

## Preparation time determines response selection when acting under conflict

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We must often select between distinct responses to the same stimulus that may have been learned at different times or in different contexts (e.g. the Simon and Stroop tasks; Fig. 1A). Classical accounts of how the brain arbitrates between competing responses assume that responses are simultaneously prepared in a race to reach a threshold, at which point the winning response is initiated. In order for slower, deliberate responses to be expressed, preparation of faster, prepotent responses must be inhibited to permit slower processes to reach threshold (van den Wildenberg et al., 2010). Failure to inhibit faster responses accounts for the fast errors typically seen in such paradigms (Figure 1A,B).

An alternative view is suggested by studies of response preparation in simple, visually-guided reaching experiments (Fig. 1C) showing that, even in simple scenarios, movement initiation does not appear to be triggered by preparation reaching completion, but rather seems to be governed by a distinct process that is independent of preparation (Haith et al., 2016). In tasks where multiple responses are possible, the motor system may initially always prepare the earliest available one, but then later replaces this with a more deliberate choice. According to this view, fast errors occur when initiation is triggered prematurely, i.e. after the prepotent response is prepared but before the deliberate response has been prepared. We conducted two experiments to test this hypothesis by forcing participants to initiate their responses prematurely and checking whether this made them more likely to generate a prepotent response.

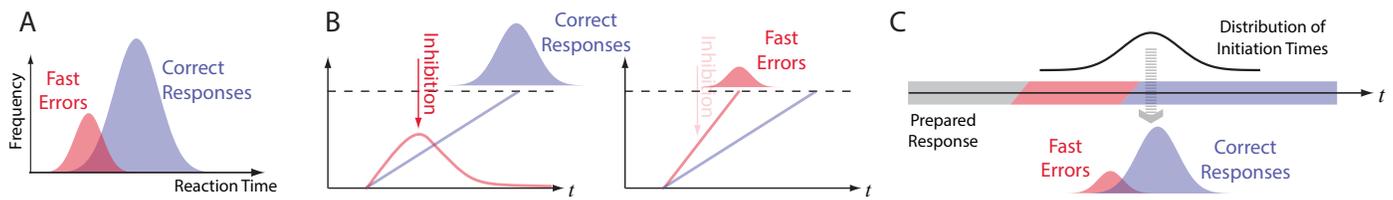
In Experiment 1, participants (N=8) generated planar reaching movements from a central start location to one of four targets (Fig. 2). The required target was cued in two different ways: In the first, Symbolic condition (Fig. 2A), the required target was cued by one of four symbols which appeared in the center of the target array, with each symbol associated with a specific target. In the second, Spatial condition (Fig. 2B), a symbol appeared within one of the targets, and participants simply moved to that *location*. In the final, Conflict condition (Fig. 2C), a symbol appeared within one of the targets, and participants were instructed to move to the target encoded by the *symbol*, ignoring its location.

During each condition, after a brief familiarization period (~50 trials), we manipulated response times using a timed-response paradigm (Haith et al., 2016); participants were trained to initiate movement at a fixed time in each trial, and the allowed response time was varied from 0-600 ms by changing the time of stimulus presentation relative to this fixed response initiation time. Participants performed 220 trials in each condition, allowing us to build a speed-accuracy trade-off (SAT) relating allowed preparation time (PT) to the probability of a correct response (computed using a 75 ms sliding window; Fig. 2, lower panels). In the Symbolic condition (Fig. 2A), performance was at chance for PTs below 200 ms, then slowly increased to maximal performance for PTs above 500 ms. In the Spatial condition (Fig. 2B), this SAT was earlier and steeper, reflecting more rapid preparation. In the Conflict condition (Fig. 2C), participants showed similar performance to the Symbolic condition, albeit slightly delayed (Fig. 2C, blue line). When PTs were limited, however, participants consistently generated movements towards the spatial location of the stimulus (red line in Fig. 2C, lower panel), confirming our prediction that reducing allowed PT would increase prepotent responding.

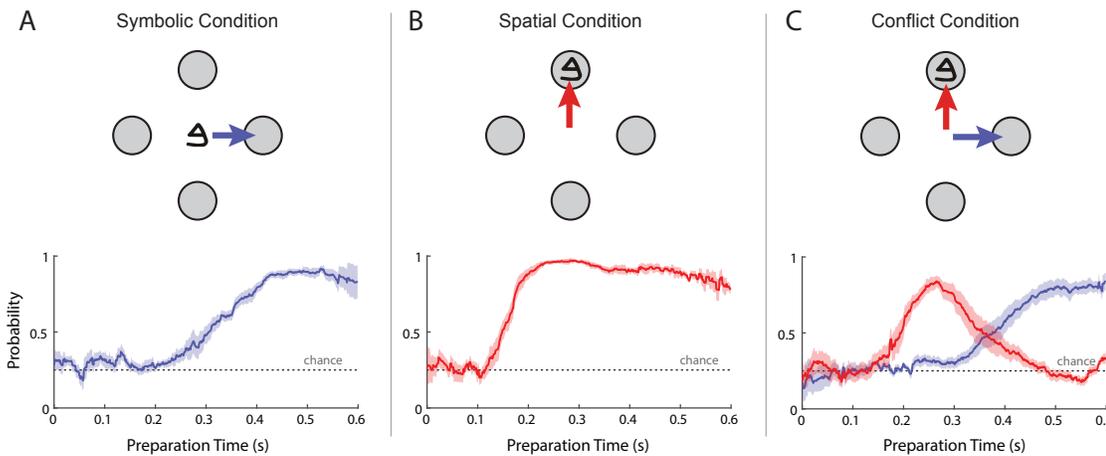
The observed dynamics of response preparation were well explained by a simple model in which we assumed that each response (spatial, symbolic) became available at a stochastic time after stimulus presentation (Figure 3A,B). The measured SATs in non-conflict conditions reflect the probability that the response was prepared by the time of initiation. Using data from non-conflict conditions, we fit independent normal distributions for the timing of Spatial and Symbolic responses via maximum likelihood (Fig. 3A,B). We used these fits to predict behavior for the Conflict condition (Fig. 3C), assuming that the Spatial response would be generated if it was the only response that had been prepared. The model accounted well for the time course response selection exhibited by participants.

To further test the generality of our framework, we conducted a second experiment (N=8) which posed a *three-way* conflict between potential responses. Participants responded based on either a spatial cue, an arrow, or a color cue (analogous to the symbolic condition) (Fig. 4A). As before, we measured the speed-accuracy trade-off for each cue type individually using a timed-reponse approach, yielding three distinct SATs (Fig. 4B). In the conflict condition, a colored arrow appeared inside one of the targets and participants were instructed to respond according to the *color* of the arrow (Fig. 4C). As predicted by the model (Fig. 4D), the most likely response depended on the allowed response time (Fig. 4D), further supporting the view that the motor system prepares all responses in sequence.

In summary, our findings demonstrate that response timing plays a critical and causal role in resolving response conflicts, consistent with the idea that movement preparation and movement initiation are distinct processes.

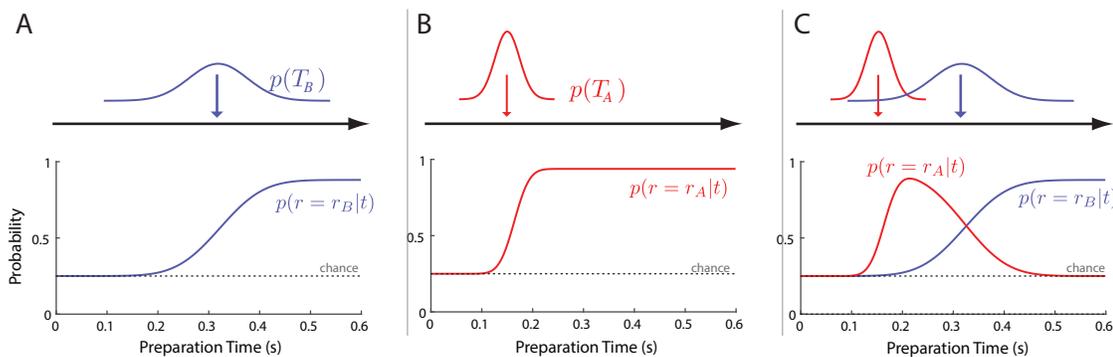


**Figure 1.** “Inhibitory control” tasks such as the Stroop or Simon tasks typically exhibit occasional *fast errors* in which an erroneous prepotent response is emitted at a low reaction time. B) Prevailing theories of behavior in such tasks propose that the prepotent response must be inhibited in order for the correct, deliberate response to be expressed; fast errors occur when this inhibition fails. C) An alternative view is that the motor system prepares responses as they becomes available, and generates whichever response is prepared at the time when response initiation is triggered. Under this theory, fast errors occur if the response is initiated before the deliberate response (blue) has been prepared.

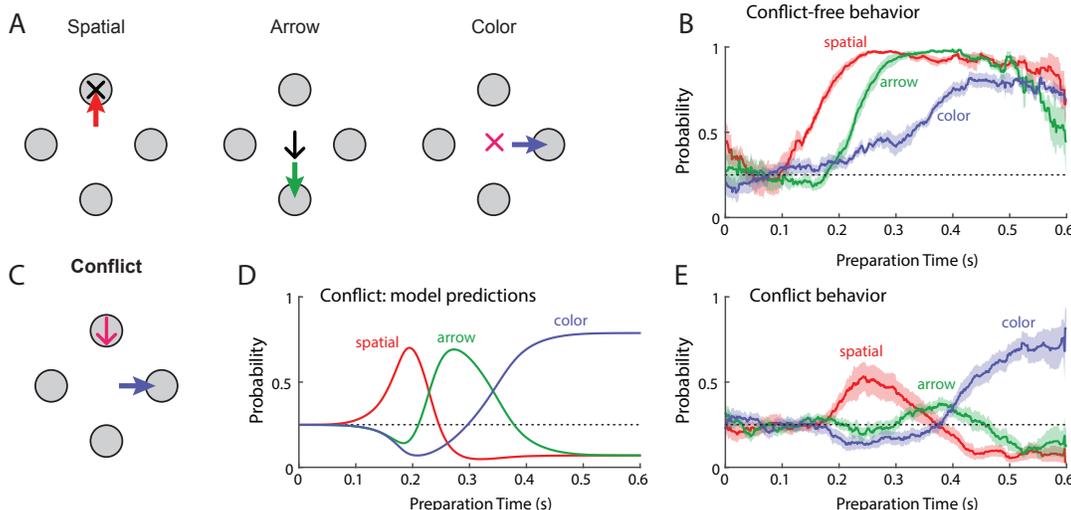


**Figure 2. Experiment 1.** A-C) Participants generated planar reaching movements towards one of four targets. The required target location was cued differently in different conditions. In initial training blocks, participants responded to (A) symbolic and (B) spatial cues. Lower panels show the corresponding speed-accuracy trade-offs - the probability of success as a function of allowed preparation time (PT) - measured using a timed-response paradigm which in which we forced participants to initiate with various PTs

between 0 and 600ms. In the conflict paradigm (C) symbols appeared at a non-central location, but participants were instructed to move according to the symbolic rules learned in (A). Participants were able to generate the correct response at long PTs (blue curve), but at shorter PTs they consistently generated erroneous movements towards the spatial location of the stimulus (red curve).



**Figure 3. Computational Model.** (A-B) We assumed that participants prepared each response at a random time after stimulus presentation in each trial (top panels), giving rise to the observed speed-accuracy trade-off (lower panels). (C) In the conflict condition, we assumed that the spatial response would be prepared and emitted if the symbolic response was not yet prepared. Lower panel shows predicted behavior.



**Figure 4. Experiment 2.** (A) Participants experienced 3 cueing conditions: Moving towards a spatial cue (left), moving in the direction of a central arrow (center), and moving according to the color of a central cue (right). (B) These conditions exhibited three distinct speed-accuracy trade-offs. (C) In the conflict condition, participants were required to move according to the *color* of an arrow, ignoring its spatial location and direction. (D) The model predicted that the most likely response would vary with RT (E) This prediction was borne out in participant’s behavior.