

Hidden cognitive states revealed in choice reaching tasks

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Perceptual and cognitive processes have largely been inferred based on reaction times and accuracies obtained from discrete responses. However, discrete responses are unlikely to capture dynamic internal processes, occurring in parallel, and unfolding over time. Recent studies measuring continuous hand movements during target choice reaching tasks reveal the temporal evolution of hidden internal events. For instance, the direction of curved reaching trajectories reflects attention, language representations and the spatial number line, in addition to interactions between the ventral and dorsal visual streams. This elucidates the flow of earlier cognitive states into motor outputs. Thus, this line of research provides new opportunities to integrate information across different disciplines such as perception, cognition and action, which have usually been studied in isolation.

Introduction

Progress in understanding how human cognition operates owes much to the information processing approach, which has adopted the computer metaphor of distinct processing units. The theoretical assumption of discrete intermediate stages has inspired cleverly designed experiments to identify sequential stages of perception, cognition, decision-making and motor output. Reaction times and accuracies obtained from discrete responses such as button presses have been viewed as useful and effective behavioral measurements to individuate sub-components, each adding its own processing times [1,2].

For decades, however, an alternative view of brain processing has also persisted, reappearing under various guises including connectionism and non-linear systems analysis: multiple internal states can be activated in parallel, and coexist [3–7]. Furthermore, these unified perspectives of perception, cognition and action have emphasized a stronger role for action in perception and cognition [5,7–9]. Although conventional discrete measurements seem adequate under the assumptions of a symbolic-computational approach to cognition, they cannot fully capture dynamic interactions of internal states over time. What has been lacking in human studies on perception and cognition are easily available behavioral paradigms to measure the temporal evolution of relevant internal events.

We shed light on ongoing endeavors to capture the dynamics of multiple cognitive states unfolding over time [4,10–14]. There has been an attempt to take advantage of

overt actions such as saccadic eye movements and manual reaching movements to read out cognitive processes. For instance, the distributions of saccadic landing positions and changes of saccadic movement trajectories have been used to examine language, attention, memory and oculomotor control [15–17]. Yet, saccades, in general, are rapid and discrete, demonstrating relatively weak trajectory modulation. In contrast, reaching movements have numerous advantages as an alternative behavioral measurement (Box 1). The continuity of reaching movements enables each sample point to be modulated by the real-time progress of a wide range of internal processes [4,18,19].

Neurophysiological studies have demonstrated the existence of simultaneous multiple motor plans and blurred distinctions between sensory, decision-making and motor processes in the brain [20–27]. This provides physiological plausibility for the view that reaching movements can reflect underlying competing cognitive states. After a brief review of these neural mechanisms, we describe examples in which the direction of curved reach trajectories reveals otherwise hidden states and processes. This new approach using reaching movements demonstrates interactive parallel processes of perception, cognition and action, bridging the gap across different disciplines in which these processes have been studied independently [5–7,9,10,28].

Perception, cognition and action: interactive parallel processes

For simplicity and convenience, theoretical models often assume separate and discrete neural substrates for perception, cognition and action. Perceptual evidence is gathered, followed by a decision process. Then the subsequent motor output is planned and executed. However, a growing number of studies have raised the question as to whether interpreting neural activity in terms of distinct perceptual, cognitive or motor processes is appropriate for bridging dynamic neural data with behavior. For instance, recent functional magnetic resonance imaging (fMRI) and neurophysiological studies have commonly demonstrated the mixture of signals appropriate for controlling higher order perceptual and cognitive decision-making processes in sensory-motor areas [20–23]. Furthermore, it has also been shown that motor planning and execution, traditionally viewed as distinct and serial, are processed within the same neurons [27,29,30]. This suggests continuous flow and blending between brain systems involved in sensory, cognitive and motor processes, in accord with the view

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Box 1. The joys of visually guided reaching

As a behavioral measurement, visually guided reaching has a number of distinct advantages. Rapid reach movements towards a target typically take about a fraction of a second, which is comparable to the time scale of many cognitive events. Thus, reach trajectories can effectively trace the evolution of internal processes. In addition, because visually guided reaching is among the most natural and practiced visuo-motor responses, various populations such as young children, aging seniors and non-human primates [63] can easily perform reaching tasks with minimum instruction and training.

More importantly, reach trajectories can map invisible internal processes into a well-defined Cartesian coordinate space. Therefore, experimental manipulations are straightforward and results can be understood intuitively. For instance, alternative choices of internal events can be spatially represented as choice targets in front of the participants, and the evolution of reach trajectories towards one target over another allows us to visualize how competing cognitive states are resolved over time (Figures 2–5).

Thanks to advancements in technology, measuring reach movements has become easily accessible and affordable using a variety of devices. Most of them are far less expensive than those to measure eye movements. The most straightforward and natural method is to directly track hand or finger positions in 3D using optical or electromagnetic devices [41,64]. These goal-directed reaching movements require no substantial training and are well understood in terms of the biological substrates [5,65,66]. There are also other tracking devices, where participants move a conventional mouse [44], a robotic arm [27,67] or a 3D device designed for games [68]. Because these devices control a cursor on a screen in which stimulus and action spaces no longer coincide under some circumstances, it sometimes requires additional training for mapping visual target and action. However, these devices can provide a cost-effective way to obtain important continuous data. Taken together, reaching movements can provide an easily accessible methodology to track the spatio-temporal evolution of internal events.

of interactive dependencies across the basic systems [5–7,9,10,28].

Neural populations in reach-related areas such as the motor cortex, the dorsal premotor area in the frontal cortex and area 5 in the parietal cortex, can represent several distinct and even mutually exclusive potential movement goals simultaneously as distinct peaks of activity [24–27]. For instance, Cisek and Kalaska [27] demonstrated that when two potential targets are presented for selective reaching, the dorsal premotor area, known to be involved in planning and executing limb movements, is able to simultaneously encode the two competing movement goals during a delay period. As the final choice is made followed by the movement, one response diminishes, and the other increases (Figure 1). This further supports the view that motor systems do not passively reflect the result of completed cognitive processes; rather, it is crucially linked to the dynamic decision-making process itself [7–9,31,32].

Goal-directed reaching movements have been viewed as consisting of two components; preprogrammed and online control phases [33,34]. Considering the linkage between cognitive and motor processes, and the concurrent processing of multiple motor plans in reach-related areas, competing cognitive states are likely to preprogram corresponding reach plans in parallel in target choice reaching tasks [13,35–38]. These preprogrammed competing motor plans could be manifested in early reach movement trajectories. In the following section, we provide

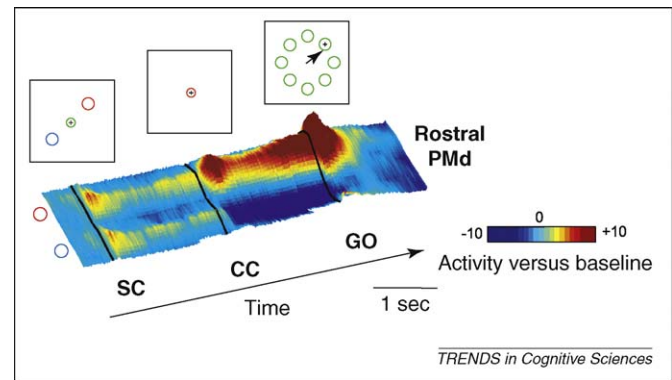


Figure 1. Neural population activity in the dorsal premotor area (PMd). Neural activity [27] is depicted as a 3D colored surface. When the spatial cues (SC) for two possible targets, one red and one blue, are presented to a monkey, two populations of cells for competing reach goals become active in parallel. The color cue (CC) indicates which colored target is the correct target, and the GO signal instructs the monkey to begin the movement. Once the decision is made, one population of cells shows an increase in activity while the other is suppressed, demonstrating that the two competing movement goals are simultaneously encoded in the PMd. Modified, with permission, from Ref. [5].

recent evidence for how continuous movement can reveal real-time flow of earlier cognitive states into motor output.

Evidence for real-time cognitive events in reach trajectories

Recent studies using target choice reaching tasks have taken advantage of the 'leakage' of earlier cognitive states into the final motor output. In these studies, the analyses of reaching movements demonstrate the current locus of attention, the nature of language representations, spatial representation of numbers, and high-level decision-making processes.

Current locus and mechanisms of attention

In the real world, most visual scenes are complex and crowded with multiple objects. Recent studies in target choice reaching have provided insight as to how attention moves from one location to another when selecting a target among competing distractors in such cluttered scenes. These studies have shown that reach trajectory and kinematics are affected by the presence of distractors. When distractors are to be ignored, and inhibited, reach trajectories deviate away from them [36,39], whereas when distractors can be potential movement targets, or when the location of a distractor is facilitated by a pre-cue or priming, reach trajectories swerve towards them [38,40–42]. Moreover, changes of the direction of curved reach trajectories have also demonstrated that inhibitory attention mechanisms are relatively slower than facilitatory ones [37]. In addition to target selection process, reach trajectories are also useful to study the time course of response competition such as in the Simon task [43].

In the color-oddy task depicted in the upper part of Figure 2, participants reach towards an odd-colored target while presented with distractors. When the colors of the target and distractors are randomly switched leading to competition between them, reach trajectories often swerve towards a distractor and are then quickly re-directed to the target as shown in the lower part of Figure 2. The rapid adjustment of trajectories shows that multiple competing

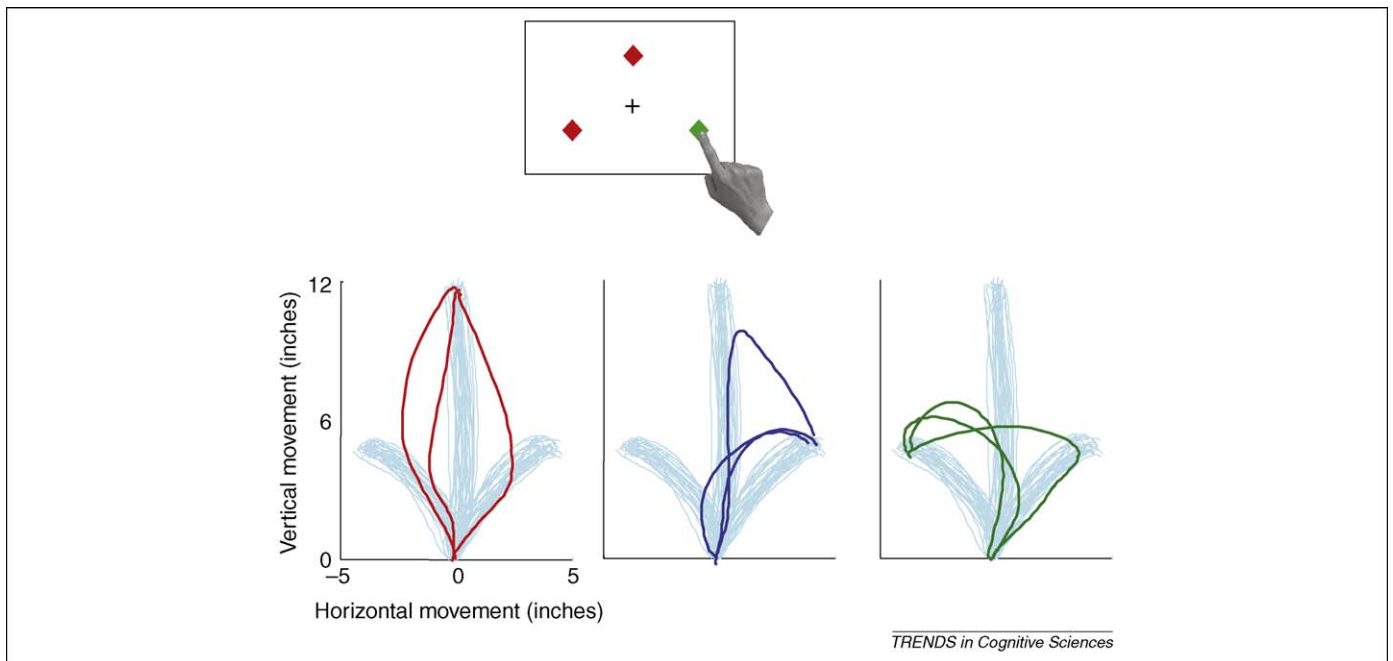


Figure 2. Effect of distractors on manual reach trajectories in a color-odddity task. The upper panel shows a schematic diagram of a trial, in which an odd-colored target is presented with two distractors, and participants search for and reach towards the odd-colored target with their index finger. The colors of the target and distractors are randomly switched in each trial. The lower panels show examples of curved reach trajectories in this task, contrasted with those in no-distractor cases (in cyan). Trajectories associated with each target location are illustrated using distinct colors in each panel: red (target at twelve o'clock position), dark blue (four o'clock), and green (eight o'clock). The trajectories are 3D, but for clarity, the most relevant x (left-right) and y (upward-downward) dimensions are plotted. Modified, with permission, from Ref. [41].

stimuli are facilitated in parallel during a target selection process well before movements are initiated [13,41,42]. This suggests that instead of completed processing at one stage passing information subsequent stages, intermediate processing is sent along as well. Moreover, the magnitude and extent of the trajectory curvature reflect the activation levels of each competing internal state [37,41].

Together, these studies have demonstrated that the evolution of trajectories reveals the current locus of attention allocation, and the time course of target selection and response competition.

Language processes in real-time

Speech is sequential with a succession of discrete words, and yet the activation of word representations occurs in parallel (Box 2). To examine the temporal dynamics of how spoken words are recognized, Spivey *et al.* [44] asked participants to move a computer mouse to click on a specified target picture, while a distractor picture was presented on the opposite side of the screen. As depicted in Figure 3, mouse-moving trajectories are attracted more towards a distractor when the names of the target and distractor are more phonologically similar (e.g. *picture* and *pickle*) than dissimilar (e.g. *picture* and *jacket*). The direction and extent of continuous curved trajectories reveal which word is activated and how strongly each word competes over time, demonstrating a dynamic online competition between simultaneously activated lexical representations. Note that this detailed temporal dynamic cannot be captured by conventional lexical decision tasks, in which participants are asked to indicate whether letter strings are words or not using a key press [18].

Similar examples can be found in a study of semantic categorization [45], in which participants categorized atypical or typical exemplars (e.g. *whale* or *cat*) into one of two categories (e.g. *mammal* or *fish*). In this study, movement trajectories curved more towards the competing category when atypical exemplars were presented, indicating graded competition in the categorization process.

A continuous reaching task is also useful for examining how different word classes such as nouns and verbs are processed. The analyses of movement kinematics reveal that compared to processing nouns, processing action verbs alter overt motor performance. This demonstrates a cross-talk between action verb processing and overt motor behavior.

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Box 2. Competing parallel activations: features, not bugs

The eminent psychologist Karl Lashley [69] challenged the ascendant behaviorism of his day. He argued that the behaviorist's associative chaining of responded stimuli fail to account for complex motor behavior in which individual components of movements happen too quickly for this chaining to occur. Rather, he suggested that there are more central autonomous processes at play to ensure well-coordinated and adaptive sequences of actions. The most important formulation for Lashley was the notion of parallel pre-motor activations. In the case of speech, he argued that words in a sentence must be pre-activated in parallel, and that by some as-yet-unidentified syntactic process, they are then ordered serially as the speech stream. Sometimes, however, these elements are not assembled as intended, and unwanted speech transpositions can occur (e.g. *our queer old dean*, instead of *our dear old queen*). This supports Lashley's claim regarding simultaneous parallel activation. Furthermore, Lashley suggested that even without external stimulation, there are multiple parallel activations in the nervous system representing different motor acts.

In accord with Lashley's pre-activation idea, recent studies have demonstrated dynamic competition in the syntactic resolution process, and motor remapping and priming processes [7,70]. Parallel activations also enable erroneous reaching movements initiated towards the wrong target to be quickly corrected towards a new goal with no loss in speed or accuracy [13].

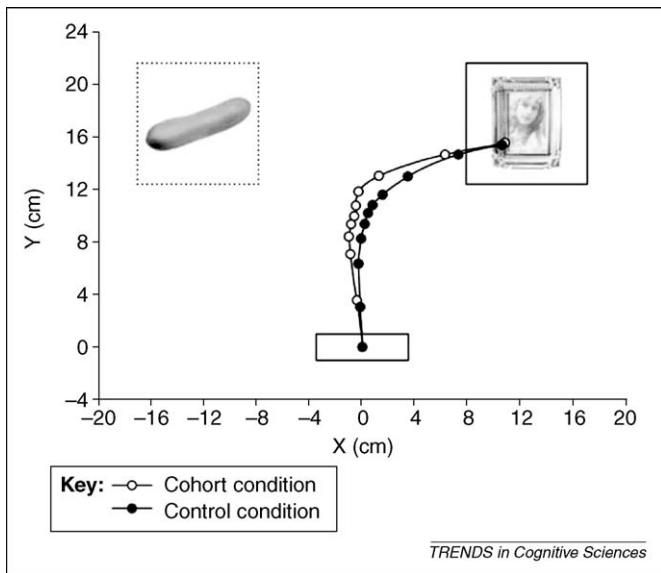


Figure 3. Effect of phonological competitors on mouse-movement trajectories. Participants are asked to click on a target (e.g. *picture*) on a computer screen after hearing a word. In the control condition (filled dot), the target and distractor are phonologically dissimilar, (e.g. *picture* and *jacket*), whereas in the cohort condition (unfilled dot), the distractor is phonologically similar to the target (e.g. *picture* and *pickle*). In the cohort condition, the trajectory is more curved towards the distractor, reflecting a graded spatial attraction due to its phonological similarity. Modified, with permission, from Ref. [44].

viator, suggesting that the motor areas are closely involved in action verb processing [46].

Spatial representation of numbers revealed by systematic trajectory shifts

The ‘numerical distance effect’, in which reaction times and error rates systematically decrease as the numerical distance between two numbers increases, suggests that

numbers are represented spatially along a continuum. This evidence of spatial number representation has been observed in adults and in infants and animals [47].

However, this is an indirect inference based on the duration for completing the entire sequence of number comparison processes. Recent studies using reaching tasks further demonstrate the association of number magnitudes with spatial response codes [13,48]. For example, in the study depicted in Figure 4 [13], participants had to determine whether a single Arabic numeral presented on the center square was less than, greater than or the same as the number five. Their task was to reach to the one of three squares on the screen: less than (left), greater than (right), or equal to (center). As shown in Figure 4, reach trajectories are systematically shifted in position according to numerical differences between the target and the number five; the greater the numeric deviation, the greater the deviation of the trajectory from the standard trajectory. This provides direct evidence that the numeric magnitude of the target is spatially encoded, and that the proximity and orders between numbers are spatially represented along a hypothesized mental number line.

High-level decision-making

Continuous choice reaching tasks can be applied not only to studies on perception, attention and language, but also to those on higher-level cognitive decision-making, closely simulating real-life situations. McKinstry *et al.* [49] examined how multiple alternatives are processed during a decision-making process. In this study, participants had to decide whether they agreed or disagreed with a presented question by moving a mouse pointer to one of two response boxes, ‘yes’ or ‘no’, located on either side of the screen. Questions were pre-classified along a continuum of ‘truth

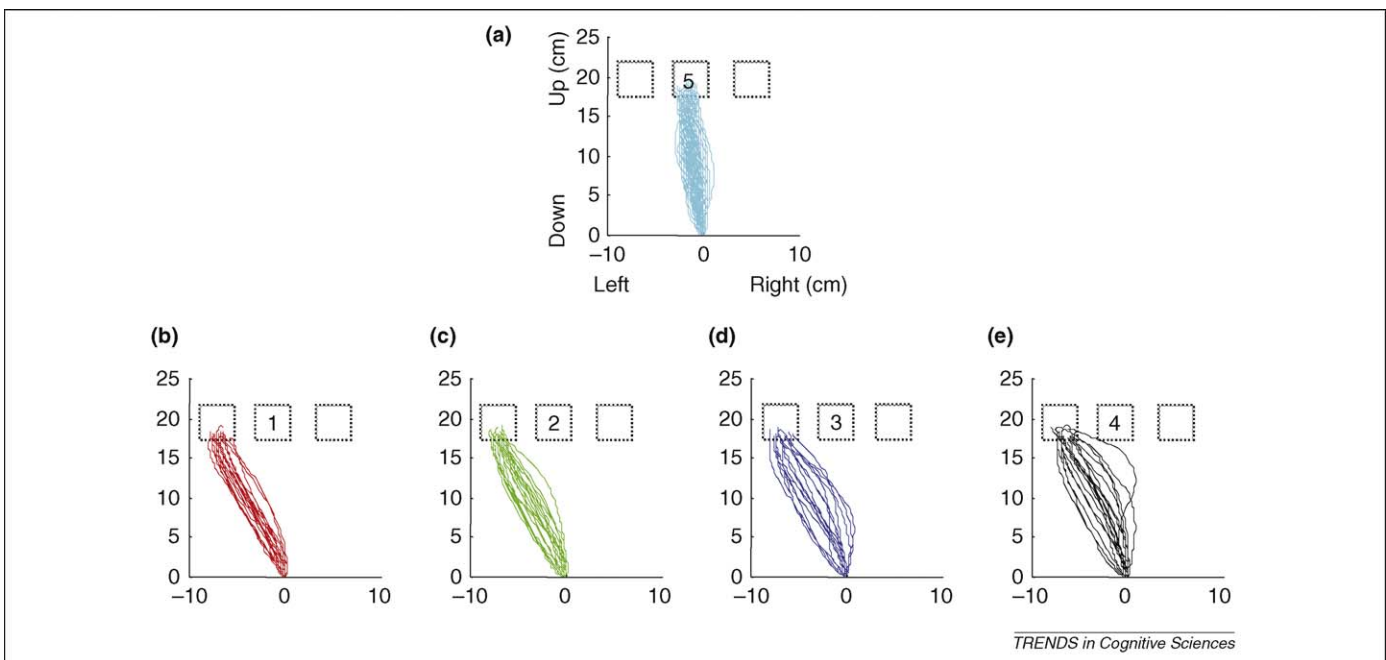


Figure 4. Spatial number representation revealed by systematic reach-trajectory shifts. Participants are shown a single-digit Arabic numeral in a center square and asked to compare its value with the standard, five. They then reach for and touch one of three squares on the screen: the left for ‘less than’, the center one for ‘equal to’, or the right one for ‘greater than’. The panels in this figure depict examples in which the value of the target is ‘equal to’ (a) or ‘less than’ (b–e) the standard. The lower panels demonstrate gradual shifts of reach trajectories towards the center square as the difference in value between the target and the standard decreases. These trajectories are 3D, but for clarity, the most relevant x (left-right) and y (upward-downward) dimensions are plotted. Reproduced, with permission, from Ref. [14].

values' (0~1 true): for instance, 'Is a thousand more than a billion?' (0 true), 'Is murder sometimes justifiable?' (.6 true), and 'should you brush your teeth every day?' (1.0 true).

When the choice was 'no', trajectories were more attracted towards the alternative than when the choice was 'yes'. This indicates that there is a prior bias towards 'true'. This bias is gradually overcome by activating the 'false' response. Furthermore, trajectories for low-truth-value questions showed significantly greater curvature than those for high-truth-value questions. In addition, peak velocity was lower in low-truth-value than high-truth-value questions. Thus, both spatial and temporal dynamics of reaching movements showed how the cognitive decision-making process behaves in response to continuous parallel competition, instantaneously sharing information with motor systems even before the decision is completed.

Taken together, a close examination of the details of reaching trajectories enables insights into a wide range of dynamic internal representations. Instead of inferring invisible internal states, cognitive processes can be mapped onto a spatial domain by measuring continuous trajectories. Furthermore, the usage of choice reaching tasks is not limited to studying conscious cognitive states.

Using reaching to identify interactions between dorsal and ventral streams

The dorsal and ventral visual streams have been identified as comprising two separate processes: an identification system in the ventral stream, and an action system in the dorsal stream [50,51]. Continuous reaching tasks have been informative in understanding how these two visual systems are dissociated. For instance, a patient with damage to the ventral portion of the visual system demon-

strates normal temporal dynamics of goal-directed reach-to-grasp movements even without recognizing objects. This suggests that the intact dorsal stream enables the patient to send appropriate motor commands in real time [51].

In spite of the accumulating evidence for the separation of these two processing streams, it is widely accepted that information from both must eventually interact with each other because many actions require semantic information about objects, which is not obvious from their raw visual characteristics [51,52]. However, it has not been easy to establish specific functional links between these streams because once a stimulus becomes visible and conscious, there is widespread activation over the whole brain and there are countless opportunities for interaction.

For this reason, reaching tasks using unseen stimuli blocked from awareness might be advantageous, as they would activate a much smaller set of neural systems, making it possible to identify early interaction between the ventral and dorsal systems [53,54]. For instance, in Schmidt [35], participants were asked to reach to one of two color targets, which were preceded by consistent or inconsistent color primes. Even when primes were completely masked by target stimuli, reach trajectories were affected by the color of the prime. In the inconsistent condition, reaching trajectories curved initially towards the non-target stimulus that was the same color as the invisible prime. This demonstrates the flow of color information, known to be mainly processed in the ventral stream, [55] into the dorsal action stream. In a similar task, Cressman *et al.* [56] further demonstrated that subliminal shape primes also influence ongoing action.

Finkbeiner *et al.* [57] extended these findings using higher-order stimuli even more closely identified with

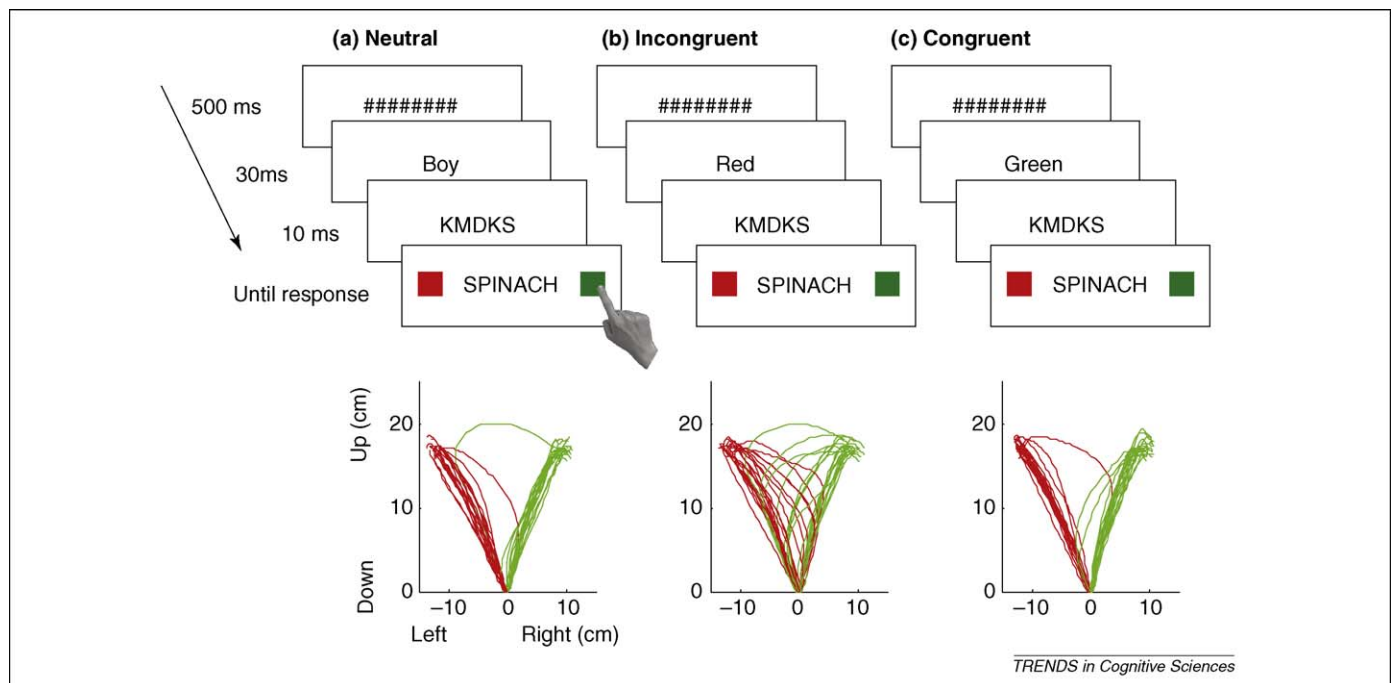


Figure 5. Effect of unseen words on reaching trajectories. The upper panel shows a schematic diagram of a trial in which participants categorize a target word (e.g. SPINACH) according to its canonical color of red or green by reaching to a corresponding square. The target word is preceded by the neutral (a), incongruent (b) or congruent (c) prime word, of which participants are unaware. In the lower panel, trajectories in correct trials associated with each target location are depicted by two distinct colors. Red trajectories represent trials in which the canonical color of the target is red (e.g. KETCHUP), whereas green trajectories represent trials in which the canonical color of the target is green (e.g. SPINACH). These trajectories are 3D, but for clarity, the most relevant x (left-right) and y (upward-downward) dimensions are plotted. Modified, with permission, from Ref. [57].

ventral stream processing, namely words. Lesion and fMRI studies have identified word form areas necessary to lexical processing in the ventral fusiform cortex [58]. In Finkbeiner *et al.* [57], participants categorized a target word (e.g. *SPINACH* or *KETCHUP*) according to its canonical color of red or green by reaching to a corresponding square. A masked prime, such as 'Red', 'Green' or 'Boy' preceded the target. Participants were not aware of the masked prime, as confirmed by a signal detection analysis in a subsequent discrimination task. They found that when the prime (e.g. Red) preceded the incongruent target (e.g. *SPINACH*), movement trajectories were initially more curved in the direction of the red square than they were when the prime was either neutral or congruent, as shown in Figure 5. This indicated that the unseen prime stimulus is processed and embedded in an initial motor plan.

These results, which take advantage of stimuli blocked from awareness and the detailed trajectory information available in the continuous choice reaching task, indicate the possible existence of an early interaction between the dorsal stream and color-specific and word-specific parts of the ventral system.

Conclusions

The detailed analysis of reaching movement provides not only insights into visuo-motor behavior itself but also reveals new information regarding otherwise hidden internal events. All of the aforementioned examples in choice reaching tasks indicate that the action is not always the final product of perception and cognition; reach trajectories can reveal multiple competing representations in addition to intermediate products. This emphasizes a more unified conception of perception, cognition and action as well as their dynamic interactions at many levels even when categorical responses are required.

Thanks to the availability of affordable devices (Box 1), the measurement of reaching trajectories could become a readily available tool for cognitive neuroscientists. The measurement of a seemingly simple action can provide rich information about widespread brain events beyond the motor system.

However, the underlying mechanism of the leakage between cognition and action is yet to be fully understood. Is the early flow of cognitive states into action an essential characteristic of brain organization, or is it largely an epiphenomena stemming from discrete modular processes? Collaborative efforts across different fields are required to elucidate the extent to which information flow is continuous or discrete between the basic systems. For instance, a more thorough examination of reach trajectories with precisely controlled inputs could show whether discrete or continuous processes feed information into motor outputs [19,59]. Furthermore, neurophysiological studies can provide a finite temporal measure of the beginning and end of each stage at the neuronal level [60]. In contrast to well-studied neural correlates of curved saccades [61,62], those of curved reach trajectories in target choice tasks have not been examined.

Taken together, we look forward to new investigations, enhancing our understanding of a wide range interactive brain states in new and unforeseen ways using easily

Box 3. Questions for future research

- In target choice reaching tasks, time-varying intermediate products of cognition are reflected in final motor outputs (e.g. Figures 2–5). To what extent does this leakage represent essential information flow across perceptual, cognitive and motor systems beyond simple crosstalk? Can we develop more refined methods to make a distinction between discrete versus continuous information flow? Can target choice reaching tasks contribute to measuring the termination of one stage and the beginning of a subsequent stage in conjunction with various other techniques such as EEG and single-unit recordings?
- Underlying neural mechanisms of curved saccade trajectories in a target selection task have been examined [61,62]. However, less is known about neural substrates of reach target selection, and curved reach trajectories. Behavioral studies demonstrating curved reach trajectories [13,35,36,38] suggest that multiple reach plans are implemented during motor preparation phase even before movement execution. To what extent would the neural activity of reach preparation or execution predict changes of curved reach trajectories?
- Can one identify neural substrates involved in resolving the various forms of competition that occur while overt action is chosen? For example, are frontal-parietal networks involved in higher-order attentional allocations responsible for target selection?
- The temporal dynamics of real-time cognition, extending from dozens to hundreds of milliseconds has been revealed in studies using choice reaching tasks. How does cognitive development and learning [68] ranging from days to years, affect the underlying mechanisms that represent and resolve multiple internal processes?
- Choice reaching tasks have revealed interactions between ventral and dorsal visual streams by using invisible colors and words representing colors. What is the range of other inputs that can have similar effects?

applicable target choice reaching tasks in combination with other techniques (Box 3).

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References

- 1 Donders, F.C. (1969) On the speed of mental processes. *Acta Psychol (Amst.)* 30, 412–431
- 2 Sternberg, S. (1969) The discovery of processing stages: Extensions of Donders' method. *Acta Psychol (Amst.)* 30, 276–315
- 3 Warren, W.H. (2006) The dynamics of perception and action. *Psychol. Rev.* 113, 358–389
- 4 Spivey, M. (2007) *The Continuity of Mind*. Oxford University Press
- 5 Cisek, P. (2007) Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362, 1585–1599
- 6 McClelland, J.L. *et al.* (2006) Are there interactive processes in speech perception? *Trends Cogn. Sci.* 10, 363–369
- 7 Rosenbaum, D.A. *et al.* (2007) The problem of serial order in behavior: Lashley's legacy. *Hum. Mov. Sci.* 26, 525–554
- 8 Barsalou, L.W. (2008) Grounded cognition. *Annu. Rev. Psychol.* 59, 617–645
- 9 Cisek, P. (2007) A parallel framework for interactive behavior. *Prog. Brain Res.* 165, 475–492
- 10 Spivey, M.J. and Dale, R. (2006) Continuous dynamics in real-time cognition. *Curr. Dir. Psychol. Sci.* 15, 207–211
- 11 Balota, D.A. and Abrams, R.A. (1995) Mental chronometry: beyond onset latencies in the lexical decision task. *J. Exp. Psychol. Learn. Mem. Cogn.* 21, 1289–1302
- 12 Coles, M.G. *et al.* (1985) A psychophysiological investigation of the continuous flow model of human information processing. *J. Exp. Psychol. Hum. Percept. Perform.* 11, 529–553

- 13 Song, J-H. and Nakayama, K. (2008) Target selection in visual search as revealed by movement trajectories. *Vision Res.* 48, 853–861
- 14 Song, J-H. and Nakayama, K. (2008) Numeric comparison in a visually-guided manual reaching task. *Cognition* 106, 994–1003
- 15 Tanenhaus, M.K. *et al.* (1995) Integration of visual and linguistic information in spoken language comprehension. *Science* 268, 1632–1634
- 16 Rayner, K. (1998) Eye movements in reading and information processing: 20 years of research. *Psychol. Bull.* 124, 372–422
- 17 Van der Stigchel, S. *et al.* (2006) Eye movement trajectories and what they tell us. *Neurosci. Biobehav. Rev.* 30, 666–679
- 18 Magnuson, J.S. (2005) Moving hand reveals dynamics of thought. *Proc. Natl. Acad. Sci. U. S. A.* 102, 9995–9996
- 19 Spivey, M.J. *et al.* Do curved reaching movements emerge from competing perceptions? A Reply to van der Wel *et al.* (2009). *J. Exp. Psychol. Hum. Percept. Perform.* (in press)
- 20 Gold, J.I. and Shadlen, M.N. (2007) The neural basis of decision making. *Annu. Rev. Neurosci.* 30, 535–574
- 21 Tosoni, A. *et al.* (2008) Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions. *Nat. Neurosci.* 11, 1446–1453
- 22 Schall, J.D. (2005) Decision making. *Curr. Biol.* 15, R9–R11
- 23 Yang, T. and Shadlen, M.N. (2007) Probabilistic reasoning by neurons. *Nature* 447, 1075–1080
- 24 Georgopoulos, A.P. *et al.* (1982) On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J. Neurosci.* 2, 1527–1537
- 25 Kalaska, J.F. (1988) The representation of arm movements in postcentral and parietal cortex. *Can. J. Physiol. Pharmacol.* 66, 455–463
- 26 Kalaska, J.F. *et al.* (1983) Cortical mechanisms related to the direction of two-dimensional arm movements: relations in parietal area 5 and comparison with motor cortex. *Exp. Brain Res.* 51, 247–260
- 27 Cisek, P. and Kalaska, J.F. (2005) Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron* 45, 801–814
- 28 Barsalou, L.W. *et al.* (2007) Cognition, as coordinated non-cognition. *Cogn. Process* 8, 79–91
- 29 Crammond, D.J. and Kalaska, J.F. (2000) Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity. *J. Neurophysiol.* 84, 986–1005
- 30 Shen, L. and Alexander, G.E. (1997) Preferential representation of instructed target location versus limb trajectory in dorsal premotor area. *J. Neurophysiol.* 77, 1195–1212
- 31 Hesslow, G. (2002) Conscious thought as simulation of behaviour and perception. *Trends Cogn. Sci.* 6, 242–247
- 32 Jeannerod, M. and Johnson-Frey, S.H. (2003) Simulation of action as a unifying concept for motor cognition. In *Taking Action: Cognitive Neuroscience Perspectives on Intentional Acts*, pp. 139–163, The MIT Press
- 33 Woodworth, R.S. (1899) The accuracy of voluntary movement. *Psychol. Monogr.* 3, 1–114
- 34 Elliott, D. *et al.* (2001) A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychol. Bull.* 127, 342–357
- 35 Schmidt, T. (2002) The finger in flight: real-time motor control by visually masked color stimuli. *Psychol. Sci.* 13, 112–118
- 36 Tipper, S.P. *et al.* (1998) Action-based mechanisms of attention. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 353, 1385–1393
- 37 Welsh, T.N. and Elliott, D. (2004) Movement trajectories in the presence of a distracting stimulus: evidence for a response activation model of selective reaching. *Q. J. Exp. Psychol. A* 57, 1031–1057
- 38 Welsh, T.N. and Elliott, D. (2005) The effects of response priming on the planning and execution of goal-directed movements in the presence of a distracting stimulus. *Acta Psychol. (Amst.)* 119, 123–142
- 39 Howard, L.A. and Tipper, S.P. (1997) Hand deviations away from visual cues: indirect evidence for inhibition. *Exp. Brain Res.* 113, 144–152
- 40 Chang, S.W. and Abrams, R.A. (2004) Hand movements deviate toward distracters in the absence of response competition. *J. Gen. Psychol.* 131, 328–344
- 41 Song, J-H. and Nakayama, K. (2006) Role of focal attention on latencies and trajectories of visually guided manual pointing. *J. Vis.* 6, 982–995
- 42 Song, J-H. and Nakayama, K. (2007) Fixation offset facilitates saccades and manual reaching for single but not multiple target displays. *Exp. Brain Res.* 177, 223–232
- 43 Buetti, S. and Kerzel, D. (2009) Conflicts during response selection affect response programming: reactions towards the source of stimulation. *J. Exp. Psychol. Hum. Percept. Perform.* 35, 816–834
- 44 Spivey, M.J. *et al.* (2005) Continuous attraction toward phonological competitors. *Proc. Natl. Acad. Sci. U. S. A.* 102, 10393–10398
- 45 Dale, R. *et al.* (2007) Graded motor responses in the time course of categorizing atypical exemplars. *Mem. Cognit.* 35, 15–28
- 46 Boulenger, V. *et al.* (2006) Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *J. Cogn. Neurosci.* 18, 1607–1615
- 47 Feigenson, L. *et al.* (2004) Core systems of number. *Trends Cogn. Sci.* 8, 307–314
- 48 Ishihara, M. *et al.* (2006) Interaction between space and number representations during motor preparation in manual aiming. *Neuropsychologia* 44, 1009–1016
- 49 McKinstry, C. *et al.* (2008) Action dynamics reveal parallel competition in decision making. *Psychol. Sci.* 19, 22–24
- 50 Ungerleider, L.G. and Mishkin, M. (1982) Two cortical visual systems. In *Analysis of visual behavior* (Ingle, D. and *et al.*, eds), pp. 549–586, MIT Press
- 51 Goodale, M.A. *et al.* (2005) Dual routes to action: contributions of the dorsal and ventral streams to adaptive behavior. *Prog. Brain Res.* 149, 269–283
- 52 Clark, A. (2007) What reaching teaches: consciousness, control, and the inner zombie. *Br. J. Philos. Sci.* 58, 563–594
- 53 Lamme, V.A. (2006) Towards a true neural stance on consciousness. *Trends Cogn. Sci.* 10, 494–501
- 54 Dehaene, S. *et al.* (2006) Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn. Sci.* 10, 204–211
- 55 Milner, A.D. and Goodale, M.A. (1995) *The Visual Brain in Action*. Oxford University Press
- 56 Cressman, E.K. *et al.* (2007) On-line control of pointing is modified by unseen visual shapes. *Conscious. Cogn.* 16, 265–275
- 57 Finkbeiner, M. *et al.* (2008) Engaging the motor system with masked orthographic primes: a kinematic analysis. *Vis. Cogn.* 16, 11–22
- 58 McCandliss, B.D. *et al.* (2003) The visual word form area: expertise for reading in the fusiform gyrus. *Trends Cogn. Sci.* 7, 293–299
- 59 van der Wel, R.P. *et al.* (2009) Trajectories emerging from discrete versus continuous processing models in phonological competitor tasks: a commentary on Spivey, Grosjean, and Knoblich (2005). *J. Exp. Psychol. Hum. Percept. Perform.* 35, 58–594
- 60 Woodman, G.F. *et al.* (2008) The effect of visual search efficiency on response preparation: neurophysiological evidence for discrete flow. *Psychol. Sci.* 19, 128–136
- 61 McPeck, R.M. and Keller, E.L. (2002) Superior colliculus activity related to concurrent processing of saccade goals in a visual search task. *J. Neurophysiol.* 87, 1805–1815
- 62 McPeck, R.M. (2006) Incomplete suppression of distractor-related activity in the frontal eye field results in curved saccades. *J. Neurophysiol.* 96, 2699–2711
- 63 Song, J-H. *et al.* (2008) Target selection for visually guided reaching in macaque. *J. Neurophysiol.* 99, 14–24
- 64 Brouwer, A-M. and Knill, D.C. (2007) The role of memory in visually guided reaching. *J. Vis.* 7, 1–12
- 65 Culham, J.C. and Valyear, K.F. (2006) Human parietal cortex in action. *Curr. Opin. Neurobiol.* 16, 205–212
- 66 Pesaran, B. *et al.* (2008) Free choice activates a decision circuit between frontal and parietal cortex. *Nature* 453, 406–409
- 67 Taylor, J.A. and Thoroughman, K.A. (2007) Divided attention impairs human motor adaptation but not feedback control. *J. Neurophysiol.* 98, 317–326
- 68 Dale, R. *et al.* (2008) Exploring action dynamics as an index of paired-associate learning. *PLoS ONE* 3, e1728
- 69 Lashley, K.S. (1951) The problem of serial order in behavior. In *Cerebral Mechanisms in Behavior; the Hixon Symposium* (Jeffress, L.A., ed.), pp. 112–146, Wiley
- 70 Farmer, T.A. *et al.* (2007) Tracking the continuity of language comprehension: computer mouse trajectories suggest parallel syntactic processing. *Cogn Sci.* 31, 889–909