Reach target selection in humans using ambiguous decision cues containing variable amounts of conflicting sensory evidence supporting each target choice

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Coallier É, Kalaska JF. Reach target selection in humans using ambiguous decision cues containing variable amounts of conflicting sensory evidence supporting each target choice. J Neurophysiol 112: 2916–2938, 2014. First published September 10, 2014; doi:10.1152/jn.00145.2014.—Human subjects chose between two color-coded reach targets using multicolored checkerboard-like decision cues (DCs) that presented variable amounts of conflicting sensory evidence supporting both target choices. Different DCs contained different numbers of small squares of the two target colors. The most ambiguous DCs contained nearly equal numbers of squares of both target colors. The subjects reached as soon as they selected a target after the appearance of the DC (“choose-and-go” task). The choice behavior of the subjects showed many similarities to prior studies using other stimulus properties (e.g., visual motion coherence, brightness), including progressively longer response times and higher target-choice error rates for more ambiguous DCs. Certain trends in their choice behavior could not be fully captured by simple drift-diffusion models. Allowing the subjects to view the DCs for a period of time before presenting the targets (“match-to-sample” task) resulted in much shorter response times overall, but also revealed a reluctance of subjects to commit to a decision about the predominant color of the more ambiguous DCs during the initial extended observation period. Model processing and simulation analyses suggest that the subjects might adjust the dynamics of their decision-making process on a trial-to-trial basis in response to the variable level of ambiguous and conflicting evidence in different DCs between trials.

ONE IMPORTANT ASPECT OF VOLUNTARY motor behavior is how the central nervous system selects one action to perform from among the many potential actions offered by the environment at any given moment (Cisek and Kalaska 2010; Gold and Shadlen 2001, 2007; Shadlen and Kiani 2013). This has been extensively studied in the oculomotor system in tasks in which subjects chose the target for saccadic eye movements from among multiple distractors in visual-search paradigms or on the basis of the direction of variable-strength coherent visual motion in random-dot kinematogram (RDK) stimuli (Carpenter and Williams 1998; Churchland et al. 2008; Ditterich 2006a, 2006b, 2010; Hanes and Schall 1996; Horwitz et al. 2004; Kim and Basso 2010; Kim and Shadlen 1999; Mazurek et al. 2003; Palmer et al. 2003; Purcell et al. 2012; Ratcliff et al. 2003, 2007; Roitman and Shadlen 2002; Sato and Schall 2003; Shadlen et al. 1996). These studies suggest that saccade target selection is accomplished by parallel neural circuits that continuously acquire sensory evidence for and against each target choice across time until the accumulated evidence in one circuit exceeds a decision criterion threshold.

Target selection for reaching movements has not been as extensively studied, but behavioral and neurophysiological studies of reaching movements using variable-strength RDK stimuli (Resulaj et al. 2009; Thura et al. 2012), visual search tasks with multiple distractors (Song et al. 2008, Song and McPeek 2010), or more complex time-varying stimuli (Cisek et al. 2009) suggest that reach target selection may likewise involve accumulation of evidence toward a decision threshold in multiple competing accumulator circuits (Cisek 2006, 2007).

Consistent with this hypothesis, Cisek and Kalaska (2005) trained monkeys to reach to one of two color-coded potential reaching targets (spatial cues) that matched the color of a delayed, centrally located color cue. They found populations of neurons in dorsal premotor cortex that appeared to process the different action-related sensory information provided by the spatial and color cues. Most importantly, they found evidence for the simultaneous neural representation of the two potential reaching movements during the delay period between the presentation of the spatial cues and the color cue. This may be the cortical neural correlate of two competing accumulators of sensory evidence for the two reach choices (Cisek 2006, 2007; Cisek and Kalaska 2010; Gold and Shadlen 2001, 2007).

The objective of the present study was to modify the task in Cisek and Kalaska (2005) to study the temporal dynamics of target selection for reaching movements on the basis of variable amounts of simultaneous conflicting sensory evidence for each target choice. One important feature of their task was that the monkeys used the color of a centrally located nonspatial color cue to choose between the two targets. Color has no inherent relevance to arm movements on its own, but the color cue provided decisive evidence about target location and reach direction via the application of a learned arbitrary color/location conjunction rule. Similarly, color (Addou et al. 2011; Krouchev and Kalaska 2003), tactile vibratory frequency (Romo et al. 2004, Romo and de LaFuente 2013), visual image identity (Brasted and Wise 2004; Buch et al. 2006; Muhammad et al. 2006) or stimulus brightness (Ratcliff et al. 2007) can become associated with particular movements or motor skills by the application of learned arbitrary stimulus-response rules. This feature of the task could make it possible to distinguish
between “sensory-discriminative” neural processes involved in identifying the critical task-related property of the sensory input vs. “action-selection” processes required to link that perceptual decision to motor action (Bennur and Gold 2011; Muhammad et al. 2006; Purcell et al. 2012; Romo et al. 2004; Romo and de Lafuente 2013).

These two potential processing stages may not be as readily dissociable in visual-search tasks with distractors, in which the unique set of properties that identify the target are presented at the location of the target of action itself and so simultaneously specify all the required properties of the action (e.g., direction, distance, final endpoint). Similarly, one can use arbitrary stimulus-response rules to dissociate the direction of coherent motion of RDK stimuli from the direction of associated saccadic eye movements (Bennur and Gold 2011; Gold and Shadlen 2003). However, the decisive sensory input and associated motor output share a common spatial attribute, direction, and, in most saccadic decision tasks using RDK stimuli, the directionality of input and output is collinear. Moreover, RDK stimuli can elicit short-latency pursuit eye movements (Schütz et al. 2010) and evoke directionally tuned responses in saccade-related lateral intraparietal neurons (Fanini and Assad 2009), showing that the motion signals in RDK stimuli have direct access to the oculomotor system. While visual target signals may have less direct access to arm motor circuits (Kubanek et al. 2013), visual motion stimuli can also alter arm movements at short lacies (Saijo et al. 2005; Gomi et al. 2006, 2013). Therefore, using color as the critical attribute of the decision cues (DCs) has experimental advantages.

In RDK tasks, decision difficulty and the duration of the sensory-evidence accumulation process are manipulated by varying the amount of coherent motion against a random-motion background. Furthermore, with rare exceptions (e.g., Bollimunta and Ditterich 2012; Niwa and Ditterich 2008), most RDK stimuli contain only a single direction of coherent motion. As a result, the most difficult decisions in most RDK tasks are a signal-detection problem: is there a weak coherent motion signal in one particular direction buried in a very noisy background?

However, many everyday decisions are made on the basis of easily detectable but conflicting evidence favoring multiple actions. In visual-search tasks with distractors, for instance, several readily discriminable potential target stimuli appear, often with shared stimulus features, and the subject must locate the stimulus that contains the specific combination of visual properties that identifies it as the target (Sato et al. 2003; Sato and Murthy 2001). Similarly, we wanted to present DCs to the subjects in which each piece of task-relevant evidence was readily discriminable and in which decisions are made more difficult not only by reducing the amount of evidence favoring the correct target choice, but also by increasing the amount of conflicting evidence supporting the other target. Therefore, we replaced the unambiguous monochromatic color cues of the Cisek and Kalaska (2005) paradigm with a checkerboard-like mosaic that contained variable numbers of small squares of the same colors as the two targets, along with other squares of a task-irrelevant color. Stimulus difficulty was manipulated by changing the relative numbers of squares of the two target colors. The stimuli that presented the least amount of evidence favoring the correct choice also contained the most amount of evidence favoring the incorrect response. As a result, rather than requiring the subjects to detect a weak signal against random noise, the stimuli that present the most difficult decisions put the subjects in a situation of conflict in which they have to choose the correct target on the basis of ambiguous sensory evidence that contained nearly equal amounts of easily discriminable but conflicting evidence for both alternatives. This could impact on the nature of the decision process compared with that in standard RDK tasks.

Finally, Cisek and Kalaska (2005) could not properly study the temporal dynamics of the target-selection process because their task imposed an arbitrary delay between the presentation of the color cue and a subsequent go signal. We eliminated that delay and permitted subjects to reach as soon as they had decided which target matched the predominant color of the central DC. This allowed us to use the onset of the reaching movement as an approximate peripheral marker for the end of the decision process.

Before using this task in neuronal recording studies, we did a psychophysical study in human subjects to assess the impact of different attributes of the variable-color DCs on task performance. The results of this behavioral study have been reported previously in preliminary form (Coallier and Kalaska 2005).

METHODS

Task Apparatus

Six subjects (S1–S6) (1 man, 5 women; mean age: 31 yr) performed arm-reaching movements in a two-alternative forced-choice task in which we recorded their reach response time (RT) to different stimuli. Two subjects (S2, S3) were very experienced, having participated in a series of pilot studies using similar task designs. The other four subjects were inexperienced. Subjects had normal or corrected-to-normal vision. They also had no known color vision deficit and readily discriminated the colored cues used in the tasks. The experimental protocol was approved by the institutional Research Ethics Committee. Subjects participated after giving their voluntary informed consent.

Subjects sat comfortably in a chair positioned in front of a horizontal digitizing graphics tablet (20 in. × 24 in., Accutab II, GTCO Calcomp, Columbia, MD). They held onto a handle attached to the free end of a light-weight pendulum-like manipulandum suspended above the graphics tablet. The subjects could move the handle freely in the X–Y plane over the tablet. The graphics tablet measured the X–Y position of a stylus installed in the handle (100 Hz, ±0.051 mm accuracy), which in turn controlled the position of a cursor displayed on a computer monitor positioned at eye level above the graphics tablet, 1 in from the subjects. Subjects did short familiarization trial sets on the first day of their participation to ensure that they understood the tasks, but did not practice the tasks extensively before beginning data collection.

“Choose-and-Go” Task

In this task, similar to the “2-target” task in Cisek and Kalaska (2005), subjects chose between two reaching movements to color-coded spatial targets in opposite directions from a central starting position, based on the color of a centrally located nonspatial color cue, according to a simple color-location conjunction rule (move to the target whose color matched that of the central color cue). Unlike the 2-target task, however, the quality of the sensory evidence used to select the target was varied by altering the color composition of the central DC. Furthermore, the subjects could move to the chosen target at any time after the appearance of the DC; there was no arbitrary

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delay period imposed after the DC appearance and no explicit go cue. Instead, the DC provided the information needed to identify the correct target and also served as the go signal to initiate the reach movement as soon as the subject had chosen the target. As a result, we called this the “choose-and-go” (CG) task.

At the start of each trial of the CG task, a central white square (1.9 cm) appeared against a black background on the computer monitor. The subject had to position the cursor in the square and hold it there for 1,000 ms. After this center-hold period, two peripheral square “spatial cues” (3.8 cm) appeared in opposite directions relative to the central square (Fig. 1A). The pair of target cues could be aligned along one of the four cardinal or diagonal axes in a given trial, for a total of eight potential target locations. The centers of the target squares were 15.2 cm apart. One target was blue, and the other was yellow, and the location of the two isoluminant-colored targets changed randomly from trial to trial. After a brief variable spatial-cue period (500 ms ± 500 ms), the central white square was erased and replaced by a multicolored DC (5.6 cm square), composed of a square “checkerboard” matrix of 225 small (3.7 mm) squares, including variable numbers of task-relevant yellow and blue squares interspersed with task-irrelevant red squares (Fig. 1, A and C). The predominant task-related color of the DC (blue or yellow) indicated which colored spatial cue was the correct target for that trial. The subjects were free to reach to the target they chose at any time after the DC appeared. If a subject chose the incorrect target in a trial, that particular trial condition (i.e., combination of spatial cues and DC) was reinserted into the remaining pseudorandom sequence of trials and repeated at a later time. Error trials were repeated until each trial condition was completed successfully.

Subjects were instructed to choose quickly but were not instructed to respond as quickly as possible at the cost of reduced success rates, or to respond as accurately as possible at the cost of longer RTs. As a result, their performance was self-paced. We found in pilot studies that subjects rarely took longer than 2,000 ms to respond to the DCs and that longer RTs were usually due to inattention or other factors. Subjects were also given no instructions to be certain of their target choice before starting to move and never alter their movement once it began, or conversely to change their mind and go to the other target if they weren’t certain of their choice. Finally, subjects were told to look at the DCs to determine its predominant color, but they were not told to fixate their gaze on any particular part of the DC.

The DC disappeared as soon as the cursor exited the central target position. This was done to reduce the possibility that subjects would continue to accumulate new sensory evidence after starting to reach (c.f., Resulaj et al. 2009). A maximum allowable movement time of 750 ms encouraged the subjects to move quickly and to avoid making multiple momentary pauses or changes of direction (“vacillating”) after exiting the central window.

The DCs contained 100 task-relevant blue and yellow squares and 125 task-irrelevant red squares. We used five different numbers of blue and yellow squares in the DCs: 100/0, 70/30, 60/40, 55/45 or 52/48 (Fig. 1C). In this way, the quality of the stimulus ranged from unambiguous (100/0; one task-relevant color only) to very ambiguous (52/48; nearly equal numbers of squares of each color). We will use these ratios to describe the DC stimuli to emphasize the increasingly conflicting nature of the evidence that they presented as the numbers of squares of the two colors approached equality. The strength of the net evidence signaling the predominant color of the DC stimuli was also quantified by their color bias, that is, the number of excess squares of the correct task-relevant color. The color bias ranged from 100 (100/0) to 4 (52/48). There were two DCs of each color ratio and bias, one predominantly blue and one yellow.
for a total series of 10 DCs (Fig. 1C). The correct target choice would be the one with the positive color bias in the DC, while choosing the other target would be an error.

The task program had a library of 100 pregenerated DC matrices for each color bias of the DC. In each trial, the DC was presented in one of two different formats. In “dynamic” DC trials, the program randomly sampled and displayed a new DC matrix of the same color bias at 20 Hz. Because the position of the blue and yellow squares varied randomly from one matrix to another, the dynamic DCs appeared to flicker but did not elicit any sense of motion of the colored squares. The sequence of DC matrices presented during a given dynamic trial was always of the same color bias. We did not attempt to modify the quality of sensory evidence during the time course of single trials in this study by changing the relative numbers of blue and yellow squares (c.f., Huk and Shadlen 2005).

In “static” DC trials, in contrast, the program randomly sampled and displayed one DC matrix until the subjects initiated a reach. The static DCs were designed to assess what performance was possible with only a single image of the color bias of the DC, and especially whether any performance advantage could be gained from the continuously changing temporal stream of sensory input about the predominant color of the DC provided by the dynamic DCs.

Subjects indicated their choice of the predominant DC color by moving the manipulandum with their right arm toward the target square of the corresponding color. To discourage guessing or anticipation of the timing of the DC, the task program also scored an error all trials in which the subject exited the central window too quickly (<150 ms) after the appearance of the DC. All factors, correct target location (8), correct target color (2), DC color ratio (5), and DC format (2), were fully balanced in a randomized-block sequence (160 successful trials). Each trial was typically 4–5 s long. There was a 500-ms intertrial interval between each trial.

To keep the subjects vigilant and motivated, we provided knowledge of results by presenting the correct target square at the end of each trial, as well as an audible “click” sound if the trial was completed correctly.

One set of trials comprised 1 complete randomized-block sequence of 160 correct target choices for all trial conditions, plus error choices. Each subject did 6 trial sets of the CG task in nonconsecutive days. The complete data set for each subject included 192 correct trials of each of the 5 DC color biases (960 correct trials in total for each subject), plus variable numbers of trials with incorrect target choices.

Interleaved with the trials in which we presented the 5 DC ratios shown in Fig. 1, we also presented trials with 100/82 and 60/49 DC ratios, to assess to what degree the subjects’ behavior was influenced by the absolute amount of sensory evidence for each choice, the relative ratio or the net color bias. As a result, subjects actually experienced 14 different DCs in each data set. However, the data from those four special DCs will not be presented in detail here.

“Match-to-Sample” Task

In the CG task, two spatial cues were presented first and had to be compared with the subsequent DC stimulus. This is an inversion of the usual sequence of stimulus events in the standard “delayed match-to-sample” paradigm. Therefore, we also tested them in a modified version of the CG task called the “match-to-sample” (MS) task, in which we presented the DC and spatial cues in the opposite order. We first presented the DC for a variable-duration DC observation period (2,250–3,250 ms) to the subjects (Fig. 1F). This initial DC observation period was significantly longer than the RTs of the subjects in the CG task after the DCs appeared and thus provided the subjects with ample time to decide upon its predominant color. After that period, the colored spatial cues appeared. The subjects had to move the cursor to the target whose color matched the predominant color of the DC. Other than the order of the stimulus events, the overall structure of the MS task was identical to that of the CG task. The same DCs were used, and all factors were fully balanced and randomized. Each subject performed six trial sets of the MS task in nonconsecutive days.

All subjects but S3 performed both the CG and MS tasks in an interleaved sequence. Those subjects did one set each of both tasks per daily session for 6 nonconsecutive days. The order of performance of the tasks varied between daily sessions for each subject and between subjects. In contrast, S3 performed all six CG task trial sets first on 3 nonconsecutive days, followed by six sets of the MS task at a later time. There was no difference in S3’s performance compared with other subjects that could be attributed to this difference in task sequence.

Data Analysis

The X–Y coordinates of the handle measured every 10 ms was differentiated to generate an instantaneous speed profile for each trial. An automatic algorithm estimated the onset of movement, as follows. We calculated the mean and the standard deviation of the variation in the speed profile for all of the X–Y coordinates measured during the last 500 ms of the center-hold period before the appearance of the DC. Starting from the time of appearance of the DC, the algorithm advanced along the speed profile to detect the first time that the instantaneous speed exceeded the mean speed calculated during the 500-ms pre-cue period by at least 3 SDs, and remained above the 3 SD criterion for at least five consecutive time intervals. The estimated RT was verified visually for each trial and adjusted manually if necessary to avoid false early or late RT estimates. These usually resulted from small twitches in hand position just before or after the DC appeared, and occurred 1–2 times on average in each data set of 200–250 trials. The same approach was used to measure the RTs in the MS task, by aligning trial data to the time of presentation of the spatial cues.

Model Simulations

We assessed the degree to which the performance of the subjects in the CG task could be explained by two versions of a bounded diffusion process (Churchland et al. 2008; Ditterich 2006a, 2006b; Gold and Shadlen 2001, 2007; Ratcliff 1978; Ratcliff and McKoon 2008; Ratcliff and Smith 2004; Resulaj et al. 2009; Shadlen and Khan 2013). We will assume in these analyses that correct and incorrect target choices result from the accumulation process and decisions related to the predominant color of the DC, and that the subjects then correctly applied the color/location conjunction rule to identify the corresponding reach target. We have some evidence that subjects applied the conjunction rule incorrectly on very rare occasions (see RESULTS), perhaps because of inattention or other factors. However, we did not attempt to account for this type of rare error. Furthermore, we focused on the final choices of the subjects and did not attempt to simulate any processes that could lead to a change of mind about the correct target or direction of movement (c.f., Resulaj et al. 2009).

These modeling simulations were not intended to identify which of the many different evidence-accumulation models is better than any other at explaining our data. Behavioral data can often be explained reasonably well by a wide range of models (Bogacz et al. 2006; Churchland et al. 2008; Deneve 2012; Ditterich 2006b, 2010; Drugowitsch et al. 2012; Eckhoff et al. 2008; Huang and Rao 2013; Palmer et al. 2005; Ratcliff and Smith 2004), even when applied to the same real (Ditterich 2006a, 2006b; Drugowitsch et al. 2012; Huang and Rao 2013; Mazurek et al. 2003; Palmer et al. 2005; Ratcliff and Smith 2004), or simulated data (Donkin et al. 2011). Instead, our objective was to assess to what degree the performance of our subjects using these multicolored DC stimuli was consistent with the performance of subjects in a range of previous decision-making tasks, especially those using RDK stimuli.

Drift diffusion model with fixed bounds. This drift diffusion model assumes that subjects sample and accumulate noisy evidence \( \mu \) at each moment in time about the DC color bias over time from a starting
point $y_0$ in each trial (where $-B < y_0 < +B$) until it reaches either an upper (+$B$) or lower (−$B$) bound that signaled a decision in favor of one of the two color choices and thus of the corresponding reach target. The value of the bound determines how much evidence must be accumulated from the starting point $y_0$ before committing to a decision and remains constant for the duration of each trial and between trials with different levels of sensory evidence. This simulation assumes a single drift diffusion process that chooses between the two alternatives, or alternatively, two diffusion modules whose sensory input is perfectly anticorrelated (Gold and Shadlen 2001, 2007; Mazurek et al. 2003; Ratcliff 1978; Ratcliff and Smith 2004; Resulaj et al. 2009).

The model assumes that the evidence accumulation process is stochastic, with variable-sized “noisy” increments of evidence at each time step in a given trial, drawn from a normally distributed random distribution with unit variance/s and mean value $\mu$:

$$\mu = k \cdot E + \mu_0$$

where $E$ was the net sensory evidence (the color bias of the DC), $k$ is a gain factor that sets the mean drift rate of the accumulation process in response to the sensory evidence, and $\mu_0$ is a bias term for the drift rate elicited by the DC. The offset of the starting point of accumulation ($y_0$) and the drift rate bias ($\mu_0$) help to capture any bias in the choice behavior of individual subjects.

The evidence $E$ provided by the DC stimuli was represented by the net color bias of the stimuli. This assumes that the integration process was driven by the difference in the activity of two populations of color-sensitive neurons that encoded the amount of evidence for each color separately (c.f., Ditterich et al. 2003; Gold and Shadlen 2001, 2007; Mazurek et al. 2003; Palmer et al. 2005). For the simulations, we divided the color bias value by 100, so that they ranged from $\pm 1.0$ (100/0 DC) to $\pm 0.04$ (52/48 DC), with $E > 0.0$ for predominantly yellow DCs and $E < 0.0$ for predominantly blue DCs. For a given simulated trial, the color choice was scored as correct when the accumulation process crossed the +$B$ bound first when $E > 0.0$, or crossed the −$B$ bound first when $E < 0.0$. Opposite outcomes were scored as simulated choice errors.

The time taken for the evidence to accumulate from the starting point $y_0$ to one of the two bounds $\pm B$ is the decision time $t_d$ for that trial. The model assumes that the RT observed in each trial comprises $t_d$ and a non-decision time $t_{nD}$, that accounts for the delay between the appearance of the DC and the onset of the bounded accumulation process, as well as the delay from the end of the process to the beginning of the movement. The model also assumes that the $t_{nD}$ varies randomly from trial to trial with an SD of $t_{nDSD}$.

The fixed-bound model had six free parameters: $k$, $B$, $t_{D0}$, $t_{nD0}$, $\mu_0$, and $y_0$. We used custom-written Matlab code and the Matlab function fminsearch to find the parameter values that would best account for the observed distributions of RTs (maximum log likelihood criterion) using analytic approaches (Resulaj et al. 2009). The simulations predicted the expected probability of the occurrence of a response to each of the DCs on a millisecond time scale, from the onset of the DCs to 300 ms after the longest observed RT in each data set, using analytic solutions based on the equations for probability density functions of absorption and first passage times, assuming normal noise (Ratcliff 1978) and the probability distributions of the decision variable and nonabsorbed times (Cox and Miller 1965) for bounded drift diffusion.

The fminsearch function typically took several hundred iterations to converge on a solution for a given data set, starting from a set of seed parameter values. If we then reinitialized the parameter search with the final parameters from the first search, fminsearch would typically find a slightly better solution involving small changes in some parameters. Ten successive iterative parameter searches usually resulted in a stable solution which could not be improved significantly. We routinely used a range of different initial seed parameters and repeated the iterative optimization process to generate a range of final solutions for each data set. These repeated fits usually converged on solutions with very similar parameter values. We chose the parameter set for each subject’s data set that yielded the maximum log likelihood.

The fixed-bound model allowed for intertrial variability ($t_{nD0}$) in the duration of the $t_{nD}$. These two parameters proved to be important in the analyses to be described later. Many contemporary decision-making models also allow for intertrial variability in the start point of integration relative to the decision bounds and in the drift rate for a given stimulus (e.g., Brown and Heathcote 2008; Heathcote and Love 2012; Ratcliff and McKoon 2008; Ratcliff and Smith 2004). However, for simplicity, we did not include these features in the fixed-bound model or in the model variant described next, with the understanding that their inclusion would have provided some improvement in the fit of both models to these data sets.

**Drift diffusion model with collapsing decision bound.** Several lines of evidence suggest that the dynamics of the decision process may change with passing time during a trial and between trials (Churchland et al. 2008; Cisek et al. 2009; Deneve 2012; Ditterich 2006a, 2006b; Drugowitsch et al. 2012; Huang and Rao 2013). Therefore, the second simulation included a time-dependent collapsing (i.e., decreasing) bound of the form

$$B_t = B_0$$

for $t < -B_{del}$

$$B_t = B - B_2 \cdot (t - B_{del})^2$$

for $t \geq -B_{del}$

where $B_0$ is the initial bound value, $B_{del}$ is the duration of the time that the bound remains at that value before beginning to collapse, and $B_2$ is the gain of the quadratic term, i.e., the decision bound collapse rate.

The two additional free parameters, $B_{del}$ and $B_2$, simulate the effect of a time-dependent decline in the threshold level of evidence required to make a decision (Deneve 2012; Drugowitsch et al. 2012), or approximately equivalently, the effect of a time-dependent additive or multiplicative signal (“urgency”; Churchland et al. 2008; Cisek et al. 2009, Ditterich 2006a; Drugowitsch et al. 2012; Janssen and Shadlen 2005; Thura et al. 2012). The eight free parameters of the collapsing-bound model were optimized simultaneously by the fminsearch function to fit the observed RT distributions for each subject, using the same iterative procedure as for the fixed-bound model. It is worth noting that the fixed-bound model is equivalent to the collapsing-bound model with a collapse rate of zero.

**Analysis of the Goodness of Fit of the Model Predictions**

The optimization procedure returned the values of the best-fit parameters for each data set and the log-likelihood value for the fit. It also returned the probability functions for the occurrence of a correct or error response with time after the presentation of each DC. These were used to quantify and compare the quality of fit of the fixed-bound and collapsing-bound models to the observed data.

The two-tailed, two-sample Kolmogorov-Smirnov (KS) test was used to test for significant differences ($P < 0.01$) in the cumulative frequency plots of observed RT distributions for different DCs in different task conditions. A two-tailed, one-sample KS test was used to test for significant differences ($P < 0.01$) in the cumulative frequency plots of observed RT distributions for each DC against the predicted cumulative response probability functions for that DC. Both KS tests were used on different combinations of data, including correct and error responses separately or pooled together, as well as for predominantly yellow or blue DCs separately or pooled together.

The difference between observed and predicted cumulative RT distributions was further quantified by calculating the sum of the squared difference between the two curves at 1-ms intervals for the time period between the fastest and the slowest observed RT to each DC.

The differences between observed and predicted responses were also assessed by generating quantile probability plots of the observed and predicted RTs for the (0.1, 0.3, 0.5, 0.7, 0.9) quantile points in the

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predicted cumulative frequency curves of correct and error responses to each DC (Ratcliff 2002; Ratcliff and Smith 2010). The quality of fit was assessed by calculating what proportion of the observed cumulative RT distribution fell within each of the quantile bins of the predicted RT distribution and comparing that against the expected proportion (0.1, 0.2, 0.2, 0.2, 0.2, 0.1) in each bin. The deviations were quantified by calculating the \( \chi^2 \) statistic:

\[
\chi^2 = \sum (\text{observed} - \text{expected})^2 / \text{expected}
\]

summed over all points in the quantile probability plot. The smaller the \( \chi^2 \) value, the better the correspondence between observed and expected RT distributions.

The log-likelihood value returned by the optimization algorithm was also used to compare the quality of the fit for the two models. However, the collapsing-bound model included two more free parameters \((B_{\text{adj}} \text{ and } B_2)\) than the fixed-bound model. We therefore used the log-likelihood values to calculate the Akaike Information Criterion (AIC), the corrected AIC (AICc) and the Bayesian Information Criterion (BIC):

\[
\text{AIC} = (-2 \cdot \log \text{likelihood}) + (2 \cdot \text{nprams})
\]

\[
\text{AICc} = \text{AIC} + \left(\frac{(2 \cdot \text{nprams}) - (\text{nobs-\text{nprams}} - 1)}{\text{nobs-\text{nprams}} - 2}\right)
\]

\[
\text{BIC} = (-2 \cdot \log \text{likelihood}) + [\text{nprams} \cdot \log (\text{nobs})]
\]

where \( \text{nprams} \) is the number of parameters in the model and \( \text{nobs} \) is the number of observations (trials) in each dataset. We used both AIC and BIC because they take into account different factors (Heathcote and Love 2012). All three information criteria penalize the fit measure for the number of parameters, but the AICc and BIC further weight that penalty as a function of the number of data points in the sample. As a result, they tend to favor simpler models than the AIC.

**Bootstrapped and simulated RT distributions.** To provide further verification of the parameter optimization procedure and to assess the significance of differences in parameter values across task conditions, we used two methods to generate artificial RT distributions. For some tests, we created bootstrapped RT distributions by random sampling with replacement from the observed RT distributions. For other tests, we created simulated RT distributions by generating the probability density functions for correct and error choices from the best-fit parameters for the data for each subject, adding stochastic noise to the density functions and then converting the resulting continuous functions into discrete RT distributions.

**Pooling of RT Data Across Subjects**

All analyses were done on the original data from each subject separately. However, to capture overall trends and for illustrative purposes, RT data were also pooled across subjects. To reduce the extra variance introduced by pooling data from different subjects, the RT data from each subject were linearly rescaled so that the median of the rescaled RT distributions from each subject was identical to the grand median value of the pooled non-rescaled RTs. This significantly reduced the spread of RT distributions for each DC that was obtained when the data from all subjects were pooled without rescaling, while retaining all other features of the results. All results from analyses of these pooled rescaled data were completely consistent with the findings from the nonnormalized data for each subject.

**RESULTS**

Because the spatial cues and DCs were presented in opposite order in the CG and MS tasks, the subjects received different prior information about their response choices during the initial spatial cue/DC period of the two tasks, respectively, and then had to process different information provided by the ensuing DC/spatial cues to select the target and initiate a reach. As a result, we will refer to the time interval between the appearance of the second cue and the onset of reach as the “response time” (RT) rather than the “reaction time,” to emphasize that the subjects were not simply reacting to the appearance of a go stimulus.

**CG Task**

Subjects were instructed to reach to the target whose color matched the predominant task-relevant color of the DC. This required them to convert a decision about the color bias of the nonspatial DC into a spatially directed differential reaching movement using a color-location conjunction rule. The subjects established their own performance rhythm and speed-accuracy trade-off and received knowledge of results at the end of each trial (see METHODS). They performed 6,733 trials with the 10 standard DCs, 5,760 trials in which they chose the correct target (192 trials × 5 DCs for each subject) and 973 incorrect-target trials.

The differing amounts of sensory evidence for both potential targets in the DCs had a strong impact on RT distributions and error rates. In all 6 subjects, RTs were shortest for the unambiguous 100/0 DCs (Fig. 2; median 381.5–585.5 ms in different subjects), and shifted towards longer values for the 70/30 to 52/48 DCs (median values for correct choices ranged from 432.5–748 ms (70/30) to 528–1,214 ms (52/48) for different subjects; Fig. 2, A–C). The RT distributions for different DCs overlapped (Fig. 3A) but were significantly different from each other for all DCs for each subject (2-tailed 2-sample KS test, \( p < 0.01 \)).

The target-choice error rate for the 100/0 DCs was zero for all subjects and increased modestly for the 70/30 (0.0–0.5%) and 60/40 DCs (0.0–5.0%) but more steeply for the 55/45 (13.5–17.6%) and 52/48 DCs (30.7–47.4%) (Fig. 2, A–D). The very low error rates for the 100/0 and 70/30 DCs (“lapse” rate) indicated that the subjects reliably applied the color-location conjunction rule when the DCs had a strong color bias; errors for those DCs were likely due to inattention. Choice errors for the other DCs were, therefore, presumably determined by the subjects’ ability to correctly identify the DC’s predominant color when the color bias was weak and there was more contradictory evidence for the incorrect choice.

Experienced subject S2 had shorter RTs for each DC than all other subjects, and the lowest error rate (30.7%) for the 52/48 DC (Fig. 2A). S5, in contrast, had the longest RTs overall, but performed at near-chance levels for the 52/48 DC (47.4% error rate; Fig. 2C). The behavior of S1 was intermediate (Fig. 2B) and more representative of the performance of the other subjects, including experienced S3. These trends indicated that the RT durations and the probability of making a choice error were strongly influenced by both the DC ambiguity and the ability of each subject to discriminate the color bias of the DCs or their willingness to commit to a target choice after a given duration of observation of the DC.
52/48 DCs after normalization to the total number of correct and error choices for each DC revealed that the RTs for error choices were systematically longer than for correct choices for the same DC (Fig. 2E). Moreover, the differences in the RT distributions for correct and error choices got progressively smaller from 60/40 to 52/48 DCs. These asymptotic trends were evident in each subject and suggest the existence of a self-imposed ceiling on the maximum observation times and RTs in the task.

Figure 3 shows the pooled RT histograms for correct and error-choice trials for each DC (Fig. 3A) and summed across all DCs (Fig. 3B), and the probability of a successful target choice as a function of time for each DC (Fig. 3C) and pooled across all DCs (Fig. 3D). Most trials had RTs <1,000 ms and nearly all were <1,600 ms (Fig. 3B).

Figure 3A reveals a subtle but important change in the shapes of the RT distributions. The distributions for the 100/0 to 60/40 DCs were left-skewed, but those for the 55/45 and 52/48 DCs were more symmetrical. This was evident for the pooled group data and also for each individual subject. This change in shape was further confirmed by plotting the RT distributions on a reciprobit scale (Carpenter et al. 2009; Carpenter and Williams 1995). The RT distributions for the 100/0 and 70/30 DCs of every individual subject and the pooled grouped data formed straight lines on a reciprobit plot, whereas those for the 55/45 and 52/48 DCs were strongly positively curved (data not shown). This indicates that the RT distributions for the latter DCs were more symmetrical than expected for a stochastic decision process terminating at a fixed decision bound, and in particular had fewer long RTs than expected.

Performance was essentially perfect at all RT latencies for the 100/0 and 70/30 DCs (Fig. 3C). Mean success rates decreased systematically for the 60/40 to 52/48 DCs (Fig. 3C), but remained relatively constant for each DC over most of the trial duration, with some evidence of a gradual decline in trials with longer RTs (Fig. 3C). Strikingly, when pooled across all DCs, the subjects experienced a nearly linear decline in the probability of a correct target choice as a function of time in a trial for the first 1,000 ms, asymptoting at ~60% for RTs in the 1,000- to 1,600-ms range (Fig. 3D). These trends were also seen in each individual subject.

This cumulative success rate curve reflects several factors. Most of the shortest RTs were evoked by the 100/0 and 70/30 DCs (Figs. 2 and 3A) for which the success rates were very high (Fig. 3C). As time progressed, more of the trials in which a decision had not yet been reached involved the more ambiguous DCs, for which subjects took increasingly longer times to make correct choices (Figs. 2 and 3A) and made more error choices which tended to have longer RTs than correct choices to the same DCs (Fig. 2E). These curves (Fig. 3, C and D), therefore, capture the subjects’ cumulative experience or expectation of success as a function both DC ambiguity and time in a trial.

This effect is also seen in the average time interval between correct choices for different DCs, which we calculated for each subject by summing the total duration of all correct and error-choice trials plus intertrial intervals, for each DC across
all sessions. The mean interval between correct choices ranged from 4,434 to 4,985 ms for the 100/0 DCs for different subjects and increased with DC ambiguity (70/30: 4,427–5,139 ms; 60/40: 4,501–5,597 ms; 55/45: 5,006–6,454 ms; 52/48: 7,840–10,603 ms) due to a combination of longer RTs and lower success rates.

Taken together, these data suggested that all the subjects showed similar behavior of observing the DCs for a variable period of time that was strongly dependent on the level of sensory evidence ambiguity or conflict in the DCs. The RT rarely lasted more than 1,200–1,800 ms for different subjects (Figs. 2 and 3). The longest RTs were associated with the lowest probability of a successful choice on a trial-to-trial basis (Fig. 3D).

Movement kinematics. Movements tended to be modestly slower for more ambiguous DCs in four of the six subjects. This was seen most clearly in the movement accelerations (Fig. 4A). This effect of DC ambiguity on reach movement acceleration was most prominent for the two most experienced subjects (S2, S3; Fig. 4A and B), present but weaker in S4 and S6, but not clear in S1 and S5.

Each subject showed small differences in RTs, movement durations and success rates across different movement directions. However, these patterns were idiosyncratic and differed as a function of both movement direction and DC in each subject and across subjects. This suggested that differences in the direction-dependent biomechanics of the reaching move-

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Fig. 3. Time course of the incidence of correct and error choices and success rates within a trial. A: histograms of the RTs for correct choices (thick lines) and error choices (thin lines, arbitrarily drawn as negatively oriented curves) for each DC in the CG task. B: cumulative histograms of the RTs for correct choices (thick lines) and error choices (thin lines) pooled across all DCs. C: success rate as a function of time for each DC. D: success rate as a function of time pooled across all DCs.

Fig. 4. Effect of DC stimuli on reach movement kinematics. A: mean acceleration curves for the reach movements to correct targets for each of the 5 DCs, for subject 3. B: mean peak acceleration as a function of DC for all 6 subjects.
ments had little systematic impact on the decision processes in this task.

Practice effects. Subjects S2 and S3 were much more experienced with similar tasks than S1, S4, S5 and S6. Furthermore, all subjects received knowledge of results about the correct vs. error choices, raising the possibility that subjects could have become more skilled across sessions.

However, there was no consistent trend for improved performance from the first to last sessions in the CG task (Table 1). Despite being very experienced, S3 showed the largest decrease in RTs of any subject, whereas S2 showed a small increase, and both showed only small decreases in error rates. S1 also showed a small decrease in RTs, but the RTs of S4, S5 and S6 increased. S1 and S6 showed reduced error rates but S4 and S5 did not.

Similar results were obtained for the MS task. Furthermore, all subjects except S3 performed the CG and MS tasks in a randomly interleaved sequence across sessions. Any differences in performance between the two tasks cannot be explained by either order or practice effects.

MS Task

The order of presentation of the spatial cue and DCs was reversed in the MS task. The subjects could observe the DCs for 2,250–3,250 ms and assess their color bias before seeing the spatial cues. The change in cue sequence was explained to the subjects, but they were given no specific instructions about how to respond and were allowed to develop their own strategy. Subjects performed 6,595 trials with the standard DCs in the MS task, 5,760 trials in which they chose the correct target (192 trials × 5 DCs for each subject) and 835 incorrect-target trials.

In the CG task, subjects initiated a reach in less than 1,600 ms after the appearance of the DCs in >97% of trials. If they processed the sensory evidence in the DCs in the same rate in the MS task, they should be able to decide on its color during the initial DC observation period in virtually all MS trials. In contrast, the shortest RTs for the 100/0 DCs were 100–125 ms longer in the CG task than in the MS task. In different subjects and the pooled group data (Figs. 2, 5, and 6), a further ~75-ms delay for the shortest RTs for the 70/30 DCs, and still further delays for the 60/40 to 52/48 DCs. This effect was more pronounced in S5 (Figs. 2C and 5C), despite her longer RTs overall in both tasks. This indicated that, in many MS task trials, most subjects decided on the predominant color of the DCs during the initial observation period and were ready to choose the matching target as soon as they appeared. In contrast, uncertainty about the nature of the impending DC before it appeared in the CG task led to delays in the earliest responses, even to the 100/0 DCs, and further delays as the amount of conflicting evidence about the correct choice increased in the 70/30 to 52/48 DCs.

If the subjects committed to a decision about the DC color during the initial observation period of every trial for the MS task, their RTs should be identical for all DCs. Subject S3 came closest to this “ideal” performance (Fig. 5A). Nevertheless, S3 still showed a few trials with longer RTs for 55/45 and 52/48 DCs. This was more pronounced in all other subjects (Fig. 5B–D). Subject S1 was typical. Her RTs showed a progressively more extended trailing edge of longer RTs for increasingly more ambiguous DCs (Fig. 5B), that were still shorter overall than her responses in the CG task (Fig. 2B).

The RT distributions of error-choice trials also shifted to correspondingly shorter values in the MS task than in the CG task, but still remained systematically longer than for the corresponding successful trials (Fig. 5E). The error rates were only modestly better in the MS task for single subjects and the pooled group data (60/40 DCs: 0.0–3.0%; 55/45 DCs: 5.9–19.3%; 52/48 DCs: 24.7–45.1%) than in the CG task (60/40 DCs: 0.0–6.8%; 55/45 DCs: 13.5–17.6%; 52/48 DCs: 30.7–47.4%), despite the extended initial DC observation period in MS trials and the further extra time that the subjects took in some trials with the more ambiguous DCs before initiating a reach after the spatial cues appeared. Error rates in the MS task also tended to be higher in subjects who showed longer RTs to the more ambiguous DCs (Fig. 5A–C), similar to that seen in the CG task. Expressed differently, subjects with higher error rates tended to observe the DCs for longer periods of time in both the CG and MS task.

Success rates in the MS task were essentially perfect at all times for the 100/0, 70/30 and 60/40 DCs (Fig. 7C). Trials with the shortest RTs to the 55/45 and 52/48 DCs had a higher success rate in the MS task (Fig. 7C) than in the CG task (Fig. 7C) but then declined rapidly with time. When pooled across all DCs, the decline in overall success rate was nearly linear and approached 60% for the trials with the longest RTs (800–1,200 ms), with late fluctuations because of small trial

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The median response times (RT; ms) and error rates (% of total trials) for data collected during the performance of the first and sixth (last) data sets in the choose-and-go (CG) task. S1–S6, subjects 1–6.
counts at the trailing edge of the RT distributions (Fig. 7D). This is reminiscent of the behavior of the subjects in the CG task (Fig. 3D).

**Static vs. Dynamic DCs: CG and MS Tasks**

We used two formats of DCs in interleaved trials. In static DC trials, the subjects saw only a single DC matrix for the duration of the trial. In dynamic DC trials, the DC matrix changed every 50 ms, so that the spatial locations of the colored squares changed continuously while maintaining the same color bias in a given trial. The dynamic DCs caused a rapid flickering of the colored squares of the matrix, without a sense of visual motion.

In the CG task, the DC format had relatively little impact on the leading edge of short-RT trials in the RT distributions for all DCs for each subject and the pooled group data (Fig. 8). There was also no statistically significant difference in the RT distributions of static and dynamic DC trials for each DC color bias, for each subject and for the grouped data (Fig. 8; 2-tailed 2-sample KS test, $P > 0.01$). Nevertheless, in the cases in which the RT distributions were not clearly overlapping, there was a consistent trend for subjects to have shorter RTs for dynamic 70/30 (3/6 subjects), 60/40 (4/6 subjects) and 55/45 DCs (3/6 subjects), but longer RTs for dynamic 52/48 DCs (5/6 subjects). These DC-dependent differences were seen in both correct and error-choice trials (data not shown). While never reaching statistical significance, these trends suggest that the format of the DCs had a modest effect on the dynamics of the subjects’ decision process on a trial-to-trial basis.

The format of the DC stimuli had a stronger effect on the pooled group error rates, which were systematically lower for the dynamic 60/40, 55/45, and 52/48 DCs (0.6%, 12.7% and 32.4%, respectively) than the corresponding static DCs (5.5%, 18.8%, 46.3%). These same trends were shown by individual subjects, with lower error rates for dynamic than static 55/45 DCs in 5/6 subjects, and in all 6 subjects for 52/48 DCs.
The differences in responses to static and dynamic DC stimuli were even smaller in the MS task, but showed the same trends as in the CG task.

**Changes of Target Choice After Movement Onset**

In occasional trials, the subjects began to move toward one target, but then reversed their movement and went to the opposite target, even though the DC was turned off at the onset of the initial reach (c.f., Resulaj et al. 2009). These “changes of mind” were more frequent in the CG task (2.5%; 235/9,433 total trials) than the MS task (1.4%; 128/9,292 trials).

In the CG task, changes of direction were very rare for 100/0 and 70/30 DCs (1/1,152 trials and 4/1,153 trials, respectively) but were increasing frequent for 60/40, 55/45 and 52/48 DC (16/1,183 trials, 1.4%; 48/1,363 trials, 3.5%; 91/1,881 trials, 4.8% respectively) (Fig. 9A).

The subjects started in the wrong direction and switched to the correct direction in 179/235 direction-change trials (76.2%), whereas they started in the correct direction but then switched to the incorrect target in only 56/235 trials (23.8%). There were no incorrect direction changes for the 100/0, 70/30 and 60/40 DCs, 8 incorrect vs. 40 correct changes (16.7%) for the 55/45 DCs and 33 vs. 58 changes (36.3%) for the 52/48 DCs. These error rates for direction-change trials were comparable to the error rates in which no direction change occurred (e.g., 55/45 DC, 203/1,315 trials, 15.4%; 52/48 DCs, 696/1,790 trials, 38.9%), indicating that no net improvement in overall target-choice accuracy resulted from the process that led to the change in reach direction.

The durations of the initial movement segments before changing direction were similar whether the initial RT was short or long (Fig. 9B), or terminated at the correct or incorrect target. The durations of the initial segments overlapped extensively for each DC (Fig. 9B), but were shorter for the 60/40 DCs than the 55/45 and 52/48 DCs (P = 0.008 and P = 0.033, respectively, one-tailed t-test). The initial movement durations were not different for the 55/45 and 52/48 DC (P > 0.1).

The trends in the MS task were fundamentally similar. Direction-change trials were rare for 100/0 and 70/30 DC trials and increasingly frequent for 60/40 (11 trials), 55/45 (22 trials) and 52/48 (41 trials) DCs. All 11 direction-change trials were from the incorrect to the correct target for 60/40 DCs. The frequency of incorrect-to-correct direction-change trials decreased for the 55/45 (18/22, 87.8%) and 52/48 (27/41, 65.9%), while the correct-to-incorrect direction-change trials increased...

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**Fig. 7.** A: histograms of the RTs for correct choices (thick lines) and error choices (thin lines) for each DC in the MS task. B: cumulative histograms of the RTs for correct choices (thick lines) and error choices (thin lines) pooled across all DCs. C: success rate as a function of time for each DC. D: success rate as a function of time pooled across all DCs.

**Fig. 8.** Cumulative frequency plots of the RTs in the CG task for correct choices and error choices combined, for static (thick lines) and dynamic (thin lines) DCs. Solid thin lines: dynamic RT distributions that were similar to the static RT distributions for a given DC [2-tailed 2-sample Kolmogorov-Smirnov (KS) test, P > 0.01].
correspondingly (4/22, 18.2%, and 14/41, 34.1%, respectively).

Model Simulations of the CG Task Data

Drift diffusion model-fixed decision bound. We used a simulation of a stochastic bounded diffusion process with fixed decision bounds (Ratcliff 1978; Ratcliff and Smith 2004; Resulaj et al. 2009) and an iterative optimization procedure to find a single set of model parameters that could best replicate the observed choice behavior of the subjects in the CG task. The fixed-bound diffusion model accounted for the central tendencies of the performance of the subjects quite well, including the success rates ($R^2 = 0.97–0.99$) and mean RTs ($R^2 = 0.97–0.99$) of the combined correct- and error-choice trials for each DC for single subjects and the pooled group data (Fig. 10A). The most systematic shortcoming was an overestimation of the rate of correct choices by 3–12% for the 52/48 DC. This was seen in four of the six subjects and in the pooled data set (Fig. 10A).

The simulation also provided the expected probability of correct and error choices as a function of time for each DC. When plotted as cumulative probability curves, the predicted probability density functions provided a reasonable fit to the observed RT distributions for each DC, but several discrepancies were evident (Fig. 11A). In particular, the observed RT distributions of correct choices for the 55/45 and 52/48 DCs were more symmetrical than the predicted distributions, which had both more shorter-latency and longer-latency correct-choice RTs than were observed (Figs. 11A and 12A). The simulation also incorrectly predicted trials in which no decision had been reached 300 ms after the longest observed RT for the group data for the 55/45 (1.9% of trials) and 52/48 DCs (3.9%), as well as for every subject (55/45 DC: 0.6%–5.9%; 52/48 DC: 1.9%–9.7%) except S2. The fixed-bound model also incorrectly predicted that error-choice RTs were similar to correct-choice RTs (Fig. 11A), which resulted in a quantile plot profile (Fig. 12A, dashed lines) that was more symmetrical than the quantile plot for observed RTs (Figs. 2E and 12A, solid lines).

To further assess how well the simulation predicted the subjects’ behavior, we compared the observed and predicted cumulative RT distributions for each DC (2-tailed 1-sample KS test, criterion threshold $P = 0.01$). The fixed-bound model successfully predicted the pooled correct-choice RTs for 70/30 and 60/40 DCs, but not for the 55/45 and 52/48 DCs nor for the 100/0 DCs, for which the model predicted significantly longer RTs than were observed (Fig. 11A). Not surprisingly, it did not predict the error-choice RT distributions (Fig. 11A).

We next compared the observed and predicted RT distributions for combined correct and error responses for each of the 10 predominantly yellow or blue DCs, for each subject and for

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**Fig. 9.** A: Mean probability of all changes in direction of the arm movement as a function of the DC color bias, averaged across all subjects (triangles), as well as of changes in direction from the incorrect to the correct target (circles) and changes of direction from the correct to the incorrect target (squares). Error bars: 1 SD. B: duration of the initial movement segment before the change of direction as a function of the RT for the start of the initial movement segment. Solid lines: regression functions for incorrect to correct direction changes. Dashed lines: correct to incorrect direction changes.

**Fig. 10.** A: regression fits of the fixed-bound model predictions for the mean success rates and mean RTs for each DC. B: regression fits of the collapsing-bound model predictions for the mean success rates and mean RTs for each DC.
the pooled group data. The fixed-bound simulation successfully predicted the RT distributions for only 35/70 (50%) of the DC data sets (2-tailed 1-sample KS test, $P < 0.01$; Table 2). Strikingly, it successfully predicted the RT distributions far more frequently for the intermediate-difficulty 70/30 to 55/45 DCs than for either the easiest (100/0) DC or the most ambiguous (52/48) DC (Table 2). The same trend was seen for the RT distributions of only the correct-choice trials (data not shown). This suggests that the failure of the model to predict many of the RT distributions for different DCs was not due only to random variability in the data or to its tendency to predict similar RTs for correct- and error-choice trials. Instead,

**Fig. 11.** A: comparison of the cumulative frequency plots of the observed (solid thick lines) and predicted (solid and dashed thin lines) RT distributions for correct choices (left) and error choices (right) for the fixed-bound model, fit to the pooled group data (same data as in Fig 2, D and E). Thin solid line: nonsignificant difference between observed and predicted RT distributions (KS test). Thin dotted line: significant difference between observed and predicted RT distributions (KS test). B: comparison of the cumulative frequency plots of the observed (thick lines) and predicted (thin solid and dashed lines) RT distributions for correct choices and error choices for the collapsing-bound model. Same format as in A. Thick black dot-dashed line: time course of the best-fit collapsing bound.

**Fig. 12.** Quantile plots of the observed RT distributions (solid lines) and predicted distributions (dashed lines) for the fixed-bound (A and C) and collapsing-bound (B and D) diffusion models, for the best-fit parameters obtained for all 5 DCs simultaneously (A and B) and when optimized for each DC separately (C and D). Each circle indicates the predicted quantile RTs for correct (right half of each graph) and error choices (left half of each graph). The color of each circle indicates the DC color ratio (c.f., Figs. 2–7). The values on the X-axis indicate the observed probabilities of correct responses to the 5 DCs (right half of the graph) and the corresponding observed probabilities of error choices to the same DCs (left half of the graph).
For both models, the main difference was in data separately for the pooled group data and for each subject static and dynamic DCs. The results were similar for both 12). Nevertheless, the collapsing-bound model still tended to predicted error RTs were longer than correct RTs (Figs. 11 and 12). Third, pre-
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The number of predicted RT distributions that were statistically similar to the observed RT distributions [Kolmogorov-Smirnov (KS) test] for each of the predominantly yellow and predominantly blue decision cues (DCs) separately for the group data and for the six subjects (14 data sets for each DC).

Drift diffusion model-collapsing decision bound. A number of behavioral, neurophysiological and modeling studies have suggested that subjects’ choice behavior not only may be driven by accumulating sensory evidence across time, but is also influenced by other time-dependent processes. One example is a time-dependent increase in a centrally generated “urgency” signal that helps to drive the accumulating evidence toward the decision bound, or nearly equivalently, by a time-dependent decrease (“collapse”) in the decision threshold, especially when presented with weak sensory evidence or in conditions in which the evidence quality and reliability are variable from trial to trial (Churchland et al. 2008; Cisek et al. 2009; Ditterich 2006a; Drugowitsch et al. 2012; Janssen and Shadlen 2005; Shadlen and Kiani 2013; Thura et al. 2012). To assess how well the choice behavior of our subjects might be captured by a decision model that permitted time-dependent changes in their decision process, we tested a version of the drift-diffusion model that implemented a decision bound that began to collapse as a quadratic function of elapsed time in the trial starting at a particular delay after the appearance of the DC.

The addition of the collapsing bound had little impact on the ability to predict the success rates ($R^2 = 0.97–0.99$) and mean RTs ($R^2 = 0.97–0.99$) of all trials for different DCs for each subject and the pooled group data (Fig. 10B). However, there was a significant improvement in the ability of the model to predict the observed RT distributions for each DC (Figs. 11B and 12B). Most (56/70; 80%) of the predicted RT distributions were not significantly different from the observed distributions (2-tailed 1-sample KS test, $P > 0.01$; Table 2). The improvement in fit resulted primarily from three changes in the shape of the predicted distributions. First, the collapsing bound truncated the trailing queue of predicted long RTs for correct trials, especially for the 55/45 and 52/48 DCs (Figs. 11B and 12B) and did not predict prolonged non-decision trials. Second, there were fewer of short RTs at the leading edge of the predicted RT distribution was reduced (Figs. 11B and 12B). Third, predicted error RTs were longer than correct RTs (Figs. 11B and 12B). Nevertheless, the collapsing-bound model still tended to predict the RT distributions better for the intermediate DCs than the 100/0 and 52/48 DCs (Table 2).

These trends were not due to pooling of data from trials with static and dynamic DCs. The results were similar for both models when they were fitted to the static and dynamic DC data separately for the pooled group data and for each subject (data not shown). For both models, the main difference was in the drift rate gain $k$, which was modestly higher for the dynamic DCs.

Model recovery and process modeling of the fixed-bound and collapsing-bound simulations. Both the fixed- and collapsing-bound models reliably predicted the mean success rates and mean RTs of each subject for each DC (Fig. 10). The collapsing-bound model predicted the shapes and timing of the correct- and error-choice RT distributions better than the fixed-bound model (Figs. 11 and 12, Table 2). However, there were details of the subjects’ performance that neither model could predict successfully. In particular, they yielded poorer fits to the RT distributions for the easiest and hardest DCs than for the intermediate DCs (Table 2). If this was due to random variability in the data, it would be reasonable to expect that the prediction failures should be uniformly distributed across different DCs, but that was not the case. This nonuniform pattern of prediction failures might reflect some inherent limitation in the ability of the optimization procedure to find the appropriate parameters for the observed results for such a broad range of stimuli, or to anomalies in some of the RT distributions that cannot be explained by the models, or to limitations in the models themselves. Moreover, the optimization procedure sought a single set of parameters for both models to fit the RT distributions across all DCs. Implicit in this procedure is the assumption that the behavior of the subjects was determined by a decision process whose temporal dynamics were stable across the entire range of stimulus quality. This assumption might not have been completely valid in this study. We did a series of tests to examine each of these alternatives.

Table 2. Drift-diffusion model best fits, two-way one-sample KS test, 1%

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Table 3. Best-fit statistics: FB and CB solutions for all DCs

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<th>S2</th>
<th>S3</th>
<th>S4</th>
<th>S5</th>
<th>S6</th>
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</thead>
<tbody>
<tr>
<td>LogL</td>
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<td>7,408.843</td>
<td>6,605.237</td>
<td>7,518.567</td>
<td>7,793.317</td>
<td>8,417.097</td>
</tr>
<tr>
<td></td>
<td>CB 45,877.159</td>
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<tr>
<td>SSDEV</td>
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<td>2.496</td>
<td>33.671</td>
<td>27.074</td>
<td>38.627</td>
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<tr>
<td></td>
<td>CB 2.961</td>
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<td>2.128</td>
<td>9.666</td>
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</tr>
<tr>
<td>χ²</td>
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<td>73.132</td>
<td>276.712</td>
<td>370.142</td>
<td>383.826</td>
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<td></td>
<td>CB 234.947</td>
<td>63.813</td>
<td>69.072</td>
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<td>13,222.475</td>
<td>15,049.134</td>
<td>15,598.634</td>
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<tr>
<td></td>
<td>CB 91,770.318</td>
<td>14,937.484</td>
<td>13,236.845</td>
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<td>AICc</td>
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<td>15,009.763</td>
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<td>14,841.766</td>
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Best-fit statistics are the fixed-bound (FB) and collapsing-bound (CB) solutions when optimized for all DCs simultaneously. LogL, maximum log likelihood of the best-fit parameters to the data set; SSDEV, summed squared deviations between the observed and predicted cumulative RT distributions; χ², summed χ² of the differences between observed and predicted RT distribution quantiles; AIC, Akaike information criterion; AICc, corrected AIC; BIC, Bayesian information criterion.
This suggests that the systematic changes in rate or start biases (data not shown) across DCs for all subjects, nor in the drift trend in the decision-bound values (Fig. 13). Longer mean RTs for more difficult DCs. There was no obvious increase in the best-fit drift rate ($k$) showed the fastest RTs overall. In parallel, there was an increase in the best-fit drift rate ($k$) and $\tau_{\text{nd}}$ for all subjects. The most consistent trend for the fixed-bound model was a progressive increase in the mean ($\tau_{\text{nd}}$) and variance ($\tau_{\text{ndsd}}$) of the non-decision time for increasingly difficult DCs (Fig. 13A). This was seen in all subjects except S2, who showed the fastest RTs overall. In parallel, there was an increase in the best-fit drift rate ($k$) for increasingly difficult DCs in all subjects, including S2, even though she had the shortest RTs of all subjects for the 55/54 and 52/48 DCs. This showed that the parameter changes were not just an artifact of longer mean RTs for more difficult DCs. There was no obvious trend in the decision-bound values (Fig. 13A), nor in the drift rate or start biases (data not shown) across DCs for all subjects. This suggests that the systematic changes in $\tau_{\text{nd}}$, $\tau_{\text{ndsd}}$ and $k$ captured specific DC-dependent changes in the observed RT distributions and were not a trivial artifact of the single-DC fit process.

Similar DC-dependent trends in $k$, $\tau_{\text{nd}}$ and $\tau_{\text{ndsd}}$ were also seen for the collapsing-bound model, although they were not quite as consistent and pronounced as for the fixed-bound model (Fig. 13B). Instead, the collapsing-bound model traded off some of the effects of those parameters on RT distributions by allowing the collapse rate $B_2$ to increase with increasingly ambiguous DCs, while $B_{\text{det}}$, the time at which the bound began to collapse, did not show systematic corresponding changes. Again, there were no strong tendencies in the initial bound value $B$ or the two bias terms. The lack of DC-dependent changes of the initial bound values seems reasonable since the subjects would not know which DC was about to appear at the start of each trial, so there was no prior expectation that could influence the initial bound value.

To assess whether these changes in parameter values were meaningful, we generated 100 bootstrapped RT distributions from the observed RT distributions for the 100/0 and 52/48 DCs for each subject and the pooled group data. We then determined the best-fit parameters for the fixed- and collapsing-bound models to the 100 bootstrapped RT distributions for the two DC separately and calculated the mean and confidence interval of the distributions of values for each parameter. For the fixed-bound model, differences in $k$, $\tau_{\text{nd}}$ and $\tau_{\text{ndsd}}$ were highly significant, with the mean values of each parameter for the 100/0 and 52/48 DCs well outside of the confidence interval about the mean value for the other DC, and with little or no overlap in the distributions of the bootstrapped parameter estimates. The sole exception was the bootstrapped $\tau_{\text{nd}}$ values for S2, which were extensively overlapping. Identical results were obtained for the bootstrapped $k$, $\tau_{\text{nd}}$, $\tau_{\text{ndsd}}$ and $B_2$ parameter estimates for the collapsing-bound model. This analysis suggested that the DC-dependent changes in parameter estimates were reliable.

Finally, to verify that these trends were not a trivial consequence of fitting individual RT distributions with different median values, dispersions and skews, we repeated the single-DC fit process on the 100 simulated RT distributions for each subject. The resulting best-fit parameter values, especially

<table>
<thead>
<tr>
<th>Group</th>
<th>S1</th>
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<td>SSDEV</td>
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<td>CB 0.740</td>
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<td>0.854</td>
<td>1.467</td>
<td>1.672</td>
<td>0.924</td>
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<tr>
<td>$\chi^2$</td>
<td>FB 127.281</td>
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<td></td>
<td>CB 98.004</td>
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<td>13,445.846</td>
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<td>16,619.225</td>
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Best-fit statistics are the FB and CB solutions when optimized for each DC individually. Same format as Table 3.
Fig. 13. Best-fit parameter values obtained from optimization of the fixed-bound (A) and collapsing-bound (B) diffusion model for the observed RT distributions for each DC separately, as well as for the collapsing bound model on one randomly selected set of simulated RT distributions from each subject (C).
for $k$, $t_{nd}$, and $t_{ndst}$, remained very consistent across DCs (Fig. 13C), without any of the trends seen from the real data. This confirmed that the optimization process will find similar parameter values for each DC when the associated RT distributions were generated by a drift-diffusion process with invariant dynamics. In contrast, the process-modeling analysis suggests that the improvements in fits and changes in parameters found by fitting the individual observed RT distributions captured real differences in the properties of the RT distributions generated by each subject in response to the range of DCs used in this particular task.

DISCUSSION

Multicolored DCs

The objective of this study was to develop a novel task paradigm to examine the processes underlying the selection of targets for reaching movements on the basis of ambiguous and conflicting sensory evidence whose critical task-relevant physical property has no inherent relationship to any attribute of arm movements per se, such as its direction. To that end, we developed a set of checkerboard stimuli with different numbers of squares of two task-relevant colors against a background of task-irrelevant red squares. However, this was not a study of color perception per se. The subjects had to ignore the task-irrelevant red color that filled the largest number of squares in the standard DCs and had to estimate which of the task-relevant yellow and blue colors filled more of the remaining squares. Each individual square was easily detectable, and its color was readily discriminable. Furthermore, most of the DCs contained yellow and blue squares, supporting both target choices. Critically, the decision was made more difficult both by reducing the total amount of evidence supporting the correct target and by simultaneously adding increasing amounts of sensory evidence supporting the alternate target. The subjects had to avoid making impulsive reaching movements to the target whose color filled fewer squares in the DC simply because they were present, not unlike the analogies in visual search tasks (Purcell et al. 2012; Sato et al. 2001; Sato and Schall 2003; Song et al. 2008; Song and McPeek 2010). This is in contrast to most RDK stimuli, which contain only one direction of coherent motion, and subjects have to detect the presence and direction of that coherent motion against a background of random motion.

As a result, there may be differences in how the sensory evidence was encoded and processed from these DCs compared with many previous studies in which the decision was based on the subjects’ estimate of the nature of a stimulus along a continuum of one physical property, such as brightness or contrast, or on their estimate of the net coherent motion signal in RDK stimuli. Nevertheless, one can assume that the subjects estimated the amount of evidence for the two target choices by processing output signals from two neural populations that are preferentially activated by the presence of squares of one or the other of the task-relevant colors in the DCs. The relative level of activity of the two color-coding neural populations presumably varied with the numbers of squares of the two colors and thus with the area of each DC occupied by each color. The subjects could have determined the color bias of the static DCs simply by counting the number of squares of one of the task-relevant colors. However, it is highly unlikely that they could have counted all the squares of one color of the 60/40 to 52/48 DCs within the 400- to 1,600-ms duration of the large majority of RTs observed for those stimuli. Moreover, this would be impossible for the dynamic DCs, which changed every 50 ms.

Choice Behavior of Subjects

Despite the unique features of the DCs used in the CG task, the performance of the subjects displayed many of the psychophysical trends seen in previous action-selection studies, in particular those using RDK stimuli to signal the target for eye saccades (Ditterich 2006, 2010; Mazurek et al. 2003; Palmer et al. 2005; Roitman and Shadlen 2002; Shadlen et al. 1996) or reaching movements (Resulaj et al. 2009; Thura et al. 2012). RTs and error rates increased as stimuli became more ambiguous, and error RTs tended to be longer than correct responses for corresponding DCs.

When questioned after completing their participation in both tasks, several of the subjects commented that, while they were confident of their target choices for the easy DCs (100/0, 70/30), they were increasingly uncertain of the correctness of their choices for the most ambiguous DCs. Some even expressed surprise that their success rates were as high as they were for the more ambiguous DCs, despite receiving knowledge of results after every trial. While anecdotal, these reports indicated that the subjects often committed to a target choice for the more conflicting DCs, even though they were not very confident that they had made the correct choice.

Furthermore, subjects occasionally reversed their initial direction of arm movement and went to the opposite target (Resulaj et al. 2009). These “changes of mind” occurred almost exclusively in trials with the most ambiguous DCs and most often corrected an initial error in target choice. These direction reversals suggest that the subjects continued to process sensory evidence about their action choice after they had chosen a target and started to reach toward it (Georgopoulos et al. 1983; Resulaj et al. 2009). This could have been based on sensory evidence that had already entered the evidence-processing pipeline but had not been fully processed before the subjects started to reach (Georgopoulos et al. 1983; Resulaj et al. 2009), or from continued introspective consideration of a short-term memory of the evidence observed before initiating the reach. These vacillations in the overt motor response are a potential physical expression of the uncertainty of the subjects about their motor decision based on weak sensory evidence. It indicates that their confidence in their initial choice was low enough in some trials that the subjects reversed their reach direction and reached to the other target.

One somewhat surprising finding was that the subjects’ performance was only modestly better in response to dynamic vs. static DCs. Error rates were lower for dynamic DCs, but there were no systematic differences in RTs between dynamic and static DCs. We had expected that a continual stream of new sensory evidence about the color bias of the dynamic DCs would allow the subjects to extract a better estimate of the color bias of the stimuli more quickly and make the subjects less susceptible to the vagaries of the evidence in any one DC matrix, such as its unique uneven distribution (“clumpiness”) of the task-relevant
squares. However, static DCs also provide a steady stream of sensory input during its presentation, which can vary from moment to moment, not only because of the stochastic nature of neural discharge, but also if subjects look at different parts of the DC while deciding on its color bias. Further study is needed about how subjects extract sensory evidence about the color bias of static vs. dynamic DCs.

Finally, the subjects showed some of the expected gains in performance offered by the initial observation period of the DCs in the MS task. RTs after the appearance of spatial cues in the MS task were significantly shorter than after the appearance of the DCs in the CG task, indicating that the subjects often committed to a decision about the predominant color of the DC during the initial DC observation period. Notably, RTs were substantially shorter even for the 100/0 DCs. The extra duration of the RTs to 100/0 DCs in the MS task may have resulted from the uncertainty of the subjects at the beginning of each trial about the quality of the evidence that would be provided by the impending DC. The appearance of a 100/0 DC was a relatively rare event, only 2 of 14 DCs that the subjects encountered. They could not prepare to respond rapidly to the presence of either of the two task-relevant colors in the DCs since most DCs contained differing amounts of contradictory evidence supporting both target choices. This uncertainty about the impending evidence may have resulted in an extra delay in the processing of even the 100/0 DCs and subsequent commitment to a target choice in the CG task. This proposed effect of stimulus uncertainty in the CG task is reminiscent of an initial sensory gating mechanism that was recently proposed to precede the process of committing to a target choice to minimize the incidence of impulsive responses to distractors in visual search tasks (Purcell et al. 2012).

Success rates were modestly higher overall in the MS task, but especially for the trials with the shortest RTs in response to the more ambiguous DCs (Fig. 7C); this was not as prominent in the CG task (Fig. 3C). This indicated that the subjects benefited from the longer imposed initial DC observation times in the MS task to improve their estimate of the color bias of the DCs. Nevertheless, even after the extended initial observation period, most subjects behaved as if they often still had not made a decision about the color bias of the more ambiguous DCs and continued to deliberate after the spatial cues appeared, as evidenced by trials with longer RTs than those for the 100/0 DCs. This variable degree of commitment about DC color bias at the end of the initial DC observation period had only a modest impact on success rates in those trials with extended RTs (Fig. 6, C and D), at the cost of significantly longer evidence accumulation (Drugowitsch et al. 2012). Alternatively, subjects may have delayed or stopped evidence accumulation before making a decision during the initial DC observation time in trials with more ambiguous DCs, and only reengaged in that process after the appearance of the spatial cues, when the task required them to make a choice. S5, in particular, may have adopted this strategy. These differences in choice behavior between the CG and MS tasks emphasize the degree to which task structure can have a strong effect on how and when subjects use sensory input to make task-related decisions.

Model Simulations

The RTs in this study were longer than often reported in similar studies, in part because we did not explicitly instruct subjects to respond as quickly as possible, but likely also in part because of the challenging nature of the sensory evidence provided by the DCs. Nevertheless, they fell within the range that is considered amenable to analysis by computational models of simple sensorimotor decisions (Niwa and Ditterich 2008; Ratcliff and Smith 2004, 2010). Simulations using simple fixed-bound and collapsing-bound drift-diffusion models indicated that the subjects’ decision-making process shared many of the same computational properties as those found in prior studies using a wide range of stimuli and tasks. The improved prediction of the subjects’ performance by the collapsing-bound model, including longer error RTs, suggested the possible existence of either a time-dependent decline in the height of the decision bound or, nearly equivalently, a time-increasing urgency signal that helped to truncate the decision process as time progressed in the trial when subjects were confronted with weak evidence (Churchland et al. 2008; Cisek et al. 2009; Ditterich 2006a; Janssen and Shadlen 2005; Shadlen and Kiani 2013; Thura et al. 2012). However, fixed-bound models that allow for trial-to-trial variability in the drift rate for a given stimulus or in the starting point of evidence accumulation can also predict long error RTs in different task conditions (Brown and Heathcote 2008; Heathcote and Love 2012; Ratcliff and McKoon 2008; Ratcliff and Smith 2004). Implementing those extra free parameters in the models would very likely lead to improved fits to our data. However, we reiterate that the objective of this initial study was to determine whether the performance of subjects in the CG task with ambiguous and conflicting DCs resembled those in many other simple two-choice decision-making studies and whether it would be suitable for subsequent neurophysiological studies. Whether their performance is best explained by a fixed or collapsing bound, urgency gating, perfect integration, leaky integration, drift diffusion, linear ballistic accumulation or many other computational models will require further studies using task variants that specifically test differing predictions of these different models.

One important finding was that the ability of both models to predict the RT distributions of subjects was systematically better for intermediate DCs than for the least and most ambiguous DCs, when the models were fit to the data for all DCs simultaneously. This systematic pattern suggested that prediction failures were not due to random variability in subject performance that occasionally violated assumptions of the diffusion model (Ratcliff 2002), since such failures should have occurred with equal probability across all DCs. Valid computational models of decision-making should explain subjects’ choice performance not just in the midrange of task conditions, but also at the extremes of the easiest and hardest task conditions (Ratcliff 2014). A process-modeling analysis (Heathcote and Love 2012; Leite and Ratcliff 2010; Mulder and van Maanen 2013; Ratcliff 2014; Ratcliff and Smith 2010; van Maanen et al. 2012) showed that both the simple fixed-bound and the collapsing-bound models used here could predict the entire range of observed RT distributions better if they were fit to the RT distributions for each DC separately. More importantly, the improved predictions involved systematic DC-
dependent changes in some but not all of the model parameters, not by random changes in the parameter values between DCs to account for random idiosyncrasies in each distribution. These analyses could be criticized as unconstrained curve-fitting. However, model recovery tests with simulated data generated by the fixed and collapsing-bound models with a single set of parameters showed that none of these trends would have arisen if the subjects’ behavior had been governed by a decision process whose dynamics were fixed and independent of stimulus quality and reliability. This suggested that the subjects’ choice behavior was influenced by factors that were dependent on DC evidence quality and thus could vary from trial to trial.

Process modeling using both the fixed-bound and collapsing-bound models suggested that the duration and variability of the non-decision time increased as DC ambiguity increased. This is consistent with other recent process-modeling studies that reported evidence of trial-to-trial changes in non-decision time and other model parameters in tasks in which stimulus quality was variable and uncertain (Heathcote and Love 2012; Leite and Ratcliff 2010; Mulder and van Maanen 2013; Ratcliff 2014; Ratcliff and Smith 2010; Teichert et al. 2014; van Maanen et al. 2012). Part of the non-decision time is presumed to be the time needed to extract from the sensory input signal the task-relevant evidence about the alternative choices that is then accumulated to make a decision. This could be fairly rapid and relatively constant for some stimuli and is usually assumed to be relatively constant across stimulus quality (Carpenter et al. 2009; Leite and Ratcliff 2010; Mazurek et al. 2003; Ratcliff and Smith 2010). However, while the color of each component square in the DCs is readily discriminable, the critical evidence is which color fills more squares, and this may take more time to estimate as the color bias gets smaller by reducing the amount of evidence supporting the correct choice and adding more evidence for the alternate choice in the DC. It is striking that the presence of just a small amount of contradictory evidence in the 70/30 DCs produced a sizable delay in the times of the earliest RTs compared with the 100/0 DCs in the CG task (Fig. 6). However, many decision models would consider estimation of the color bias part of the evidence accumulation phase, not the sensory-encoding stage. Nevertheless, when allowed to fit the RT data for each DC separately, the models could better predict the data for the more ambiguous or conflicting DCs by prolonging the duration and variability of the non-decision time, as well as that of the decision time itself.

The process-modeling analysis also suggested DC-dependent changes in the gain of the evidence integration process (both models) and in the rate of collapse of the decision bound (collapsing-bound model). These changes suggest that, when the DC is relatively unambiguous, subjects began to commit to a decision quickly and could keep the gain of the accumulation process relatively low because the sensory evidence was strong. In contrast, when the DC is relatively ambiguous, the subjects behaved as if they weighted the weaker evidence more heavily and reduced the decision bound more quickly as time progressed to hasten a decision in the face of weak evidence. Dynamic within-trial changes in both drift rate gain and decision bound height have also been invoked to explain the computational processes underlying changes of reach direction in trials with low-coherence RDK stimuli (Resulaj et al. 2009).

We do not imply from this process-modeling analysis that the subjects’ decisions were made by a computational mechanism with 30–40 free parameters indexed to DC ambiguity. We only infer from these findings that the subjects’ choice behavior was not just driven by the available evidence, but may also be susceptible to central processes related to the level of conflicting evidence in the DCs and to the passage of time. These influences may be more prevalent in the arm movement system than the oculomotor system because of its longer RTs, much greater metabolic costs and the far greater risks inherent in physical interaction of the arm and hand with the environment, compared with saccadic rotations of the eyes in their protective orbits to sample sensory input from different parts of the visual scene.

Limitations of Interpretation of the Process Modeling Findings

These interpretations assume that the subjects’ decision process was captured successfully by the different parameters of the diffusion models. However, other processes may also come into play that cannot be explained readily by the models. For instance, because each local piece of evidence (the colored squares) in the DC matrix is unambiguous, the earliest evidence accumulation period for the more ambiguous DCs may be a particularly noisy and unreliable estimate of the true color bias of the entire DC matrix, if the accumulation process begins shortly after each DC appears. In contrast, standard drift diffusion models assume that variability of the estimate of net evidence is constant across time. Alternatively, as the DCs become more ambiguous, the decision process may become more susceptible to abrupt fluctuations in the value of the accumulating decision variable due to top-down cognitive reinterpretation of the sensory evidence (“mental vacillating”) that would tend to prolong the decision process. The changes of reach direction are an overt physical expression of that vacillation, which might also occur during evidence accumulation period without crossing one or the other decision bounds for the two reach options. Evidence of covert subthreshold mental vacillations has been reported in neurophysiological studies (Bollimunta et al. 2012; Kiani et al. 2014). The models can only explain such events on the basis of the parameters available to them, and so might erroneously attribute any tendency of these mental vacillations to prolong RTs to an increase in the duration and variability of the non-decision time and changes in other parameters, rather than to transient fluctuations in the evidence accumulation process itself. Such influences could be accommodated within the drift-diffusion model, at the cost of increased complexity of the model (e.g., Resulaj et al. 2009).

Alternate Hypotheses for Choice Behavior in the CG Task

As just noted, the earliest evidence accumulation period might be particularly noisy for the most conflicting DCs because of their unique nature. For that and other reasons, it might be advantageous for the subjects to begin to formulate an initial belief about the color bias of the DCs before beginning to accumulate that evidence in favor of one or the other of the two targets. This would presumably take longer for the more ambiguous DCs. This is consistent with other findings that the initial evidence extraction stage may be longer and more variable before the evidence accumulation process can begin.
when it requires an analysis of more complex global features of a sensory input, such as the presence of a target among multiple distractors (Purcell et al. 2012; Sato et al. 2001; Sato and Schall 2003), or the identity of letters masked by noise (Leite and Ratcliff 2010; Ratcliff and Smith 2010), or may be prolonged to increase decision accuracy (Mulder and van Maanen 2013; Teichert et al. 2014).

This suggests a model for this task with two sequential stages: an initial variable-duration sensory coding stage to begin to extract an estimate of the color bias of the DCs, followed by a conversion of that evidence into a decision about action. Neural correlates of sensory and motor decision stages have been identified for the arm motor system when they are linked by arbitrary sensory-motor mapping rules (Muhammad et al. 2006; Romo et al. 2004; Romo and de Lafuente 2013) and have even been identified in lateral intraparietal when the direction of RDK motion direction and saccade direction are likewise dissociated by an arbitrary stimulus-response association rule (Bennur and Gold 2011).

This also raises the possibility that, during the initial stimulus processing stage, subjects began to formulate a belief about the reliability of their estimate of the color bias of the DCs in the presence of variable amounts of contradictory “distractor” evidence and began to adjust the decision process on the basis of their estimate of sensory quality and reliability, knowledge of likely outcomes based on prior experience with similar stimuli and a comparison of the benefits and the costs of continued evidence acquisition vs. immediate action (Churchland et al. 2008; Cisek 2009; Denève et al. 2012; Ditterich 2006a,b, 2010; Drugowitsch et al. 2012; Hanks et al. 2011; Huang and Rao 2013; Kiani and Shadlen 2009; Shadlen and Kiani 2013; Zylberberg et al. 2012). Subjects did report anecdotally that their confidence in their decisions was lower with more ambiguous DCs. This was further supported by the changes in reach direction in trials with more ambiguous DCs, and by increasingly frequent delays in initiating a movement to a target, even after the extended initial DC observation period in the MS task as the DC ambiguity increased.

A related hypothesis is that the longer non-decision time values in trials with more ambiguous DCs may reflect the operation of an initial gating mechanism that momentarily delays evidence accumulation toward a target choice to permit more time to extract a reliable signal about the color bias from the conflicting evidence in the DCs, to avoid integration of noisy and misleading evidence leading to impulsive movements to the target supported by the contradictory “distractor” evidence (Purcell et al. 2012; Ratcliff and Smith 2010; van Maanen et al. 2012). This gating process may be particularly prominent with these multicolored DCs, since most of them contain evidence for both competing action options, unlike RDK stimuli that usually contain only one direction of coherent motion.

Both of these hypotheses predict that the evidence accumulation stage may be progressively delayed for DCs with greater levels of conflicting evidence for the two choices, until the subjects have accumulated enough evidence in the initial signal encoding and extraction stage to establish an initial estimate of the color bias of the DCs.

Yet another hypothesis is suggested by the finding of Cisek and Kalaska (2005) that the presentation of the two spatial cues simultaneously activates two populations of dorsal premotor cortex neurons that prefer the two potential reach directions, even though the net evidence favoring either target during the spatial cue epoch of the trials was zero. The appearance of DCs with increasing amounts of conflicting evidence supporting both choices may lead to a further transient increase in the activity of both populations that would take progressively longer to resolve as further evidence about the color bias of the DC is sampled. Because drift diffusion models assume that the evidence accumulation process is driven only by the net evidence from a common starting point, they cannot account for the effects of a transient simultaneous activation of the accumulators for both alternatives by the conflicting evidence. It may only be able to account for the effects of the transient activation by including it in the non-decision time parameters.

This last hypothesis is consistent with reach target selection by a biased competition mechanism between representations of the two alternate choices (Cisek 2006, 2007; Cisek and Kalaska 2010). It is also reminiscent of the neural mechanisms underlying saccade and reach target selection in visual search tasks (Kim and Basso 2010; Purcell et al. 2012; Song and McPeek 2010). Ultimately, neural recordings will be needed to provide more definitive evidence for the neural mechanisms leading to reach target selection in the CG task.

**Total Evidence, Net Evidence, or Evidence Ratio?**

Many two-choice decision-making models assume that subjects accumulate a decision variable proportional to the net difference in evidence supporting the two alternative choices. Our model simulations likewise accumulated signals proportional to the color bias (net evidence) in each DC. However, the evidence provided by each DC could be quantified by the total evidence for each choice, the net evidence for the correct choice or the relative ratio of evidence. These three factors are all confounded in the standard DCs used in this study, but the design of the DCs permits independent manipulation of each factor. For instance, along with the standard DC series, we also presented the subjects with DCs with 100/82 and 60/49 yellow/blue or blue/yellow squares, with a corresponding reduction in the number of task-irrelevant red squares. These special DCs presented the same total evidence for the correct choice as the 100/0 and 60/40 DCs, the same color ratio as the 55/45 DCs, and color biases (18 and 11, respectively) that fell between the 60/40 and 55/45 DCs. The RT distributions and success rates of all six subjects for these special DCs fell between the 60/40 and 55/45 DCs. The RT distributions and success rates of all six subjects for these special DCs fell between the responses to the 60/40 and 55/45 DCs. Thus their performance was driven more by the net evidence or relative evidence ratio than by the total evidence for the correct choice provided by the DC. However, more extensive tests with a greater range of DCs will be required to verify and expand on these preliminary findings (Liston and Stone 2013).

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Author contributions: E.C. and J.F.K. conception and design of research; E.C. performed experiments; E.C. and J.F.K. analyzed data; E.C. and J.F.K. interpreted results of experiments; E.C. and J.F.K. drafted manuscript; E.C. and J.F.K. edited and revised manuscript; E.C. and J.F.K. approved final version of manuscript.

REFERENCES

Addou T, Krouchev N, Kalaska JF. Colored context cues can facilitate the ability to learn and to switch between multiple dynamical force fields. J Neurophysiol 103: 163–183, 2011.


Ditterich J. A comparison between mechanisms of multi-alternative perceptual decision making: ability to explain human behavior, predictions for neurophysiology, and relationship with decision theory. Front Neurosci 4: 184, 2010.


