesis, which is the starting premise of the present work (Gopal et al. 2015; Gopal and Murthy 2015). Visual cues (isoluminant colored squares), which subtended a visual angle of 1° , were used as targets in no-step trials (60%) and step trials (40%), which were randomly interleaved (Fig. 1). Both trials were initiated when a white unfilled square box appeared at the center of the screen with luminosity of 0.01 cd/m^2 and subjects fixated and pointed with their index finger on it. After a fixation period of $300 \pm 100 \text{ ms}$ (accurate to the nearest monitor refresh rate), a peripheral green target with luminosity of 34.42 cd/m^2 appeared, on either the right or the left of the fixation box at an eccentricity of 12° . Subjects were instructed to make a saccade and point, as quickly and accurately as possible, to the target. Trials were aborted if subjects did not respond within a time limit of 600 ms. Trials were scored as successful if subjects fixated and pointed within $\pm 5^\circ$ of the target, which was determined online by means of an electronic window centered on the target. Auditory feedback was given on successful trials.

In step trials, a yellow target with luminosity of 34.48 cd/m^2 appeared in a position opposite (180°) to that of the green target with the same eccentricity (12°) after a temporal delay, known as the target step delay (TSD). On these trials, subjects were instructed to redirect their response to the final target. When a subject inhibited the response to the initial target and responded to the second target with a gaze shift and simultaneous pointing response, the trial was scored as successful, hereafter called a compensated trial. When subjects failed to redirect the response to the initial target and made a saccade and a pointing movement to the green target, it was considered an erroneous response, hereafter called a noncompensated response. At larger TSDs, the redirect cue appeared much later in time; hence the subjects found it harder to redirect the initial response, consequently making more erroneous noncompensated responses. This relationship between the probability of error and TSD was quantified in the form of a psychometric function called a compensation function (see Fig. 4, A and B).

In *experiment 1* subjects performed the redirect task in three different conditions, eye-alone, hand-alone, and eye-hand, in separate blocks on separate sessions. To get reliable compensation functions, TSDs were selected to sample the no-step RT distribution adequately. The no-step RT distributions across conditions were distinctly different from each other; hence we selected different TSDs for each condition separately.

Eye-alone. Subjects positioned their pointing finger at the central fixation throughout the trial, while they made saccades to the targets. A trial was aborted if the hand moved out of the fixation box at any time during the trial. Six hundred trials were recorded per subject under the eye-alone condition with six TSDs ranging from 50 to 300 ms in steps of 50 ms.

Hand-alone. Subjects maintained their gaze at the central fixation box throughout the trial, while hand movements were made to the target. A trial was aborted if the gaze shifted out of the fixation box any time during the trial. Seven hundred trials were recorded per subject under the hand-alone condition with seven TSDs ranging from 100 to 700 ms in steps of $\sim 100 \text{ ms}$.

Eye-hand. Subjects made coordinated eye-hand movements to the targets. Only those trials in which both the eye and the pointing finger satisfied the redirect condition were considered successful. One thousand trials were recorded per subject under the eye-hand condition with 10 TSDs, which were a combination of TSDs used in the eye-alone and hand-alone conditions.

Experiment 2

Subjects performed an eye-hand version of the redirect task under three separate task instructions, in separate blocks. On 60% of the no-step trials subjects made coordinated eye-hand movements to the peripherally appearing green target. On the remaining 40% of step trials subjects responded to the red second target depending on the instruction given in that block. Within a session, three blocks, each consisting of 160 trials, were counterbalanced and recorded for each subject.

Eye redirect. Subjects were instructed to redirect their eye movement to the second target. The response of the hand, during step trials, was irrelevant.

Hand redirect. Subjects were instructed to redirect their hand movement to the second target. The response of the eye, during step trials, was irrelevant.

Eye-hand redirect. Subjects were instructed to redirect their eye and hand movements to the second target. A step trial was scored as successful only if both eye and hand movements were redirected.

Setup for Data Acquisition

Experiments were under the control of TEMPO/VDOSYNC software (Reflective Computing, St. Louis, MO), which displayed the stimuli and collected data at a temporal resolution of 1 ms. Eye movements were monitored by a pupil tracker (ISCAN) at a sampling

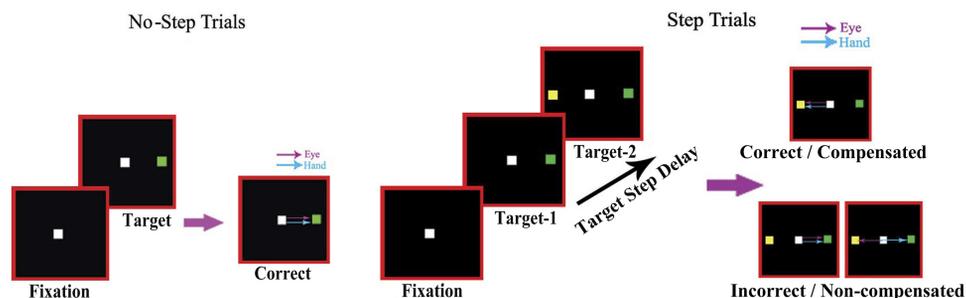


Fig. 1. The task. In a no-step trial, subjects were instructed to make a saccade, a pointing movement, or both, to targets that could appear 12° on either side of fixation in an eye-alone, hand-alone, or eye-hand condition, respectively. In a step trial a second yellow target appeared in the opposite hemifield after a target step delay. The different responses are shown.

frequency of 240 Hz and interfaced with TEMPO in real time. Hand movements were tracked by an electromagnetic tracker (LIBERTY, Polhemus) that read the movement of a sensor strapped on the pointing finger at a sampling frequency of 240 Hz and also interfaced with TEMPO in real time. Stimuli were presented on a CRT (SONY SGI 21 in., 60 Hz refresh rate) monitor in *experiment 1* and an LCD (Dell Ultra Sonic) monitor in *experiment 2* and housed overhead on a custom-made wooden frame. Stimuli that were calibrated for physical isoluminance with a colorimeter (Minolta CR-96) remained on the screen until the subject made a response to the stimulus or until the trial was aborted. A plane mirror (25% transmission, 75% reflectance) was placed below the monitor at an angle, to reflect the CRT monitor display conveniently for the subjects. An acrylic sheet was kept in the same plane as that of the virtual image of the monitor, constraining the pointing hand movement on the same virtual plane. A schematic of the setup used is shown in a previously published paper (Gopal et al. 2015).

Recording Procedure

At the beginning of each session subjects were given written as well as verbal instructions followed by ~50 practice trials. In a typical session that lasted ~1 h, subjects performed ~500 trials on average, with breaks between 250 trials. Each subject performed five to eight sessions. Trackers were calibrated by having subjects point and fixate at the two target positions. The accuracy of the eye tracker as measured by the standard deviation (SD) of the eye position during the 80-ms fixation period at the central fixation spot was 0.15°. The accuracy of the eye tracker at the two target positions, measured in the same manner, for 80 ms after saccade offset was 0.70° (Kornylo et al. 2003; Ramakrishnan et al. 2010). Similarly, the accuracy of the hand tracker at the central position was 0.04 mm and 4.7 mm at the two target positions. Subjects were comfortably seated in a position to see and point at the virtual image of the CRT monitor formed by the mirror in a darkened room. Head movements were restrained with a chin rest, a head bar, and two side bars that were placed at the temple to avoid the contamination of eye traces. Additionally in *experiment 2*, to track the eye movements, a head-mounted camera was used that automatically canceled out minor head movements. The pointing hand was placed over the acrylic sheet over which the virtual image of the monitor was formed. A battery-powered LED was also strapped with a sensor onto the pointing finger to provide visual feedback.

Analysis

Custom algorithms were written in MATLAB to detect the onsets of saccade and hand movements. A velocity threshold of 30°/s was used to mark the beginning and end of a saccade. Blinks were removed from the saccade trace. Similarly, a threshold of 10 cm/s was used to mark the start and end of a pointing movement. Eye and hand RT distributions and the compensation function were the variables of interest, which were calculated for each condition separately. The compensation function for each subject, in each condition, was fitted to a cumulative Weibull function, and the Weibull mean, which was the midpoint of the fitted function, was calculated. The population means along with SDs are reported throughout this article. Paired or unpaired *t*-tests, and ANOVAs where appropriate, were performed after confirmation of normality with the Lilliefors test. To quantify the goodness of fit between the predicted and the observed data, we calculated r^2 , which measures the proportion of the observed variability that can be explained by the model. The χ^2 -test was used instead of r^2 when comparison between the predicted and observed data was in the form of frequencies.

Race Model Framework

The race model suggests that behavior in the redirect task can be explained by a race between a stochastically accumulating GO pro-

cess that initiates the response to the initial target and a stochastically accumulating STOP process that attempts to inhibit the GO process. The GO process is initiated when the initial target appears and the STOP process after the appearance of the final target during step trials. These two processes race against each other to a decision threshold, and the outcome of this race determines the behavior. Noncompensated responses occur when the STOP process fails to reach the threshold before the GO process. Compensated responses occur when the STOP process crosses the threshold before the GO process.

Calculation of Target Step Reaction Time

The target step reaction time (TSRT) measures the time it takes to change a movement in the redirect task and is analogous to the SSRT of the countermanding paradigm (Camalier et al. 2007; Kapoor and Murthy 2008; Ramakrishnan et al. 2010). Being a covert process, TSRT is not directly available from the behavioral data, but the race model provides a means for estimating its duration (Logan 1994; Logan and Cowan 1984). The RT of no-step trials along with the compensation function provide the necessary data to estimate the time to change a planned movement.

TSRT was calculated in three ways using slightly different methods based on the logic described by Logan and Cowan (1984). The first approach assumes that TSRT is a random variable. The mean TSRT equals the difference between the mean no-step RT and the mean of the compensation function. The TSRT was also calculated by subtracting the median of the compensation function from the median of the no-step RT distribution. In the integration method, TSRT was estimated by integrating the no-step RT distribution until the integral equaled the observed proportion of erroneous noncompensated responses at that TSD. The RT at the integrated value yielded the finish time of the race—i.e., the longest RT at which the GO process finished before the STOP process. TSRT can be calculated by subtracting the TSD from the finish time of that TSD. To obtain a more robust estimate, the three estimates of TSRT were averaged to provide a single composite measure.

Calculation of STOP Variability

While TSRT gives the mean of the STOP process, variability of the STOP process is another measure that can provide insight into the architecture of the control process. Like TSRT, variability of the STOP process is also measured indirectly with the no-step RT distribution and the compensation function by applying the race model framework. Since the compensation function is determined by the interaction of the GO and STOP processes, the variability in these processes is reflected in the slope of the resultant compensation function. The variability in the GO process can be directly quantified from the no-step RT distribution and is used to normalize the compensation function by replotting the probability of error based on the standardized relative finishing time (ZRFT) instead of the TSD. The ZRFT can be calculated for each subject across each TSD by applying the normalization procedure formulated by Logan and colleagues (Logan and Cowan 1984; Osman et al. 1986).

$$\text{ZRFT} = \frac{\text{NSRT} - \text{TSD} - \text{TSRT}}{\text{SD(No-Step RT)}} \quad (1)$$

where NSRT is the mean RT of no-step trials, TSD is the target step delay, and TSRT is the target step reaction time. The slope of this normalized compensation function now reflects the variability of the STOP process and was estimated by linear regression fitted to the data points on the normalized compensation functions. In this analysis we restricted the ZRFT values between -3 and +3 to ensure that the tails of the distributions did not distort the estimates.

Modeling

Model parameter estimation. The underlying processes responsible for behavior in the redirect task are the GO and STOP according to the race model framework. The individual units (GO and STOP) in the model are modeled as noisy accumulators of sensory information (Ratcliff 2006; Ratcliff and Rouder 1998; Ratcliff and Van Dongen 2011; Usher and McClelland 2001).

GO process. The GO process represents the preparatory activity of a movement plan that builds up to a threshold, following stimulus presentation (Hanes and Schall 1996). The movement is triggered when the accumulation crosses a preset threshold. The rate of accumulation is governed by Eq. 2:

$$a_{GO}(t) = a_{GO}(t-1) + \mu_{GO} + \xi_{GO} \quad (2)$$

where a_{GO} represents the GO unit activation at time t . The mean growth rate of the GO unit is given by μ_{GO} , which represents the mean strength of the sensory signal. ξ_{GO} is a Gaussian noise term with a zero mean and a standard deviation of σ_{GO} that represents the noise in the sensory signal. The accumulation process is simulated with a time resolution of 1 ms between a baseline fixed at 0 and a threshold fixed at 1, after a visual afferent delay of 60 ms. Given these model constraints, the strength of the mean growth rate (μ_{GO}) and the standard deviation of the noise (σ_{GO}) were optimized by scanning a range of parameters (0.001–0.1) that can produce behaviorally relevant RT distributions with RTs that range from 1 ms to 1,000 ms. The details of the Monte Carlo simulations are given in Gopal et al. (2015).

We used a common command model to simulate the GO process of coordinated eye hand movements (Gopal et al. 2015; Gopal and Murthy 2015). The common eye-hand GO accumulator was modeled with Eq. 1, but when the threshold was crossed an eye movement was generated, while the hand movement was initiated after a stochastic temporal delay, which was modeled as a Gaussian distribution characterized by two free parameters μ_{DELAY} and σ_{DELAY} . These parameters are estimated based on the hand RT distribution with the Monte Carlo methods described above.

STOP process. The STOP process represents the inhibitory activity (Schmidt et al. 2013) that also builds up to a threshold, following the appearance of the second stimulus onset. Movement is inhibited when the STOP accumulator reaches a threshold earlier than the GO process. The rate of accumulation in the STOP accumulator was governed by Eq. 3:

$$a_{STOP}(t) = a_{STOP}(t-1) + \mu_{STOP} + \xi_{STOP} \quad (3)$$

where a_{STOP} represents the STOP unit activation at time t . The mean growth rate of the STOP unit is given by μ_{STOP} , and ξ_{STOP} is a Gaussian noise term with a mean of zero and a standard deviation of σ_{STOP} that characterizes the noise in the sensory signal. The same model constraints were applied as in the case of the GO process. Using Monte Carlo methods, we estimated the strength of the mean growth rate (μ_{STOP}) and the standard deviation of the noise (σ_{STOP}) that could explain redirect behavior.

The parameters of the STOP process were estimated by simulating step trials. In a step trial, the GO accumulator—simulated based on the parameters obtained by fitting the no-step trials—was instantiated after the appearance of the first target. A STOP accumulator began to rise to the same threshold, following the appearance of the final target, controlled by the μ_{STOP} and σ_{STOP} values randomly chosen from a range (0.001–0.1) that generates behaviorally acceptable compensation functions. GO RTs as well as STOP RTs were estimated based on the time that the respective accumulators took to cross the threshold in each trial. For each TSD 350 such step trials were simulated. The proportions of trials in each TSD that were noncompensated (GO RT < STOP RT) and compensated (GO RT > STOP RT) were calculated. By determining the fraction of compensated to noncompensated trials as a function of TSD, we constructed the simulated

compensation function. The least squares error (LSE) was calculated between the simulated and observed compensation functions. The LSE was used as an index that was minimized in the parameter space. We chose the set of μ_{STOP} and σ_{STOP} parameters with the least LSE value.

Models for Redirection

We tested two different models of control of coordinated eye-hand movements.

Multiple-stop model. The multiple-stop model assumes that two separate, effector-specific inhibitory control signals are recruited during the control of coordinated eye-hand movements (Fig. 2A). They are thought to independently control eye and hand movements. These separate STOP processes of eye and hand compete with the common GO process, and the outcome of this race determines the behavior on a given trial. The parameters of these effector-specific STOP processes are estimated from the observed eye and hand compensation functions, separately, with the Monte Carlo method described above.

Unitary stop model. The unitary stop model assumes that a unitary, global, effector-independent inhibitory mechanism controls both eye and hand effectors simultaneously. The race between the common GO and the unitary STOP is thought to determine the behavior in a step trial (Fig. 2B).

For such a STOP process to be able to successfully explain the hand compensation function, an additional ballistic stage (Fig. 2C) was incorporated during the motor programming of hand. A ballistic stage is defined as a phase during the motor preparation of a movement that is impervious to any form of inhibitory control from higher centers and hence cannot be controlled (Bartlett 1958; Osman et al. 1986). When the motor programming crosses a point of no return, which is a hypothetical point that separates the initial controllable stage from the final ballistic stage of movement preparation, movement execution is inevitable. The duration of the ballistic stage was estimated from the hand compensation function in the eye-hand condition with the race model framework, as done in previous studies (Kornlyo et al. 2003; Ramakrishnan et al. 2010).

The GO process for the hand was modeled based on the parameters estimated with the common command architecture. We also assumed that this GO process has two stages, an initial controllable stage and a final ballistic stage separated by a point of no return (Fig. 2B). The STOP process is allowed to inhibit the GO only if it reaches the threshold before the GO process crosses the point of no return. Three hundred fifty step trials were simulated for each of the 10 TSDs. The STOP process parameters were estimated from the eye compensation function in the eye-hand condition with the method described above. The duration of the ballistic stage was randomly chosen from a range of values (1–200 ms). The GO process was made impervious to the STOP during this interval, and the proportion of trials that were noncompensated per TSD was calculated to simulate the compensation function. The LSE was calculated between the simulated and the observed compensation function, which was minimized with the same function and procedures described above.

RESULTS

The redirect task, which is the modified version of a double-step task with a countermanding signal incorporated in it, was used to test computational mechanisms underlying the control of coordinated eye-hand movements. The race model framework that has been successful in explaining behavior in the classical countermanding task (Logan and Cowan 1984; Verbruggen and Logan 2008, 2009) and the redirect task (Camalier et al. 2007; Kapoor and Murthy 2008; Ramakrishnan et al. 2012) was used to understand the control of eye-hand coordination.

Target Step Reaction Time

We computed the TSRT for eye and hand effectors separately in the coordinated condition as well as when they were instructed to be redirected in isolation. We found a significant [2-way ANOVA: $F(1,28) = 30.77, P < 0.001$] main effect for the effector type (eye vs. hand) on the TSRT while that for the condition type (alone vs. eye-hand) was not significant [2-way ANOVA: $F(1,28) = 1.50, P = 0.2316$]. More specifically in the eye-hand condition, the TSRT for the hand (152 ± 29 ms)

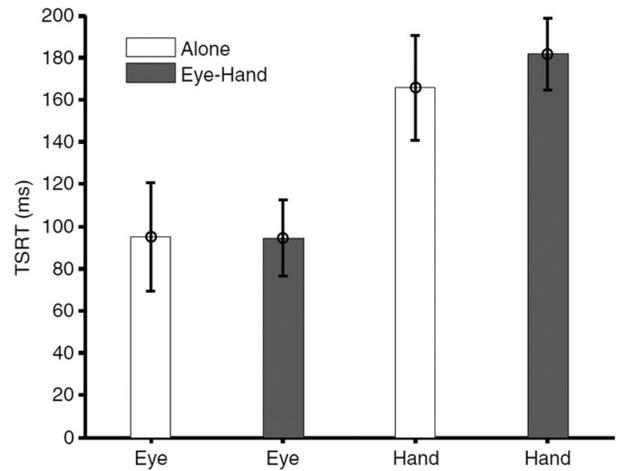
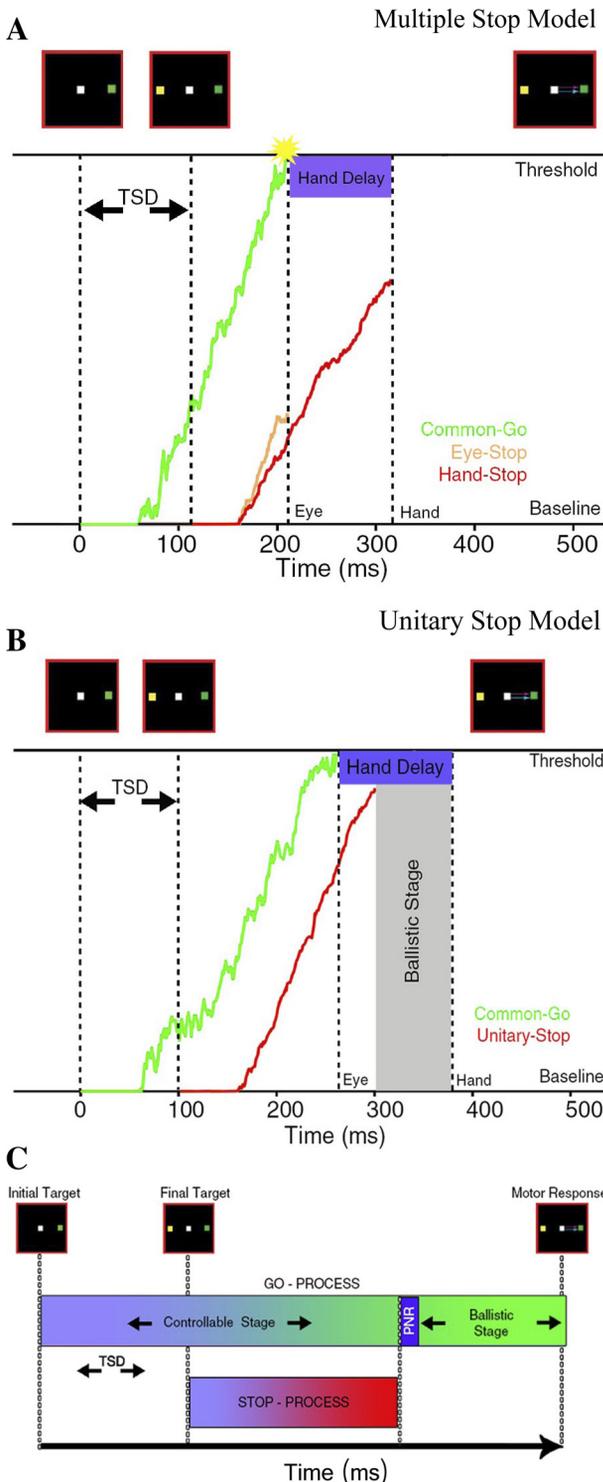


Fig. 3. The TSRT estimated from an independent race model for eye and hand effectors in the alone and eye-hand conditions.

was significantly greater than the TSRT for the eye (93 ± 20 ms) by 59 ms ($t = -3.402, df = 21, \text{Bonferroni-corrected } P = 0.003$). Interestingly, the same pattern was found when the TSRT was compared between the eye-alone and hand-alone conditions. The hand-alone TSRT (131 ± 23 ms) was significantly greater ($t = -5.234, df = 21, \text{Bonferroni-corrected } P < 0.001$) than the eye-alone TSRT (93 ± 25 ms). Moreover, we also found that the eye in eye-hand TSRT and the eye-alone TSRT were similar ($t = -0.0384, df = 21, \text{Bonferroni-corrected } P = 0.9697$). Likewise, the hand in eye-hand TSRT was comparable to the hand-alone TSRT ($t = 1.869, df = 21, P = 0.075$). Taken together, this first-pass analysis (Fig. 3) is consistent with independent control of the eye and hand when the two effectors are executed in isolation or when they are coordinated.

Compensation Functions

Although the TSRTs of eye and hand effectors were observed to be distinct from each other, we observed interesting differences between the effector-alone and coordinated conditions when compensation functions were compared. Consistent with the TSRT analysis described above, we found that the eye-alone and hand-alone compensation functions were significantly different (KS test: $P = 0.0310, \text{KS statistic} = 0.6$; Fig. 4A) from each other for a typical subject. However, for the same subject in the eye-hand condition eye and hand compen-

Fig. 2. Models for redirection. A: the multiple-stop model. The common accumulator initiating eye and hand movements is shown in green. The eye movement is elicited as soon as the accumulator reaches the threshold and the hand movement occurs after a temporal delay denoted by the violet bar. Two effector-specific STOP signals responsible for redirecting eye (orange) and hand (red) start accumulating and race against the common GO process to reach the same threshold. B: the unitary stop model. A race to a threshold between the common GO process (green) and the unitary STOP process (red) is shown. In this example trial, the STOP process did not inhibit the hand movement since it did not cross the threshold before the GO process reached the ballistic stage, shown in gray. C: a schematic depicting the ballistic stage. A GO process responsible for initiating the movement and a STOP process responsible for redirecting the movement are depicted. The GO process is divided into two parts—an initial controllable phase and a final ballistic phase that is close to movement execution and separated by a point in time called the “point of no return” (PNR).

sation functions were comparable (KS test: $P = 0.3129$, KS statistic = 0.4; Fig. 4B), despite having dissimilar TSRTs. The same trend was seen across all subjects. The midpoint of the compensation function, the Weibull mean, was used as a metric for comparison. We also found a strong interaction effect of condition (alone vs. eye-hand) on the Weibull means of eye and hand effectors [2-way ANOVA: $F(1,28) = 20.36$, $P < 0.001$]. The mean of the Weibull means across subjects for the eye-alone condition was 163 ± 44 ms, while the mean of the Weibull means for the hand-alone condition was 345 ± 30 ms and was significantly different ($t = -9.637$, $df = 14$, Bonferroni-corrected $P < 0.001$; Fig. 4C). However, in the eye-hand condition the mean of the Weibull means for the eye (217 ± 50 ms) was comparable ($t = -1.200$, $df = 14$, Bonferroni-corrected $P = 0.249$) to the mean Weibull means of the hand (250 ± 59 ms). Moreover, the Weibull means of the eye and hand in the coordinated condition were better correlated ($r = 0.925$, $P = 0.0012$) with each other than in the effector-alone condition ($r = 0.757$, $P = 0.02$). This evidence suggests that the initial assumption of two separate independent control signals may be applicable only when eye and hand movements

are executed in isolation and not during the control of coordinated eye-hand movements.

Differences between the compensation functions of the alone and coordinated conditions in and of themselves do not necessarily prove different control mechanisms, since compensation functions are also influenced by the no-step RT distributions. Thus if the no-step RT is faster then the time for the STOP process to act is consequently lesser, making it harder to stop the movement, which will be reflected in the compensation functions. Hence the shift in the compensation function that we observed may reflect changes in the no-step RT distribution.

To quantify the relationship between no-step RT distribution and the compensation function, we calculated the relationship between the means of the no-step RT and the means of the compensation function. The means of no-step RT and the compensation functions were well correlated with each other in the eye-alone ($r = 0.86$, $P = 0.006$; Fig. 4D) and hand-alone ($r = 0.97$, $P < 0.001$; Fig. 4D) conditions. The same trend was also seen for the eye ($r = 0.89$, $P = 0.003$; Fig. 4E) and hand ($r = 0.86$, $P = 0.006$; Fig. 4E) effectors in the eye-hand condition. To compare across conditions we fitted means of the

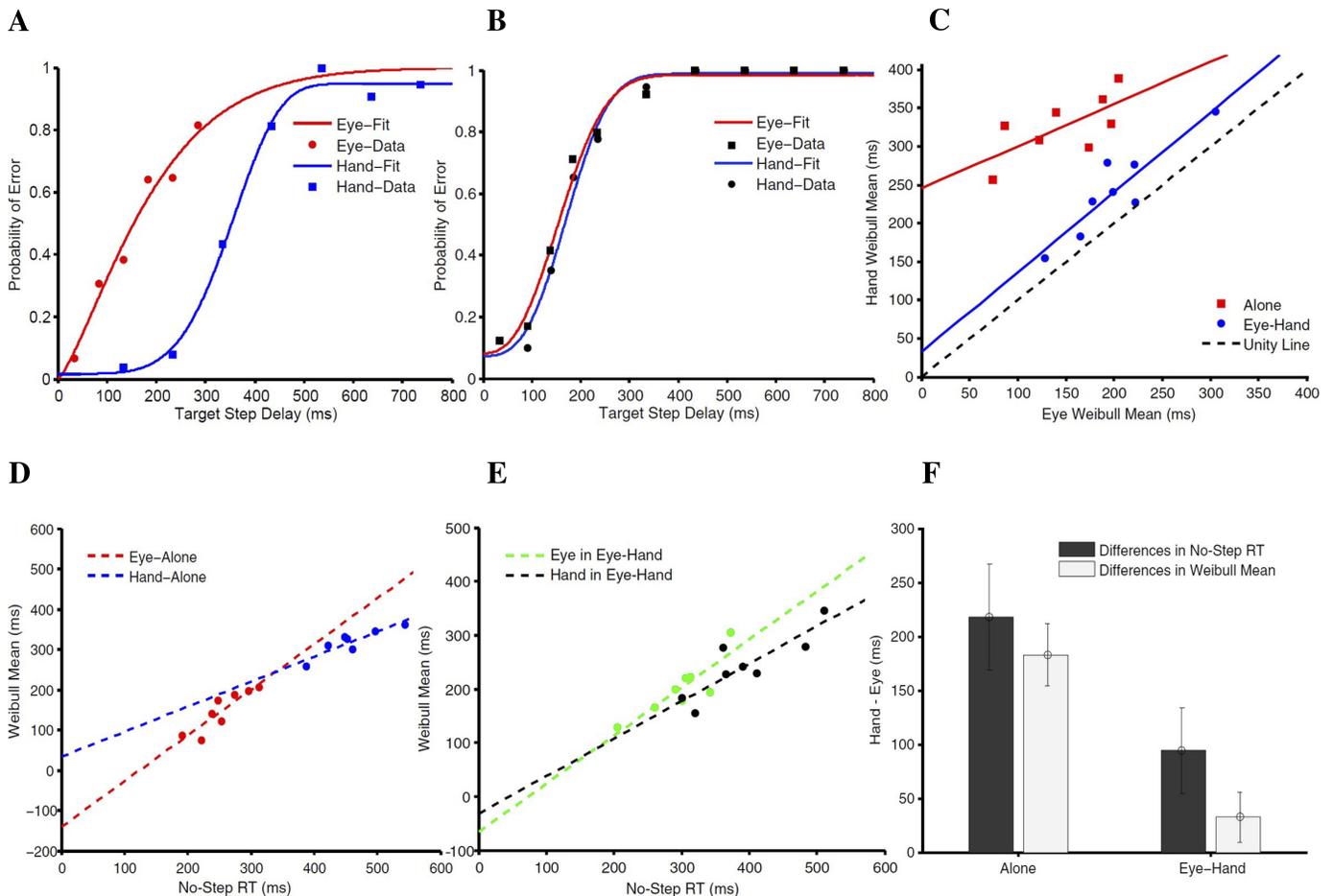


Fig. 4. Signatures of control in the alone vs. the coordinated condition. *A* and *B*: eye and hand compensation functions in the alone (*A*) and eye-hand (*B*) conditions for a typical subject. *C*: scatterplot between the Weibull means of the eye and hand calculated from their respective fitted compensation functions across subjects in the alone and eye-hand conditions. The dashed black line is the unity line. The best fit lines (solid lines) are also shown for reference. *D*: scatterplot between the means of the no-step RT and the Weibull means of the compensation function across subjects for the eye and the hand in the alone condition. The best fit lines in each condition are shown as dashed lines. *E*: scatterplot between the means of the no-step RT and the Weibull means of the compensation function across subjects for the eye and the hand in the eye-hand condition. *F*: bar plot comparing the change in means of the no-step RT distributions between eye and hand effectors and changes in the Weibull means of the compensation functions for the same effectors in the alone (*left*) and eye-hand (*right*) conditions separately.

no-step RT and the means of the compensation function to a linear regression for each condition separately. The slopes of the best fit lines ($\text{slope}_{\text{eye}} = 0.963$, $\text{slope}_{\text{hand}} = 0.491$) were significantly different ($F = 5.38$, $t = 2.32$, $P = 0.03$) from each other in the alone conditions (Fig. 4D). However, in the coordinated eye-hand condition (Fig. 4E), the slopes of the best fit lines ($\text{slope}_{\text{eye}} = 0.883$, $\text{slope}_{\text{hand}} = 0.689$) were comparable ($F = 0.56$, $t = 0.75$, $P = 0.467$). This further suggests that the control mechanism employed during the redirection of coordinated eye-hand movements may be distinct when these movements are executed in isolation.

We tested this hypothesis further and found that the mean hand-alone RT (472 ± 60 ms) in the no-step trials was significantly greater than the mean eye-alone no-step RT (254 ± 40 ms; $t = -8.5442$, $df = 14$, $P < 0.001$). The mean of the compensation functions also followed a similar pattern. Across subjects, the average Weibull mean of the hand compensation function (346 ± 30 ms) was significantly greater than the average Weibull mean of the eye-alone compensation function (163 ± 44 ms; $t = -9.6372$, $df = 14$, $P < 0.001$). Nevertheless, the change in means of no-step RT between eye and hand effectors was comparable to the change in the means of the compensation functions ($t = 1.7337$, $df = 14$, Bonferroni-corrected $P = 0.1049$; Fig. 4F).

Inferring a Ballistic Stage During Planning of Eye-Hand Movements

Contrary to the result shown above, in the eye-hand coordinated condition the mean hand RT (393 ± 74 ms) was significantly different ($t = -2.98$, $df = 14$, $P = 0.009$) from the mean eye no-step RT (299 ± 50 ms), while the means of the eye (217 ± 50 ms) and hand (250 ± 59 ms) compensation functions were comparable ($t = -1.2005$, $df = 14$, $P = 0.249$). The change between the means of the eye and hand no-step RT (94 ± 40 ms) was significantly greater than the change in the means of the compensation functions (32 ± 23 ms; $t = 3.76$, $df = 14$, Bonferroni-corrected $P = 0.002$; Fig. 4F). This peculiar shift of the no-step RT, without affecting the compensation function, was reported earlier in certain experimental manipulations of the classical countermanding task (Osman et al. 1986). Such nonsymmetric shift in the RT without an accompanying shift in the compensation function is thought to occur when the experimental manipulation has affected the ballistic stages of movement preparation. Interestingly, we found this unequal shift only during the control of coordinated eye-hand movements, not when these effectors were controlled in isolation. This suggests that the nature of control during the coordinated condition may be different from the control mechanism employed during the alone conditions. Furthermore, this analysis raises the possibility of a point of no return in the hand movement preparation during coordinated eye-hand movements, after which the response is ballistic, producing compensation functions comparable to that of the ensuing eye movement.

We estimated the ballistic stage from the existing redirect data, using simulations detailed in MATERIALS AND METHODS. Figure 5A shows the comparison between the best fit compensation function predicted by the ballistic stage model and the observed data for a typical subject. The goodness of fit was quantified with r^2 for each subject. The average r^2 ($0.971 \pm$

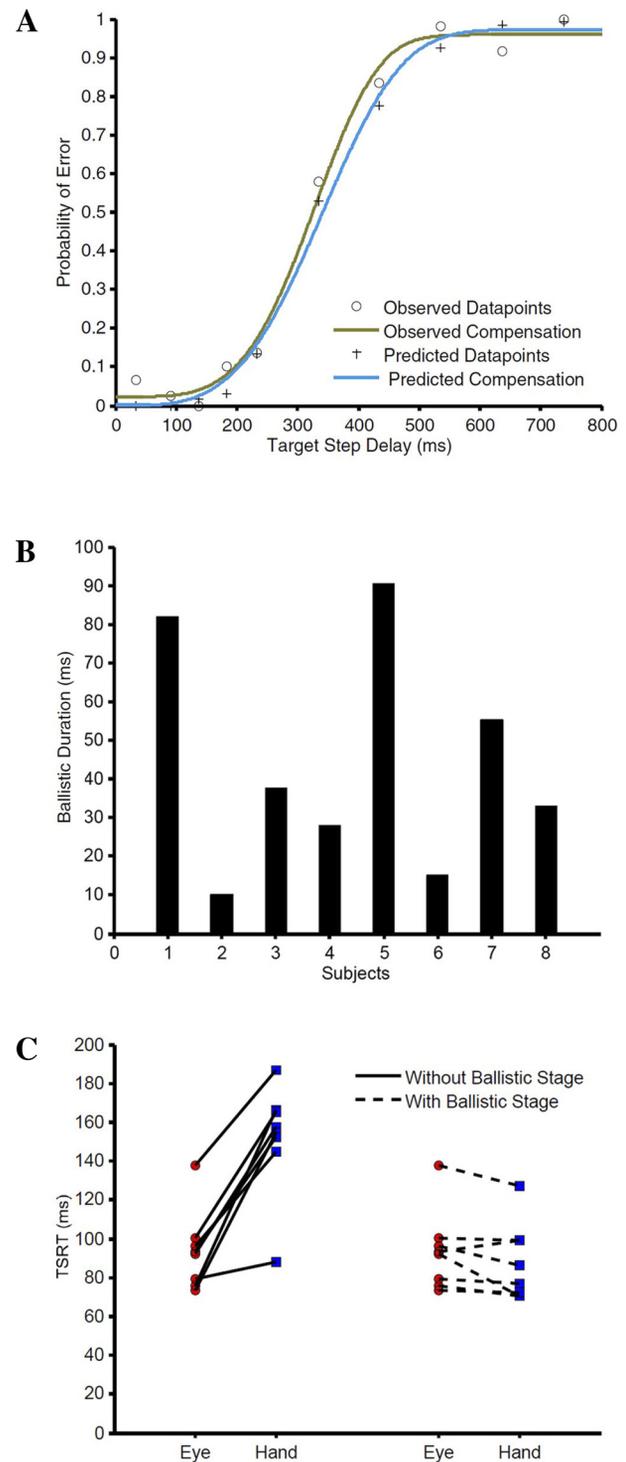


Fig. 5. Evidence of a ballistic stage during the programming of coordinated eye-hand movements. *A*: comparison between the observed compensation function and the compensation function predicted by the ballistic stage model for the hand in a typical subject. *B*: the duration of the ballistic stage estimated for each subject. *C*: comparison between the mean TSRTs of the eye (red) and the hand (blue) calculated with the classical race model (solid line) and the ballistic stage model (dashed line).

0.02) across subjects suggested a good fit between the prediction of the model and the observed data. Using this approach, we estimated the ballistic stage for the hand in the eye-hand condition across subjects to be 44 ± 30 ms on average (Fig.

5B). As a consequence of incorporating a ballistic stage in the motor preparation of the hand, the duration of the STOP process, and consequently TSRT, is reduced since the GO process can only be stopped before it crosses the point of no return. The TSRT calculated for the hand in the eye-hand condition, on average across subjects, with the classical race model was 152 ± 29 ms, as shown above. However, when a ballistic stage was incorporated the hand TSRT became 88 ± 20 ms on average, which is significantly lower ($t = 6.991$, $df = 7$, $P < 0.001$) than the earlier estimate. More interestingly, the TSRT of the hand with ballistic stage (88 ± 20 ms) now becomes comparable to the TSRT of the eye (94 ± 20 ms; $t = 1.954$, $df = 7$, $P = 0.091$) in the eye-hand condition (Fig. 5C). This result is consistent with a unitary, global, effector-independent mechanism being recruited in the coordinated eye-hand condition.

Testing Models of Redirection

Incorporating a ballistic stage for the hand during the programming of coordinated eye-hand movement suggests that a unitary stop mechanism may be recruited for the control of both eye and hand effectors. To test this hypothesis in a more rigorous manner, we used the race model to simulate the behavior in the eye-hand redirect condition and compare the predictions between the effector-specific multiple-stop model

and the unitary stop model. We compared the compensation function of the eye predicted by the two models to the observed data. For a typical subject, the predicted eye (Fig. 6A) and hand (Fig. 6B) compensation functions of the multiple-stop model (eye KS test: $P = 0.675$; hand KS test: $P = 0.675$) as well as the unitary stop model (eye KS test: $P = 0.675$; hand KS test: $P = 0.312$) were not significantly different from the observed data. The goodness of fit as accessed by the r^2 across subjects for both effectors was comparable between the multiple-stop and unitary stop models (eye: $t = 0.070$, $df = 14$, $P = 0.945$; hand: $t = 1.782$, $df = 14$, $P = 0.09$). To test this more rigorously across subjects, the mean of the compensation function was accessed by computing the Weibull mean as before. The Weibull means of the eye compensation function averages across subjects predicted by the multiple-stop model (204 ± 48 ms) and the unitary stop model (204 ± 47 ms) were comparable [1-way ANOVA: $F(2,21) = 0.12$, $P = 0.8879$] to the observed data (215 ± 51 ms). Similarly, the average Weibull means of the hand compensation function predicted by the multiple-stop (251 ± 61 ms) and unitary stop (248 ± 55 ms) models were also comparable [1-way ANOVA: $F(2,21) = 0.01$, $P = 0.9949$] to the observed mean of the hand compensation function (248 ± 60 ms). This suggests that both models predicted the observed compensation functions well (Fig. 6C).

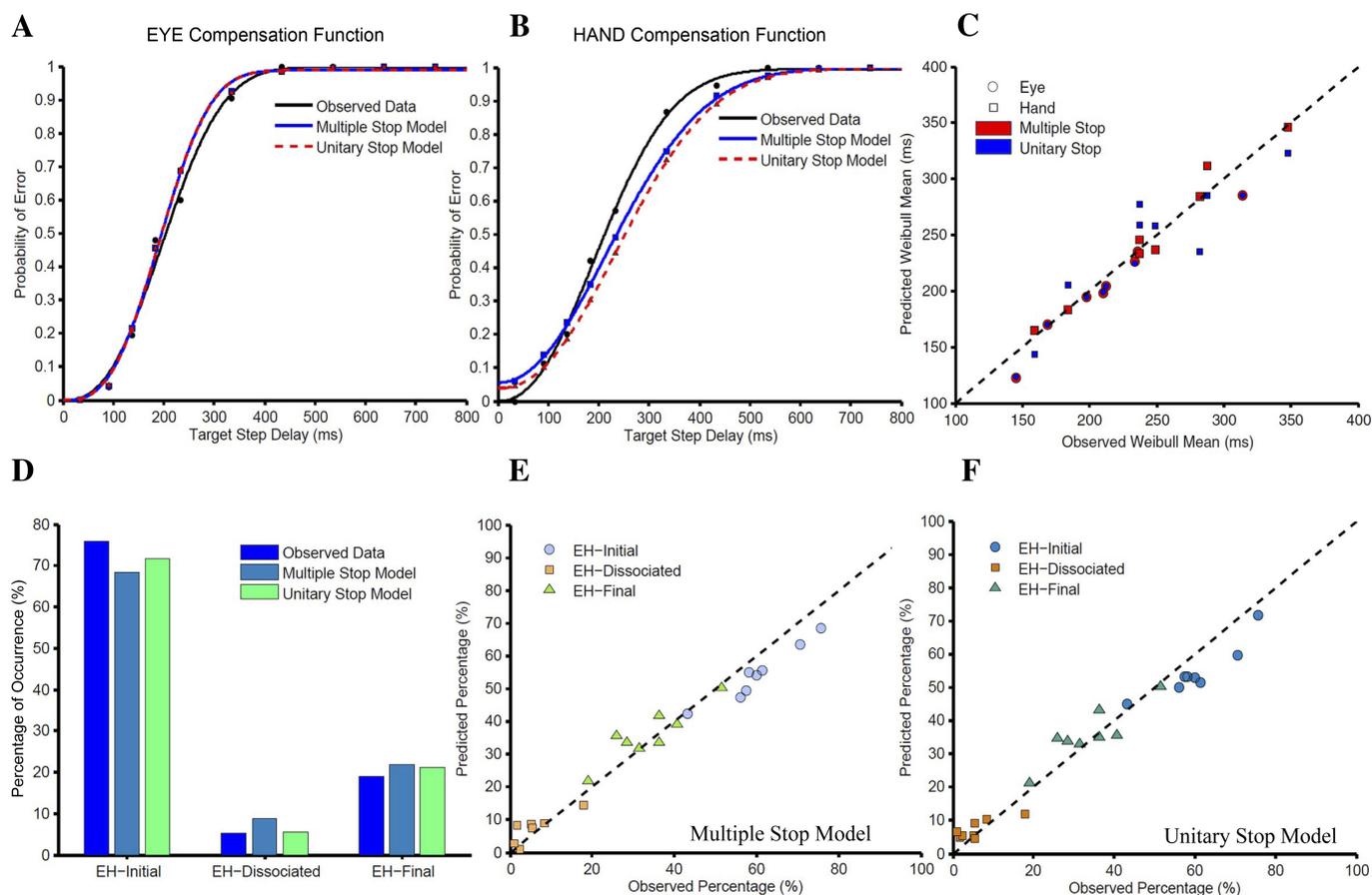


Fig. 6. Testing models of redirection. *A* and *B*: comparison between the observed and predicted compensation function of the eye (*A*) and hand (*B*) by the multiple-stop and unitary stop models for a typical subject. *C*: scatterplot of the Weibull means derived from the observed and predicted compensation functions of eye and hand by the multiple-stop and unitary stop models across subjects. *D*: comparison between the observed and the predicted frequency of the 3 trial types by the multiple-stop and unitary stop models for a typical subject. *E* and *F*: scatterplot of the predicted and observed frequencies of the EH-initial, EH-dissociated, and EH-final trials is shown across subjects for the multiple-stop (*E*) and unitary stop (*F*) models.

In addition to the compensation functions, the two models predict different types of behavioral responses based on the outcome of the race. When the common GO process wins the race against the STOP process(es) then both eye and hand effectors are directed to the initial target, called an EH-initial response. When the common GO process wins the race against the STOP process of the eye, but not against the STOP process of the hand, then the eye movement is made to the initial target while the hand is redirected to the second target, called an EH-dissociated response. In the unitary stop model, EH-dissociated responses occur when the common GO accumulator reaches threshold before the STOP process, resulting in an eye movement to the initial target, and the STOP process manages to reach threshold before the ballistic stage of the hand is initiated, resulting in the hand being redirected. When the STOP process(es) win the race against the common GO process, both eye and hand movements are redirected to the second target, called the EH-final response. The model predicted these different behavioral responses to occur with varying degrees of probability, which can be used to test the validity of these models by comparison to the observed data.

We compared the observed frequencies of response types in the data to the frequencies of EH-initial responses, EH-dissociated responses, and EH-final responses predicted by the multiple-stop and unitary stop models for a typical subject (Fig. 6D). To test this across subjects, we compared the means of the observed and predicted frequencies of each response type separately. We found that the predicted frequencies of the EH-initial trials were not significantly different [1-way ANOVA: $F(2,21) = 0.16$, $P = 0.333$] for the multiple-stop model ($54.4 \pm 8.5\%$; Fig. 6E) as well as the unitary stop model ($54.5 \pm 8.0\%$; Fig. 6F) compared with the observed frequencies ($60.3 \pm 9.8\%$). In addition to this, the frequencies of occurrences of EH-dissociated and EH-final trials were also well predicted across population. The mean percentage of EH-dissociated trials as well as EH-final trials predicted by the multiple-stop model (EH-dissociated = $7.4 \pm 4.0\%$, EH-final = $36.0 \pm 8.1\%$; Fig. 6E) and the unitary stop model (EH-dissociated = $7.2 \pm 2.7\%$, EH-final = $35.9 \pm 8.4\%$; Fig. 6F) were comparable [1-way ANOVA: $F_{\text{DISS}}(2,21) = 0.29$, $P_{\text{DISS}} = 0.7478$, $F_{\text{FIN}}(2,21) = 0.17$, $P_{\text{DISS}} = 0.8449$] to the observed percentages (EH-dissociated = $5.9 \pm 5.4\%$, EH-final = $33.7 \pm 9.8\%$). We did not find any significant difference between the predictions in the frequency of the three trial types by the multiple-stop model or the unitary stop model, suggesting that both models could predict the behavior equally well. To test this more rigorously, the χ^2 -statistic was calculated for each subject and the mean χ^2 -statistic across subjects was used as a measure to compare the models. The mean χ^2 -statistic, across subjects, for the multiple-stop model (48 ± 28) was comparable ($t = -0.8077$, $df = 7$, $P = 0.4458$) to the mean χ^2 -statistic computed for the unitary stop model (54 ± 32). This suggests that both models of redirection were equally good in predicting the behavior.

Validating the Unitary Stop Model

To validate the unitary stop model we tested other behavioral measures. Specifically, a multiple-stop model predicts a particular type of dissociated trial, in which the eye is directed to the second target (successful compensation) while the hand

is directed to the first target (failed compensation). This is possible only if two distinct stop processes are recruited. Interestingly, this type of dissociated trial in which the faster eye movement is successfully compensated while the slower hand movement is not compensated is not predicted by the unitary stop model. Consistent with this prediction, we found no evidence of this behavioral response.

Second, the unitary stop model assumes that the final phase of the motor preparation of the hand movement in the eye-hand condition is ballistic in nature. Hence we wanted to test the relationship between the ballistic stage and the estimated hand delay, which is thought to reflect the interval between the onset of the EMG and the observed RT, sometimes referred to as the electromechanical delay (Gribble et al. 2002; Karst and Hasan 1991; Wadman et al. 1979). We found that the mean ballistic stage duration (44 ± 30 ms) was significantly lower ($t = -3.893$, $df = 7$, $P = 0.006$; Fig. 7A) than the hand delay (83 ± 44 ms) predicted by the common command model. Moreover, we also found a strong correlation ($r = 0.767$, $P = 0.02$) as well as a linear relationship (slope = 1.146; Fig. 7B) between the duration of the hand delay and the duration of the ballistic stage. This suggests that the point of no return may be initiated at some fixed interval during the hand delay period after the rise of the EMG signal but before the start of the hand movement.

To further test this hypothesis more rigorously we ran the unitary stop model as above without assuming a ballistic stage during the programming of the coordinated eye-hand movement. This ensured that the unitary stop process could stop the hand movement, throughout the duration of the hand delay, until the movement was initiated. This model predicted the percentage of EH-dissociated responses ($12 \pm 5.6\%$) to be significantly greater ($t = -3.67$, $df = 7$, $P = 0.008$; Fig. 7C) than the observed data ($6 \pm 5.4\%$). This overestimation of the model clearly suggests that a portion of the hand delay is ballistic in nature and impervious to inhibitory control. As a corollary of this hypothesis, the time interval within the hand delay that is not ballistic should be correlated with the extent of EH-dissociations seen in each subject. We tested this and found that the time difference between the hand delay and the ballistic stage that is not ballistic in nature is highly correlated ($r = 0.904$, $P = 0.002$; Fig. 7D) with the frequency of EH-dissociated responses. This evidence suggests that a significant part of the duration of the hand delay in the motor preparation of a coordinated eye hand movement is ballistic in nature.

In addition to the ballistic stage and its relation with the dissociated trials, the unitary stop model also has a specific prediction regarding the variability in the STOP processes of eye and hand. Since the model assumes that a unitary stop process as a single accumulator, the variability of the estimated STOP processes controlling the eye and hand are expected to be comparable. To test this prediction, we estimated the variability of the STOP process with a procedure that is detailed in MATERIALS AND METHODS. Briefly, the compensation functions were replotted using ZRFT normalization instead of TSDs. The transformed compensation functions of eye and hand coincided with each other in the eye-hand condition (Fig. 8A), suggesting a unitary control, but were distinctly different in the alone condition (Fig. 8B). To quantify the variability of the STOP process, a linear regression was used to fit separate lines on the

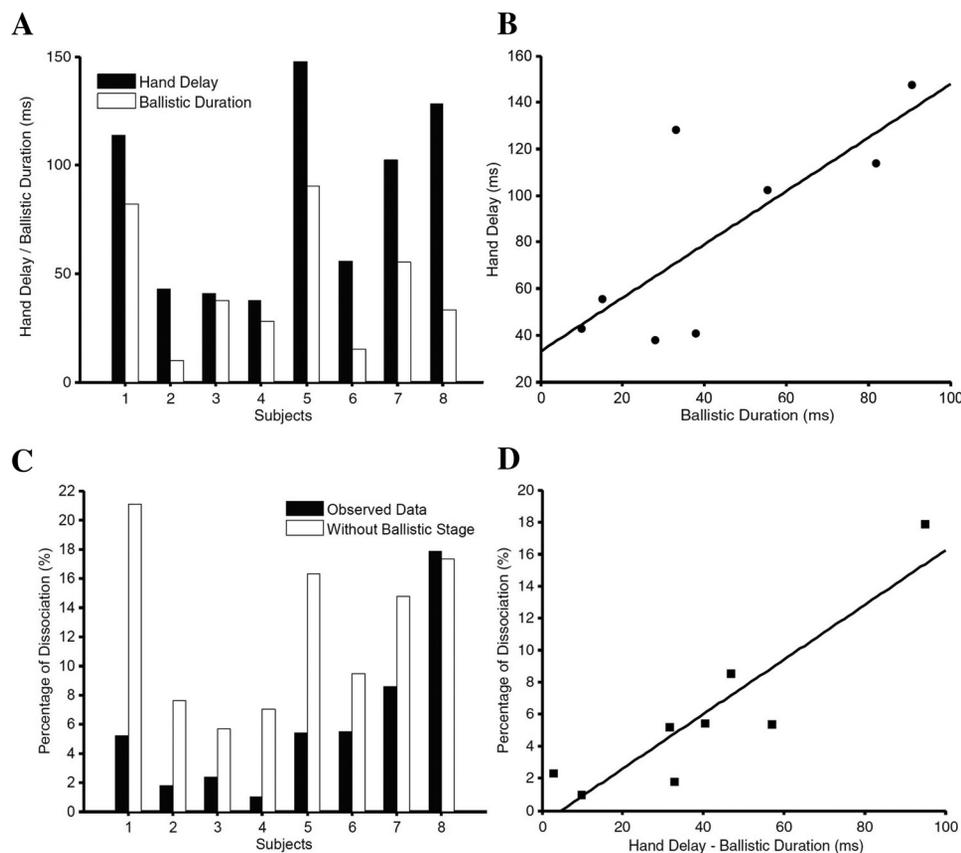


Fig. 7. Verification of the ballistic stage. *A*: bar plot comparing the duration of the hand delay estimated through the common command model using the no-step RT distributions and the duration of the ballistic stage estimated using the compensation functions for all subjects. *B*: scatterplot showing the linear relationship between the hand delay predicted by the common command model and the ballistic stage estimated across subjects. The best fit line is also shown for reference. *C*: bar plot comparing the frequency of predicted EH-dissociated trials in the absence and presence of a ballistic stage relative to the observed frequency of EH-dissociated trials. *D*: scatterplot showing the linear relationship between % of dissociated trials and the hand delay duration prior to the ballistic stage. The best fit line is shown for reference.

compensation functions of the eye and hand, which were clipped between -2 and $+2$ to avoid the tails of the distributions. For a typical subject (Fig. 8A) the best fit lines of the eye and hand coincided with each other in the eye-hand condition. Across the population (Fig. 8C), the mean slope of the best fit lines, which was an indirect measure of the STOP variability, was comparable ($t = 1.385$, $df = 7$, $P = 0.2085$) for eye (-0.26 ± 0.03) and hand (-0.28 ± 0.03) movements. Interestingly, when the eye and hand movements were executed in isolation, the variability of the eye (-0.22 ± 0.04) and hand (-0.28 ± 0.03) STOP processes were significantly different ($t = 3.520$, $df = 7$, $P = 0.009$) for the same typical subject (Fig. 8A) as well as across the population (Fig. 8C).

To experimentally test the unitary stop model, subjects performed a modified version of the redirect task (*experiment 2*) in which coordinated eye-hand movements were generated to a peripherally appearing green target on no-step trials that constituted 60% of the trials. In separate blocks, subjects were instructed to redirect their eye, hand, or both eye and hand when the second target appeared after a TSD in the remaining 40% of the step trials. We hypothesized that if multiple effector-specific stop signals are recruited to redirect coordinated eye-hand movements, then performance in the three task conditions would be distinctly different from each other. Stopping only the eye should not affect the performance of the hand in the eye-redirect condition and vice versa in the hand-redirect condition if multiple effector-specific stop signals are recruited. In contrast, if a global effector-independent unitary stop mechanism is recruited, instruction to stop one of the effectors should automatically affect the performance of the other, even in the absence of explicit instructions. Such a

unitary stop mechanism should produce identical behavioral performance in all three conditions of the task.

To test the two models of redirection, we compared the compensation functions of the eye in the three task conditions—eye-redirect, hand-redirect, and eye-hand-redirect. We found that the compensation functions of the eye and hands were similar across conditions for a typical subject (Fig. 9, *A* and *B*). To test this qualitative finding more rigorously, we computed the means of the compensation function by calculating the Weibull mean across conditions. Across subjects, the average Weibull means of the eye compensation function in the eye-redirect (227 ± 33 ms), hand-redirect (215 ± 40 ms), as well as eye-hand-redirect (209 ± 47 ms) conditions were comparable. Similarly, the mean of the hand compensation functions across subject in the eye-redirect (252 ± 60 ms), hand-redirect (238 ± 46 ms), as well as eye-hand-redirect (257 ± 46 ms) conditions were comparable [2-way ANOVA: $df = (2,30)$, $F = 0.23$, $P = 0.7924$; Fig. 9C]. The TSRTs of the eye ($\text{redirect}_{\text{eye}} = 110 \pm 12$ ms, $\text{redirect}_{\text{hand}} = 104 \pm 18$ ms, $\text{redirect}_{\text{eye-hand}} = 105 \pm 20$ ms; Fig. 9D) and hand ($\text{redirect}_{\text{eye}} = 151 \pm 25$ ms, $\text{redirect}_{\text{hand}} = 155 \pm 33$ ms, $\text{redirect}_{\text{eye-hand}} = 144 \pm 19$ ms; Fig. 9D) were significantly different [2-way ANOVA: $df = (2,30)$, $F = 34.61$, $P < 0.001$] from each other but were comparable across conditions [2-way ANOVA: $df = (2,30)$, $F = 0.29$, $P = 0.7514$]. As expected, the frequencies of the three different behavioral responses were significantly different [2-way ANOVA: $df = (2,45)$, $F = 102.6$, $P < 0.001$] from each other while the frequencies of the three behavioral response observed during the three different redirect conditions were comparable for a typical subject (Fig. 9E), as well as across subjects [2-way ANOVA: $df = (2,45)$, $F < 0.001$, $P =$

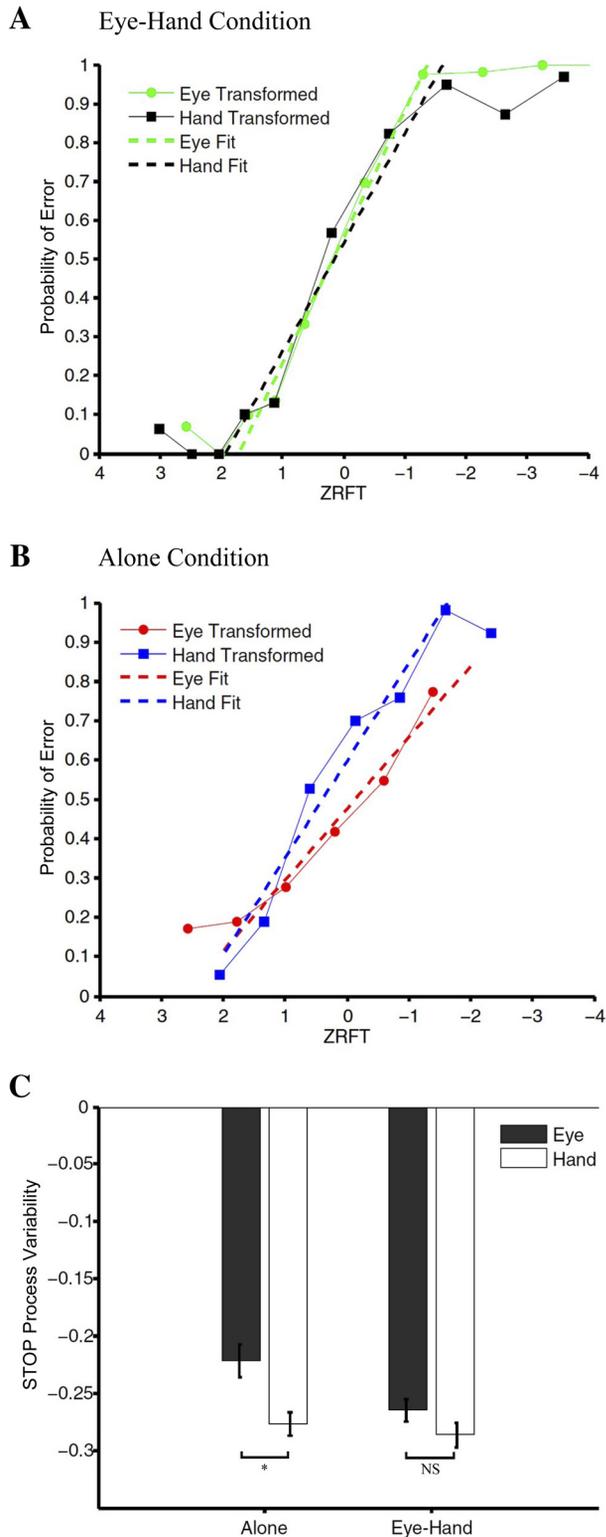


Fig. 8. Variability of the STOP process. *A*: normalized compensation functions for eye and hand when replotted as a function of ZRFT in the eye-hand condition. The best fit lines of the compensation functions are shown as dashed lines. *B*: compensation functions for eye and hand when replotted as a function of ZRFT in the alone condition. The best fit lines of the compensation functions are shown as dashed lines. *C*: bar graph comparing the average slopes of the best fit lines for eye and hand across subjects, in the alone (*left*) and eye-hand (*right*) conditions. * $P < 0.05$; NS, not significant.

1; Fig. 9*F*]. These results indicate that redirecting the eye affected the performance of the hand and vice versa, leading to similar behavior across conditions despite distinct instruction given during each condition. Since the performance of the subjects in the three conditions of eye-redirect, hand-redirect, and eye-hand-redirect were comparable, we conclude that a unitary, effector-independent stop process was recruited that controlled both eye and hand movement plans simultaneously.

DISCUSSION

We showed that a single control signal provides a parsimonious explanation of eye-hand control. In the process we also showed that the preparation of the hand movement reveals a small but significant ballistic component just prior to movement execution.

Relationship Between the Redirect and Classical Countermanding Task

Earlier studies have investigated the mechanism of control using the countermanding task and the race-model architecture. Unlike the countermanding task in which the subject withholds a preplanned response, in the redirect task the subject redirects the planned response to a second target. Hence redirect performance can also be modeled as a race between two GO processes—one that initiates a movement to the initial target and a second that initiates a response to the second target. However, recent studies from our laboratory have shown that aspects of redirect behavior are better understood as requiring an explicit STOP process. For example, in a redirect task, when control is manifested during saccade execution, hypermetric movements are produced (Ramakrishnan et al. 2010) that are characterized by asymmetric velocity profiles (shorter deceleration phase compared with the acceleration phase) indicating that an active braking mechanism is involved. In addition, the time it took to control the hypometric movements was correlated with TSRT, suggesting that it is a manifestation of the same central control process during execution that results in hypometry. In contrast, during the generation of sequential saccades, subjects typically produce midway or averaged saccades but very few hypometric saccades (Bhutani et al. 2012). Second, the ability to redirect movements improves when subjects make memory-guided saccades or visually guided delayed saccades that entail an inhibition of planned eye movement (Kapoor and Murthy 2008). Third, the pattern of responses following microstimulation of frontal eye fields during redirection is best explained with an intervening STOP process (Ramakrishnan et al. 2012). Finally, a rather simple calculation based on the average RTs to the first and second targets in both reaching and saccade redirect suggests a race between a GO and a STOP process. Since compensated responses were generally observed to be ~ 50 ms faster than noncompensated responses, at TSD of 50 ms the finish times of compensated and noncompensated responses should be the same, producing the two responses with equal probability ($P[\text{error}] = P[\text{cancel}] = 0.5$). However, the observed compensation functions for both eye and hand (Fig. 4, *A* and *B*) reveal that at such TSDs the probability of making an error was a lot less than 0.5. Thus a simple direct race between GO_1 and GO_2 cannot account for the observed data and requires a covert inhibitory STOP process for both eye and hand effectors. All

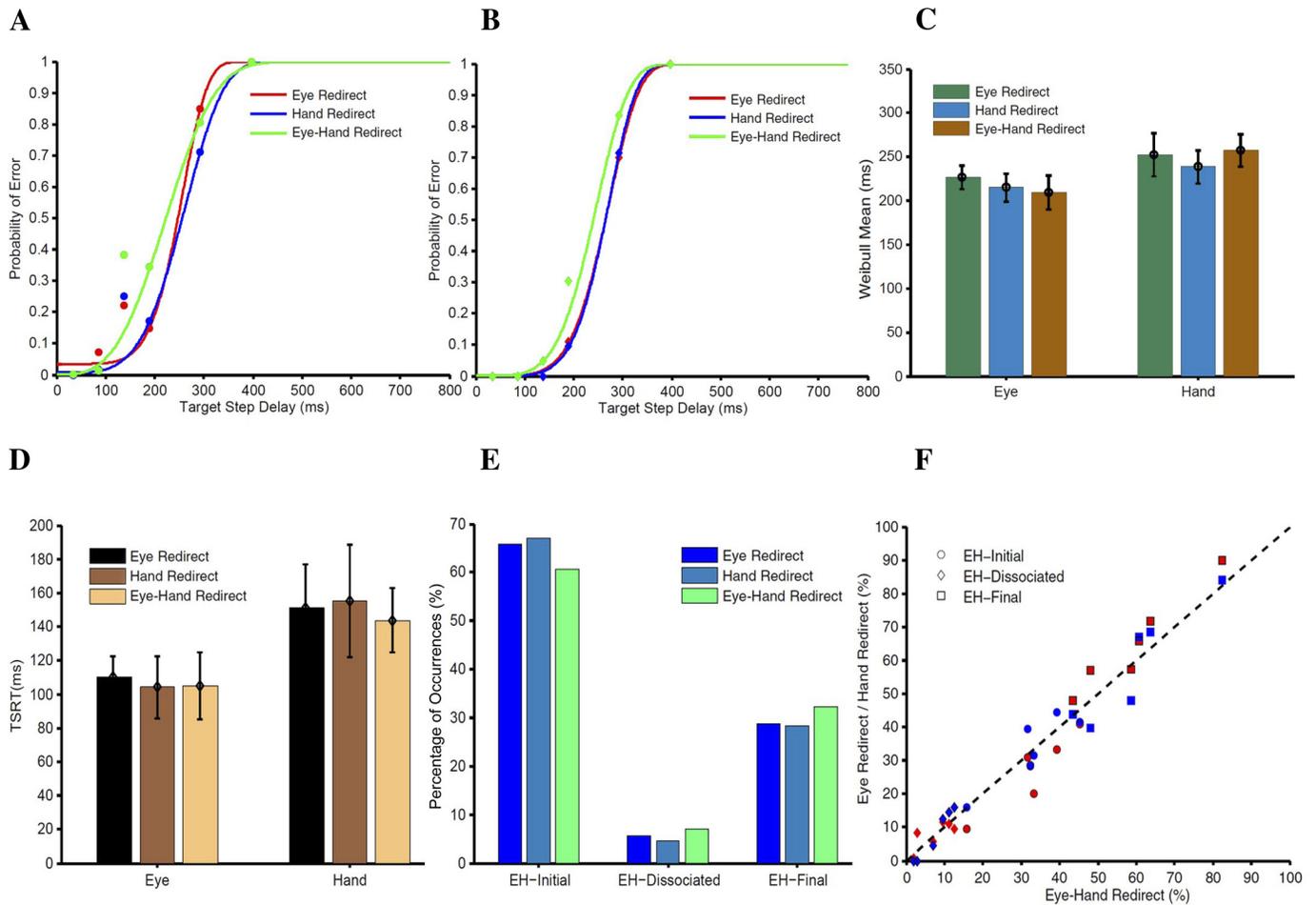


Fig. 9. Validation of the unitary stop model. *A* and *B*: compensation functions of the eye (*A*) and hand (*B*) derived from the eye redirect, hand redirect, and eye-hand redirect trial conditions in a typical subject. *C*: bar plot comparing the average Weibull mean across subjects calculated from the individual compensation functions during the eye redirect, hand redirect, and eye-hand redirect conditions for eye (*left*) and hand (*right*) effectors. *D*: bar plot comparing the mean TSRTs from the eye redirect, hand redirect, and eye-hand redirect conditions for eye (*left*) and hand (*right*) across subjects. *E*: bar plot comparing the frequency of EH-initial (*left*), EH-dissociated (*center*), and EH-final (*right*) trials during the eye redirect, hand redirect, and eye-hand redirect conditions for a typical subject. *F*: scatterplot comparing the frequency of trial types (EH-initial, EH-dissociated, and EH-final) observed during the eye-hand redirect condition relative to the frequencies observed during eye redirect (blue) and hand redirect (red) conditions across subjects. The points lying close to the unity line (dashed black) suggest that the frequencies of trial types observed across the 3 conditions were comparable across subjects.

these observations notwithstanding, the main finding of a common control signal for coordinated eye-hand movements is not dependent on the form of the control signal involved in the race model (GO-STOP or GO-GO) but is based on the observation that compensation functions of the eye and hand effectors are similar despite the differences in their mean RTs.

Control of Hand Movements Executed in Isolation

The vast majority of studies have studied inhibitory control using eye and hand movements executed in isolation. The general consensus is that although the similar principles of a race model are applicable to both eye and hand movements, the control signals, as assessed by the SSRT or TSRT, are much longer (~ 200 ms) for hand movements (Logan and Irwin 2000; Mirabella et al. 2006) compared with eye movements (~ 100 ms for saccades) (Hanes et al. 1995; Hanes and Carpenter 1999; Kapoor and Murthy 2008; Ramakrishnan et al. 2010). Our results are consistent with these results in the eye-alone and hand-alone conditions when the movements are executed in isolation. Moreover, the change in the means of the no-step RT distributions of eye and hand across conditions affected the

compensation functions to the same extent (Fig. 4*F*), implying that the controllable stage of movement preparation occurs until the point of the hand RT (McGarry and Franks 1997; Osman et al. 1986). However, the finding that longer TSRTs necessarily imply entirely distinct control processes for eye and hand movements is questionable because the difference between TSRTs could be a consequence of a larger peripheral interval (~ 100 ms) between the onset of the EMG and the ensuing hand RT compared with the corresponding interval in the case of eye movements (~ 40 ms). Consistent with this interpretation is the finding that hand movements are subject to peripheral inhibitory control when central control fails (De Jong et al. 1990, 1995) as well as the absence of a clear point of no return in hand movement control (Ko et al. 2012; McGarry et al. 2000; McGarry and Franks 1997; Mirabella et al. 2008). In this context, it is rather surprising that, despite extensive work, hand stopping has not been studied relative to the EMG. By our estimate, accounting for the peripheral delays of ~ 100 ms should decrease the estimate of hand stopping to ~ 100 ms, making it comparable to the eye stopping time. Thus the difference between eye and hand stopping may not neces-

sarily reflect differences in central processing per se but rather be a consequence of a peripheral stop that gets engaged for hand movement control (De Jong et al. 1990, 1995).

Control of Hand Movements During Eye-Hand Movements

Previous work from our laboratory (Gopal et al. 2015) showed a systematic difference in the scaling of mean RT and its associated variance between the hand-alone and hand in eye-hand conditions such that the variance in the latter appears to be determined by the variance of the associated eye RT distribution. This peculiar scaling of the hand RT variance with mean eye RT and not mean hand RT could only be modeled by assuming a common eye-hand command signal that instantiated the GO signal. Furthermore, attempts at decoupling the eye-hand movements by introducing a redirect signal produced far fewer trials in which dissociated eye and hand movements were generated to a different target than predicted by an independent or interactive model of separate eye-hand accumulators (Gopal and Murthy 2015). If coordinated eye-hand movements reflect a dedicated circuit, it stands to reason that the control of such movements may also entail a dedicated control mechanism. Consistent with this notion, we found that performance of the eye and hand on redirection, as accessed through compensation functions, are comparable in the coordinated condition and in stark contrast to their corresponding eye and hand-alone conditions. Unlike the alone condition, we also found that the differences in the mean no-step RT distribution between eye and hand were not entirely reflected in the compensation functions (Fig. 4F). A behavioral consequence of this effect is that controlling the hand becomes much harder in the presence of a preceding eye movement, as if it was being dictated by the same mechanism that controls eye movements. We surmise that this shift to eye control reflects the loss of peripheral control, producing a pseudoballistic stage for hand movement control during coordinated eye-hand movements. When such a ballistic stage is incorporated in the race model and is used to calculate the time course of redirection, the eye and hand movements have comparable TSRTs (Fig. 5C), suggesting a unitary stopping mechanism to control coordinated eye-hand movements.

A conceptually similar model was also proposed to explain eye-head control. An extension of a race model with a ballistic stage incorporated showed that a unitary stop mechanism could also account for the control of coordinated eye-head movements (Corneil and Elsley 2005). Although the neural basis of such a common stop is beyond the scope of the present study, it is noteworthy that application of TMS on the task-irrelevant hand representation in the motor cortex evoked MEPs of lower amplitude on compensated saccade trials relative to noncompensated trials (Wessel et al. 2013). Moreover, a potential common stopping network comprising the ventrolateral prefrontal cortex is activated when both manual and saccadic responses are countermanded (Leung and Cai 2007). Nevertheless, contrary to our interpretation, two other studies using a countermanding task have shown that eye and hand movement planning and control are consistent with an independent model (Boucher et al. 2007; Logan and Irwin 2000). There were some critical differences between the two studies that could explain this discrepancy. The major difference was the use of joysticks and button presses instead of the natural

pointing movements used here. We hypothesize that the coupling between the eye and hand movements during a button press or a joystick manipulation is minimal compared with a naturalistic pointing movement. Consistent with this idea, RT correlations between the eye and hand reported by Boucher et al. (2007) were much lower (0.3–0.5) than reported here (0.56 ± 0.19). Moreover, the shift in the no-step RT distribution that we and others (Bekkering et al. 1994; Mather and Fisk 1985) have observed during eye-hand pointing movements is not reported in their study. Hence, it is likely that independent eye and hand signals would also recruit separate control signals for redirection.

A Ballistic Stage for Hand Movement Control During Coordinated Eye-Hand Movements

We have shown that even though the hand RT is longer than the eye RT, it is not reflected in the ability of the hand to change an erroneous response. In other words, the longer hand RT does not make the control of it easier; instead, the hand compensation function is very similar to the eye effector. This result can be explained by a ballistic stage that is impervious to inhibitory control that was estimated to be ~ 44 ms on average, prior to movement initiation. Since EMG onsets typically begin ~ 100 ms before movement initiation, we surmise that the ballistic stage during the movement preparation of the hand begins after the EMG onsets (~ 50 ms) but before the initiation of the movement.

Although some studies have attempted to detect ballistic stages during the programming of hand movements, none has conclusively shown its existence (De Jong et al. 1990; McGarry et al. 2000; McGarry and Franks 1997; Osman et al. 1986). We believe this is because these studies involved observing hand movements in the context of button presses that are not necessarily the ethological equivalent of reaches. Furthermore, these studies did not instruct eye movements. The latter is critical because the presence of a ballistic stage is apparent only during the programming of a coordinated eye-hand movement as shown in this study. This suggests that a ballistic stage of hand may not be universal but sensitive to the context in which the movement is generated. In addition, these studies have also reported that the movements could be interrupted or modified anytime during its execution, which was taken as evidence against a ballistic stage (De Jong et al. 1990; Mirabella et al. 2008). Contrary to this notion, we have defined the ballistic stage as a time interval within the RT, most likely the final stage of the RT, during which the onset of the hand movement cannot be interrupted. This definition of a ballistic stage does not imply that hand movements cannot be controlled online after its initiation. In fact in this data set itself we have seen evidence of hypometric corrections in which the hand movements were corrected midway before it reached the initial target.

Finally, it is equally possible that the ballistic stage that we detected in this study might not reflect an actual stage in the programming of hand movements. Rather, it might be a consequence of the recruitment of a unitary stop process, which after failure to redirect the prior eye movement gets extinguished. This lack of a control signal would effectively produce a pseudoballistic stage in the hand system. Further research needs to resolve this issue.

Mechanism of Dissociated Trials

If coordinated eye and hand movements are initiated by a common GO process and controlled by a unitary global stop process, then the compensation functions of eye and hand should be identical. Nevertheless, there was consistently a low fraction ($5.9 \pm 5.4\%$) of dissociated trials. Although such dissociations may be construed as evidence against the unitary stop model, it can be accounted for by assuming the recruitment of slower peripheral stopping mechanism for the hand. Earlier work has shown that such a peripheral stopping system exists that is capable of aborting the overt response even though EMG responses in the muscles have started to build up (De Jong et al. 1990; Goonetilleke et al. 2010, 2012).

Consistent with the notion of a ballistic stage for hand movement control, it is interesting to note that the peripheral stop for the hand does not appear to act throughout the entire period of hand delay. If that had been the case, then the portion of dissociated trials would have been much larger than what was observed (Fig. 7C). Thus we hypothesize that the peripheral stop acts for only a short interval after the common central GO accumulator crosses the threshold, winning the central race, until the EMG buildup in the muscles crosses the point of no return, generating dissociated trials. Consistent with this hypothesis, we found the frequency of dissociated trials to be strongly correlated with the time difference of hand delay and ballistic stage, which is the duration of the hand delay that is not ballistic in nature.

In conclusion, this study has provided a framework to understand the mechanism underlying the control of multiple effectors that are coordinated. We have shown evidence of a flexible mechanism of control in which a unitary stop is recruited when coordinated eye and hand movements are redirected and multiple stop processes when the same effectors are redirected in isolation. Such flexible control, we believe, is necessary given the versatile repertoire of visually guided actions that involve multiple independent effectors that are coordinated in the service of goal-directed behavior.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

A.G. and A.M. conception and design of research; A.G. performed experiments; A.G. analyzed data; A.G. and A.M. interpreted results of experiments; A.G. prepared figures; A.G. drafted manuscript; A.G. and A.M. edited and revised manuscript; A.G. and A.M. approved final version of manuscript.

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