

## BRIEF REPORT

# Losing the Boundary: Cognition Biases Action Well After Action Selection

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For selecting an action, traditional theories suggest a cognitive architecture made of serial processing units. Others suggested that action selection emerges from the parallel implementation of and competition between multiple action plans. To disentangle these 2 hypotheses, we created a reaching task assessing the temporal dynamics of action selection. Crucially, our design did not force action selection processes to operate in parallel, allowing an informative comparison between the hypotheses. We manipulated the probability of congruence between a cue and a delayed reach target to investigate, in an unbiased way, whether congruence probability interacts with reach trajectory. Our results show that reach trajectories are modulated by the probability of congruence. Hence, action selection is temporally spread, continues after movement onset, and emerges from a competition between multiple afforded action plans, in parallel biased by relevant task factors (e.g., probability of reach).

*Keywords:* decision making, action selection, movement planning, parallel processing, reaching

When a tennis player responds to a serve, he quickly analyzes the stance and grip of his opponent and computes the probability of a successful forehand or backhand return. Traditionally, cognitive psychology explained action selection in such situations within the framework of serial processing. This suggests a brain architecture based on the computer metaphor of sequential processing modules (Heitz & Schall, 2012; Murthy, Ray, Shorter, Schall, & Thompson, 2009; Sternberg, 1969). Various methods assessed the processing stages between stimulus and response (Sternberg, 2011). Essentially, the serial architecture posits that perception, cognition and action proceed serially, are not coacti-

vated, and thus do not interact. The tennis player would first analyze the visual scene (perception), leading to a representation of the success probabilities linked to forehand and backhand (cognition). Based on this he would then choose (again cognition) the best upcoming movement to finally execute it (action).

It is important to clarify beforehand that the serial model architecture we address is that of perception, cognition, and action, and specifically the critical link between cognition and action. Serial versus parallel processing between tasks (e.g., Han & Marois, 2013) or between task components (e.g., Zylberberg, Fernández Slezak, Roelfsema, Dehaene, & Sigman, 2010) is outside the scope of this article. The idea of a strict serial link between selection (cognition) and execution (action) is present in various recent influential studies. For instance, Hare, Schultz, Camerer, O'Doherty, and Rangel (2011) suggest that

decision-making can be broken down into several component processes: assigning values to stimuli under consideration, selecting an option by comparing those values, and initiating motor responses to obtain the reward. Although much is known about the neural encoding of stimulus values and motor commands, little is known about the mechanisms through which stimulus values are compared, and the resulting decision is transmitted to motor systems. (p. 18120)

Others studies in value-based response selection share the same view (for review, see Rushworth, Kolling, Sallet, & Mars, 2012). This serial architecture is also a key feature of accumulator-to-bound models, such as the drift diffusion model (Ratcliff, 1978). The latter contains one parameter representing time for encoding and response, a collapse of input (perception) and output (action) stages, distinct from the actual diffusion process (cognition/selection).

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This article was published Online First June 15, 2015.

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We thank Craig S. Chapman for sharing information on functional data analysis and functional ANOVA procedures, as well as Julie Duqué, Philippe Peigneux, Filip Van Opstal, and the reviewers for valuable comments. Cristian Buc Calderon is supported by a fellowship from the National Fund for Scientific Research (FRS - FNRS Belgium, Grant Number 1.A.188.13F).

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This idea was questioned by studies showing that monkeys plan for all possible actions before selecting the relevant one. Prior to action, multiple action plans are represented in parietal reach region (Klaes, Westendorff, Chakrabarti, & Gail, 2011), dorsal premotor cortex (Cisek & Kalaska, 2005), and primary motor cortex (Bastian, Schöner, & Riehle, 2003; Thura & Cisek, 2014). These observations in sensorimotor regions suggest that no clear boundaries exist between perception, action selection, and action execution (Koch, Keller, & Prinz, 2004; O'Regan & Noë, 2001; Shadlen, Kiani, Hanks, & Churchland, 2008). This view is advocated in the "affordance competition hypothesis," proposing that decision making emerges from a biased competition of multiple action options afforded by the environment (Cisek, 2007). Action specification, selection, and execution would occur in parallel. The tennis player would represent both forehand and backhand action (action specification), and the probability information would bias the competition between both action plans (action selection).

In humans, this hypothesis has gained support from Transcranial Magnetic Stimulation (TMS) studies. Klein-Flügge and Bestmann (2012) demonstrated that corticospinal excitability (CSE; measured through motor evoked potentials) before movement onset correlated with the amount and probability of reward associated with the subsequently chosen action. Moreover, it was shown that CSE increases for preferred food stimuli and higher monetary reward (Gupta & Aron, 2011), even if the response side press is implicitly associated with a higher reward (Klein, Olivier, & Duque, 2012). TMS in combination with CSE measurement allows sampling the biased representation of multiple action plans. However, this sampling takes place prior to movement onset, and thus one cannot assess if this biased competition continues after action initiation.

Whether cognitive variables are processed and influence action during movement execution can be addressed using a reaching task (e.g., Sullivan, Hutcherson, Harris, & Rangel, 2015; Welsh & Elliott, 2005). This task captures the temporal dynamics of interactions between perception, cognition, and action. Broadly, three types of reaching tasks can be identified, ranging from least to most informative to disentangle serial from parallel activation of action selection and execution (hereafter termed *serial* and *parallel processing hypotheses*, respectively). The first class of studies reveals the information relevant for decision making only after movement initiation (e.g., Boulenger, Roy, Paulignan, Deprez, & Jeannerod, 2006; Chapman et al., 2010; Cressman, Franks, Enns, & Chua, 2007; Spivey, Grosjean, & Knoblich, 2005). Because stimuli allowing response selection processes to begin are given after movement initiation, it is impossible to assess if these selection processes continue at movement initiation. Hence, these designs induce a bias toward parallel processing and are not particularly suited to disentangle the serial from the parallel processing hypothesis. The second class of studies maximizes the chances of observing parallel processing by making use of explicit distractors that remain on screen after movement initiation. In the studies of Song and Nakayama (2006, 2008b), subjects are presented with three targets. Suddenly, a target changes color and participants must reach for it as fast as possible. The remaining targets become distractors, staying on screen until the relevant target has been reached. Explicit distractors attract trajectories if subjects focus their attention on these distractors at movement onset. When attention refocuses on the relevant target, the trajectory redirects

toward the relevant target. Thus, fast reaching designs may induce trials in which the redirection toward the relevant target happens during movement execution, specifically when attention refocuses on the relevant target after movement initiation. Finally, a third class of studies further reduces the possibility of parallel processing by accounting for the aforementioned biases (e.g., Finkbeiner, Song, Nakayama, & Caramazza, 2008; Resulaj, Kiani, Wolpert, & Shadlen, 2009; Santens, Goossens, & Verguts, 2011; Song & Nakayama, 2008a). However, in these studies, task difficulty is increased either by embedding the go signal in a rather high-level task (e.g., semantic categorization or number comparison) or by increasing ambiguity of where to reach. For instance, when subjects had to indicate whether a number was smaller or larger than "5" by reaching the left or the right square, trajectory redirections were more common when the numbers "4" or "6" were given compared with "1" or "9" (Song & Nakayama, 2008a). Indeed, a smaller numerical distance induces an increased overlap of activation (i.e., increased competition) between the neural codes associated with the left and right reaches compared with higher numerical distance. Resulaj and colleagues (2009) instructed subjects to reach toward a left or right target depending on the movement direction of random dots display. Parallel processing (instantiated as movement change during a trajectory) was observed, but only with very low coherences, thus when there was maximal ambiguity of where to reach. Even with these low coherences, changes in trajectory only occurred in 10% of the cases. Moreover, when coherence increased to 90%, a steep drop in trajectory changes was observed (approximately in only two to three out of 100 trials). In sum, high task difficulty increases the competition between reach options, which, in situations of rapid reaching, enhances the chance of observing a leakage of this competition into overt movement execution (i.e., favoring the parallel hypothesis).

Chapman and colleagues (2010) demonstrated that subjects' trajectories were initially directed toward the midpoint between two targets when these had equal probabilities of being reached and deviated toward a side when it had more probability of being reached. Their results suggest an online simultaneous biased representation of competing reach plans. With this finding and the previous comments in mind, we designed a study providing equal opportunities for this biased parallel competition to stop (serial hypothesis) or continue (parallel hypothesis) evolving at movement initiation. First, the "go" signal was given before movement onset. Second, no explicit distractors were used. Third, the go signals were unambiguous (i.e., 100% coherent, easily interpretable arrows), and the information differentiating between two relevant conditions (e.g., low- and high-reach probability) was presented several hundreds of milliseconds before the go signal, further simplifying the task. Moreover, in case of parallel processing, another advantage of our design is the ability to assess up until where in the reach parallel processing is observed.

Cue and target could be congruent or incongruent; the cue indicated both a movement direction and the probability that this movement direction was correct (i.e., probability of cue-target congruency). The serial processing hypothesis holds that action execution can begin only when it receives action selection output. Participants start moving once an action is selected. Consequently, probability of cue-target congruency would be reflected in initiation time. However, the trajectories and movement times would be

unaffected by the probability of cue–target congruency. Alternatively, the parallel processing hypothesis holds that action selection emerges from the simultaneous processing of probability information and potential action plans, with the first biasing the competition in the second. Hence, action selection may not be over before action execution, and thus could be reflected in movement time and reach trajectory. Incongruence (relative to congruence) between cue and target side would lead to a more curved trajectory toward the competing target and a slower movement time. In sum, both hypotheses predict slower initiation times in the incongruent condition, but only the parallel hypothesis predicts slower movement times in the incongruent condition.

## Method

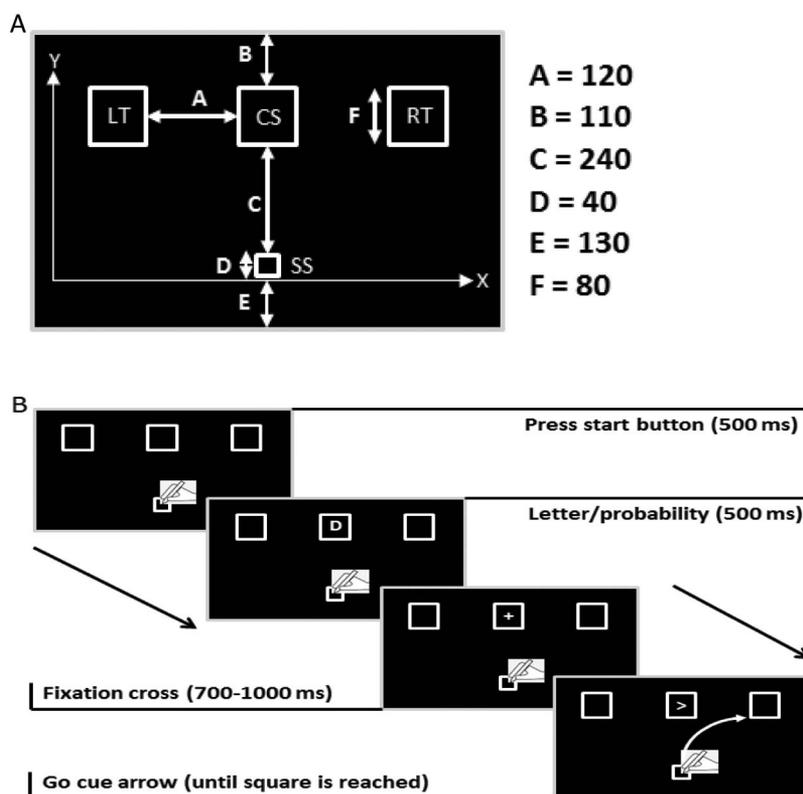
### Participants

Eighteen right-handed subjects (14 females;  $M = 23.1$  years,  $SD = \pm 3.69$ ) performed the study in exchange for monetary compensation. The local committee approved this study and participants were naïve regarding the purpose of the experiment. The

sample size was determined based on a previous reaching task investigating the influence of probability on trajectories (Chapman et al., 2010).

### Experimental Design

Reach trajectories were recorded with a Wacom LCD tablet DTF-720. The resolution was  $800 \times 600$  pixels, trajectory coordinates were sampled at 60 Hz, and stimuli were white on a black background (Figure 1A). Participants started the trial by touching (with a cordless pen) the start square during 500 ms. Subsequently, the letter “D,” “d,” “G,” or “g” (500 ms) appeared randomly on the central square (for *droite* and *gauche*, meaning “right” and “left,” respectively). The letter was replaced by a fixation cross presented for an amount of time randomly drawn from a uniform distribution between 700 and 1,000 ms. This jitter was added to prevent anticipatory responses based exclusively on the cue. The fixation cross was substituted by a target arrow (e.g., “<” or “>”) and participants rapidly reached the left or right target indicated by the arrow (Figure 1B). There was no response time limit, but it was stressed to participants that they were to respond as fast as possible. If participants left the start square before the go



*Figure 1.* (A) Screen display dimensions; units are pixels and all polygons are squares. The experiment was implemented on 17-in. Wacom touchscreen with a resolution of  $800 \times 600$  pixels. The angle between the screen and the table was  $30^\circ$ , and participants were placed in a way that allowed them to reach both targets without moving the body trunk. (B) Experimental design: Participants start by touching the start square (SS) for 500 ms, then a letter appeared on the central square (conditional stimulus [CS], 500 ms), followed by a jittered fixation cross (700 to 1,000 ms), and finally the appearance of the target signal indicating to reach as fast as possible either target left (LT) or target right (RT). The target signal disappeared when a target was reached. In the illustrated trial, cue and target are congruent.

signal (target) onset or lifted the pen during the trial, they received an error message and the trial was counted as null. Participants performed a training block of 16 trials with feedback (1,200 ms). Participants then performed five blocks of 80 trials. In each block, letters were presented equally frequent (20 trials per letter). Participants were instructed that if they saw an uppercase letter “D” or “G,” there was a high probability (0.8) that the following target signal arrow would be congruent with the cue. For lowercase letters “d” or “g,” there was a low probability (0.6) of cue–target congruency. Therefore, across the entire experiment, there were 80 high- and 60 low-probability congruent trials, and 20 high- and 40 low-probability incongruent trials, respectively, for right and left reaches.

## Trajectory Analyses

Movement trajectory analyses were threefold. To test main effects and interactions, we extracted orthogonal distance (X-dimension) of the trajectory to the display midline (connecting the start square to the central square) for each trial at 10 equally spaced time points (10% to 100% of movement time; details in Santens et al., 2011; Song & Nakayama, 2008; Spivey et al., 2005). To perform planned comparisons between high and low probability within congruent and incongruent trials, we used functional ANOVA (fANOVA; Gallivan & Chapman, 2014). Finally, to plot normalized mean trajectories, we used functional data analysis (Ramsay & Silverman, 2005). To simplify the trajectories’ plot, left reach trajectories were collapsed within right reach trajectories.

## Results

### Error Rates

Table 1 reports mean error percentages for each cell of the 2 (cue–target congruency: congruent, incongruent)  $\times$  2 (probability: high/0.8, low/0.6) design. A repeated-measures ANOVA on error percentages revealed a main effect of probability,  $F(1, 17) = 6.02$ ,  $p < .05$ ,  $\eta_p^2 = .261$ . We did not find a significant interaction or a significant difference between low- and high-incongruent trials. Hence, the interaction reported in the subsequent analyses is not induced by differences in error rates.

For the following analyses only correct trials ( $95.22 \pm 3.73\%$ ) were analyzed (i.e., trials in which participants reached for the side indicated by the target signal). Moreover, to ensure that movement time results were not induced by trials in which subjects based their action on the cue letter rather than the go signal (target), we also discarded trials with initiation times below 100 ms.

Table 1  
2 (Cue-Target Congruency: Congruent or Incongruent)  $\times$  2 (Probability: High or Low) Table for Mean Percentage Error Rates

Probability	Cue–target congruency	
	Congruent	Incongruent
High	1.10	1.44
Low	0.88	1.15

### Response Time

Both initiation time (time between target signal onset and crossing the start square) and movement time (time between crossing the start square and crossing a target square) were recorded. A 2 (cue–target congruency: congruent, incongruent)  $\times$  2 (probability: high/0.8, low/0.6) repeated-measures ANOVA was performed on both measures.

The repeated-measures ANOVA on initiation time revealed a main effect of congruency,  $F(1, 17) = 12.7$ ,  $p < .01$ ,  $\eta_p^2 = .428$ . Participants were faster to initiate movements for congruent ( $417 \pm 66$  ms) than incongruent ( $466 \pm 107$  ms) trials. Moreover, an interaction was observed between congruency and probability,  $F(1, 17) = 12.567$ ,  $p < .01$ ,  $\eta_p^2 = .425$ . High probability reaches were initiated faster than low-probability reaches for congruent trials, and the reversed pattern was observed for incongruent trials (Figure 2 left). Planned comparisons between high- and low-probability revealed a significant difference within congruent trials,  $F(1, 17) = 27.8$ ,  $p < .001$ ,  $\eta_p^2 = .620$ . High probability trials were initiated faster than low-probability trials ( $410 \pm 69$  ms and  $424 \pm 67$  ms, respectively)

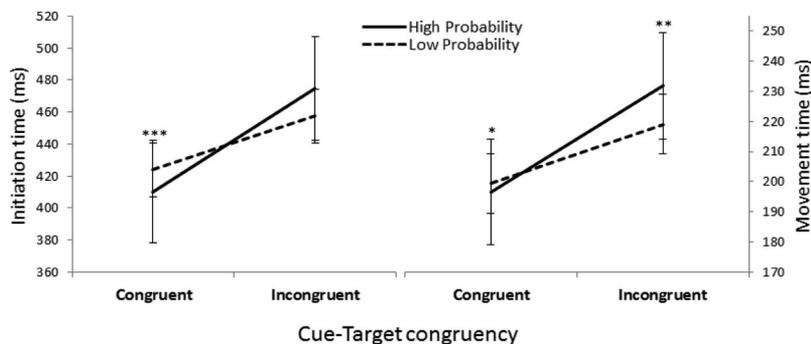
Movement times revealed a main effect of congruency,  $F(1, 17) = 13.4$ ,  $p < .01$ ,  $\eta_p^2 = .440$ . Participants were faster to reach targets in congruent ( $198 \pm 37$  ms) compared with incongruent trials ( $225 \pm 53$  ms). A main effect of probability was observed,  $F(1, 17) = 5.96$ ,  $p < .05$ ,  $\eta_p^2 = .260$ . Movement times were shorter for low-probability ( $209 \pm 46$  ms) compared with high-probability ( $214 \pm 50$  ms) trials. Crucially, the interaction between congruency and probability was also observed for movement time,  $F(1, 17) = 10.7$ ,  $p < .01$ ,  $\eta_p^2 = .387$  (Figure 2, right). Planned comparisons between high and low probability revealed significant differences for both congruent and incongruent trials,  $F(1, 17) = 5.02$ ,  $p < .05$ ,  $\eta_p^2 = .228$ , and  $F(1, 17) = 9.02$ ,  $p < .01$ ,  $\eta_p^2 = .347$ , respectively.

### Movement Trajectories

A 2 (cue–target congruency: congruent, incongruent)  $\times$  2 (probability: high/0.8, low/0.6) repeated-measures ANOVA was performed on the X-dimension values, independently for the 10 time points (see the Method section). There was a main effect of congruency for Points 4 to 9 ( $p < .05$ ;  $\eta_p^2$  ranging from .248 to .328) and probability for Points 7 and 8 ( $p < .05$ ;  $\eta_p^2$  of .233 to .252, respectively). Crucially, a significant interaction for Points 5 to 8 ( $p < .05$ ;  $\eta_p^2$  ranging from .222 to .332) was observed. Illustrating this interaction, a significant quadratic regression of  $\eta_p^2$  as a function of time ( $R^2 = .633$ ) was observed; the interaction effect climbs and attains its highest point between the sixth and seventh time points before decreasing again (Figure 3B).

Paired comparisons between low versus high probability (Bonferroni corrected  $p < .05$ ) were performed with fANOVA (see the Method section). Importantly, this revealed a significant difference within incongruent trials (Figure 3A). Low-probability trajectories (black dashed lines) deviated from the midline significantly more than high-probability trajectories (black solid lines). Thus, on average, high-probability trajectories are longer compared with low-probability trajectories, yielding shorter movement times for low-probability reaches.

One may argue that differences in movement trajectories derive from averaging between straight correct and “partial error” trials (i.e., trials in which subjects first reached for the incorrect target



*Figure 2.* (Left) Cue-target congruency and probability interaction for initiation times, calculated as the time interval between go cue onset and the crossing of the start square. (Right) Cue-target congruency and probability interaction for movement times, calculated as the time interval between crossing the start square and crossing the target square. On both graphs, probability of cue-target congruency is indicated by full (high probability) and dashed (low probability) lines. Significant planned comparisons between high and low probabilities within congruency are highlighted by asterisks (\*  $p < .05$ , \*\*  $p < .01$ , \*\*\*  $p < .001$ ). Error bars denote the standard error of the mean.

and later redirect toward the correct target). However, standard errors are small throughout the entire reach for all conditions (Figure 3A). Furthermore, an averaging artifact would cause larger standard deviations for high-compared with low-probability incongruent trials. In contrast, no significant difference was observed between the standard deviations of the 10 equally spaced time points (mean standard deviation of 15.18 and 15.82 for low- and high-probability, respectively).

## Discussion

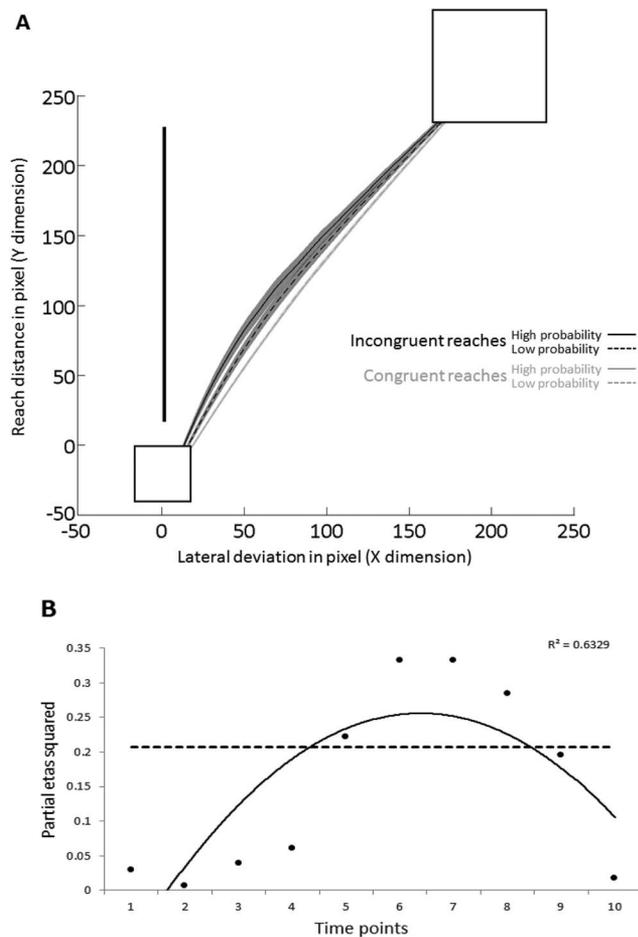
An adapted reaching task was designed to compare the serial and parallel processing hypotheses in action selection. The probability of congruence between cue and target side was reflected not only in the reaction time but also in movement time and movement trajectory. The current study shows that action probability is processed in parallel to movement execution even when task settings were calibrated to maximize serial processing. When selecting a reach, participants specify both competing reach plans (Baumann, Fluet, & Scherberger, 2009; Cisek & Kalaska, 2010; Shadlen & Newsome, 2001), while relevant task factors (e.g., prior probability associated with each action execution) bias the competition (Lauwereyns, Watanabe, Coe, & Hikosaka, 2002; Louie, Gratton, & Glimcher, 2011; Pastor-Bernier & Cisek, 2011). This mechanism is observed in a variety of continuous response designs with response modalities such as reaching (Cisek & Kalaska, 2005), grasping (Baumann et al., 2009), and saccade selection (Van der Stigchel, Meeter, & Theeuwes, 2006). It can also be observed using electromyographic recordings in button-press tasks (Burle, Allain, Vidal, & Hasbroucq, 2005). In sum, parallel processing is revealed with various tasks and response modalities.

Importantly, our findings are in contradiction with the idea that once the activity in favor of a motor plan reaches the execution threshold, the selected action would be executed ballistically. In other words, motor behavior would not be entirely defined by the execution of a single motor plan but rather by the constant representation of simultaneously afforded biased motor plans. Notably, our trajectory analysis reveals that this representation may influ-

ence motor behavior up until the very late phases of its execution. Thus, action selection consists of an interplay between action specification, selection, and execution. This idea is present in dynamical systems theory (Erlhagen & Schöner, 2002; McClelland et al., 2010; Schöner & Thelen, 2006), in which “decisions are seen as emerging within the dynamical system describing an agent’s interaction with the world” (Cisek & Pastor-Bernier, 2014, p. 4). Here, the initial state of the system (reflecting the aiming point of the reach) is determined by the amount of activity in favor of each action plan (e.g., probability cue). With new information (e.g., target signal arrow), the system evolves and activity in favor of a specific reach builds up while activity for the opposite reach diminishes (Pastor-Bernier & Cisek, 2011). When enough activity has built up for a specific reach plan, movement starts. However, the dynamical system does not stop evolving at movement initiation. Instead, trajectories continue reflecting the evolving state of the dynamical system.

Alternatively, one could argue that subjects shift their aiming point according to the probability cue before the go signal and that movement trajectories are entirely defined by this initial shift of aiming. However, this is unlikely. First, the interaction effect holds up until 80% of the movement time and climbs to reach its maximal effect slightly after mid trajectory. This strongly suggests that probability is still being processed after movement initiation. Second, the aiming shift hypothesis would predict differences between the initial directions of the high- and low-probability congruent trials, which are not observed in our data.

The affordance competition hypothesis, as it stands, leaves some unresolved issues. First, one could argue that the proposed mechanism is limited to fast action selection. Under speed constraints, a good speed-accuracy strategy would be to start moving before the competition between the afforded reach plans is resolved. However, the aforementioned mechanism may also account for slow action selection, for instance, when accuracy is emphasized. In the latter, participants may prioritize waiting for the dynamical system representing the competition between both reaches to stabilize in favor of a specific reach. This would increase accuracy at



**Figure 3.** (A) Average reach trajectories stemming from the cue–target Congruency  $\times$  Probability interaction. Left reach trajectories were collapsed with right reach trajectories to simplify the figure. Congruent high- and low-probability (plain and dashed gray) trajectories partly overlap in the figure. Planned comparisons between low and high probability revealed a significant difference for incongruent reaches, depicted by the black significance bar on the left of the figure. The latter shows at which point during the reach the functional ANOVA resulted in a significant difference. Shaded error bars symbolize the average standard error across all participants. (B) Plot showing partial  $\eta^2$  stemming from the interaction as a function of the 10 equally spaced movement time points. A significant quadratic regression was revealed with  $R^2 = 0.63$  suggesting that the effect of the three-way interaction attains its peak between the sixth and seventh time points. The significance threshold is depicted by the dashed line.

the expense of rapidity, hiding the underlying dynamics. Indeed, if the reach is executed once the system has stabilized, the trajectory would have the empirical signature as predicted by the serial processing hypothesis. However, the underlying mechanism is fundamentally different. Second, although formal descriptions of how dynamic systems integrate relevant task factors to bias the competition between afforded action plans have been elaborated (Erlhagen & Schöner, 2002), implementations accounting for movement trajectory data are currently lacking.

In conclusion, cognitive psychology is undergoing a paradigmatic shift toward emphasizing the interaction between perception,

decision variables (i.e., cognition), and motor representations (i.e., action) afforded by the milieu. This trend is apparent in a number of recent theoretical frameworks, including predictive coding (Friston, 2010) and the affordance competition hypothesis (Cisek & Kalaska, 2010). However, its core idea was already proposed in James Gibson’s “ecological psychology” (Gibson, 1979), as well as in William James’s ideomotor theory (James, 1890). The current research supports this tight coupling between perception, cognition and action.

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Received January 9, 2015

Revision received May 6, 2015

Accepted May 7, 2015 ■