Ann. N.Y. Acad. Sci. ISSN 0077-8923

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Special Issue: *The Year in Cognitive Neuroscience*
REVIEW

# Models, movements, and minds: bridging the gap between decision making and action

Nathan J. Wispinski,[1] Jason P. Gallivan,[2,3,4] and Craig S. Chapman[5,6]

[1]Department of Psychology, University of Alberta, Edmonton, Alberta, Canada. [2]Centre for Neuroscience Studies, Queen's University, Kingston, Ontario, Canada. [3]Department of Psychology, Queen's University, Kingston, Ontario, Canada. [4]Department of Biomedical and Molecular Sciences, Queen's University, Kingston, Ontario, Canada. [5]Faculty of Kinesiology, Sport, and Recreation, University of Alberta, Edmonton, Alberta, Canada. [6]Neuroscience and Mental Health Institute, University of Alberta, Edmonton, Alberta, Canada

Address for correspondence: Nathan J. Wispinski, Department of Psychology, University of Alberta, P-217 Biological Sciences Building, Edmonton, AB T6G 2R3, Canada. nathan3@ualberta.ca

**Decision making is a fundamental cognitive function, which not only determines our day-to-day choices but also shapes the trajectories of our movements, our lives, and our societies. While immense progress has been made in recent years on our understanding of the mechanisms underlying decision making, research on this topic is still largely split into two halves. Good-based models largely state that decisions are made between representations of abstract value associated with available options; while action-based models largely state that decisions are made at the level of action representations. These models are further divided between those that state that a decision is made before an action is specified, and those that regard decision making as an evolving process that continues until movement completion. Here, we review computational models, behavioral findings, and results from neural recordings associated with these frameworks. In synthesizing this literature, we submit that decision making is best understood as a continuous, graded, and distributed process that traverses a landscape of behaviorally relevant options, from their presentation until movement completion. Identifying and understanding the intimate links between decision making and action processing has important implications for the study of complex, goal-directed behaviors such as social communication, and for elucidating the underlying mechanisms by which decisions are formed.**

**Keywords:** decision making; value; action; movement; perception

## Introduction: two halves of a whole decision

Imagine opening a refrigerator on a hot summer's day. To the left, a pitcher of iced tea, and to the right, a bottle of sparkling water with lemon. How do you decide between these two options, and how does this decision result in the movement required enacting it? As with all decisions, this involves reducing many choice options to only one goal. And, as with the types of decisions we focus on in our review, most goals require a physical action.

The first question at the heart of our review is, In what representational space is an option selected? According to good-based decision theories,[1–3] choice options are represented and are selected in an abstract value space where multiple sources of information are combined to construct a single subjective value for each of the options in a common neural currency.[4] In the most rigid of these theories, the highest value, winning option is selected and only then is an action planned to enact the decision.[2] At the other end of the spectrum are action-based decision theories,[5–9] wherein choice options are represented and selected within sensorimotor maps of space that directly reflect how each option is physically situated in the environment. Under this view, the representation of every option is sensorimotor in nature, reflecting details of the movement associated with acting on each alternative.

doi: 10.1111/nyas.13973

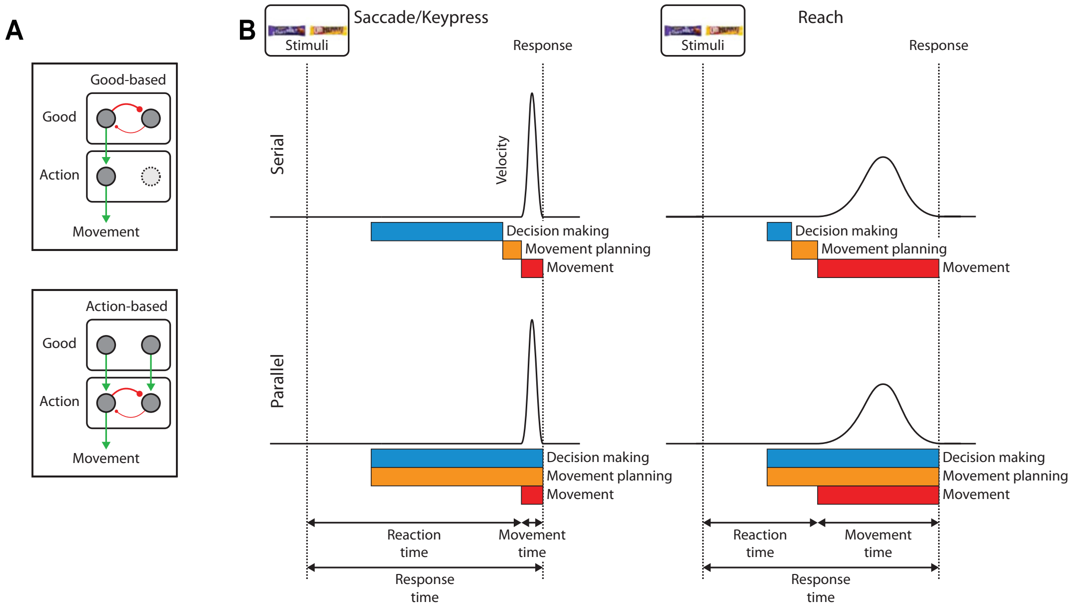

**Figure 1.** (A) Good-based models (top) state that a decision is made at the level of abstract values before an associated action is planned, while action-based models (bottom) state that a decision is made at the level of physical movements. (B) Serial and parallel processing timelines of decision making (blue), movement planning (orange), and movement (red) during a simple decision like choosing between chocolate bars. Choices requiring ballistic, short duration responses like saccades or key presses are shown on the left and those requiring longer duration responses like reaches are shown on the right. Good- and action-based schematics adapted from Ref. 158.

Following from this distinction, the second question central to our review is: When does a decision get made? Returning to the cold-drink-on-a-hot-day conundrum, good-based theories generally argue that you first choose the drink and then you plan the movement toward it; that is, the decision is made before the associated movement is specified. Conversely, action-based theories generally argue that movement representations toward both drinks are maintained in parallel; that is, the decision does not end until the movement is complete (Fig. 1). However, while good-based theories are often implicitly associated with serial processing and action-based theories are often implicitly associated with parallel processing, neither framework strictly requires that they conform to these specific temporal sequences of decision making.

When decisions are made and at which level options are selected has a profound impact on understanding the underlying neural architecture involved, why we choose certain options over others, and how we behave in between. For example, most action-based models would predict diverse and intimate neural connections between motor and perceptual systems for sensory decision information to shape motor representations, whereas good-based models would instead predict that an abstract value space mediates many of these connections. Additionally, action-based models would predict quicker responses after target selection, as the motor response associated with the selected option has already been specified in the sensorimotor system. It would also predict, however, that unselected movements might seep into movement execution.

Our review is broadly structured into three parts. The first two parts address good- and action-based models each in turn and reviews formal models, and behavioral and neural data in support of the theory. In the last part, we review recent models, behavior, and neural findings that have made progress in bridging the gap between good- and action-based decision-making models. As with most problems in cognitive neuroscience, what initially appears to be a stark divide in theory is likely a result of dichotomous thinking—the real answer likely lies somewhere in between. In this review, we do not attempt to put forth a unifying theory of decision making, but rather identify gaps in our understanding and aim to outline current evidence for the three lines of thought.

## Good-based models: from stimulus to reaction time

Good-based models of decision-making state that the selection of available options occurs at the level of abstract value representations.[2,3] In this review, our use of the term *value* is specific to the task at hand. For example, in a perceptual decision task, like deciding in which direction a pattern of noisy dots is moving[10] (Fig. 2A), value is derived from perceived motion direction. By comparison, in a task like deciding between two chocolate bars,[11] value is derived from subjective preference. One of the most parsimonious features of a good-based model is that it is agnostic with respect to what information is used to construct value, since there is an abstract common currency on which an arbiter can judge. With respect to the relationship between a decision and the action associated with enacting it, a good-based model treats the decision process as a distinct module in a serial process (Fig. 1). Once perceptual processes have delivered a representation of the choice options, and decision processes have selected one for action, only then is the corresponding movement planned. To expand upon this serial architecture of decision making and movement, we first describe bounded evidence accumulation decision-making models. These models are distinct from good-based decision-making models since bounded accumulator models are typically agnostic regarding the level at which options are selected, and instead focus on how selection occurs. However, most bounded accumulation and good-based models share the common assumption that decision making is complete before movement processes that enact the decision begin.

### *Model*

The most prominent (though by no means only) class of decision-making models are those based around the accumulation of evidence to a threshold.[12,13] Here, the information relevant to a decision (i.e., evidence) is repeatedly sampled from the external world, or from internal sources such as memories.[14] Evidence for or against a particular option is added over time. When this accumulated evidence in support of a particular option crosses some threshold, the decision is made (Fig. 2B). For example, in the random dot motion (RDM) task,[10] moving dots are presented to a participant who is asked to discriminate the net direction of the dots (e.g., left versus right) (Fig. 2A). Decision difficulty is manipulated by the amount of dots moving in the same direction on each trial (i.e., coherence). Additionally, the stimulus is noisy, as the remaining "noncoherent" dots move in random directions. Evidence accumulation models argue that subjects arrive at decisions in this task by sequentially sampling small portions of the motion stimuli. This information is processed to extract whether, and how much, the motion sample favors responding left or right. This evidence is then added to left and right accumulators in the brain and sampling continues until some decision criterion based on accumulated evidence is met (Fig. 2B).

Two of the most widely used evidence accumulation models are deemed race[15] and drift-diffusion/random walk models.[16,17] Race models state that a decision is made the first time any one of multiple independent accumulators crosses some fixed decision threshold. In contrast, drift-diffusion models state that decisions are made based on relative evidence—the difference in evidence between options is accumulated until reaching an upper or lower bound corresponding to the two options under consideration (Fig. 2B). It is beyond the scope of our review to summarize the support for and against the many kinds of bounded evidence accumulation models, but in general, these models account for behavior in a wide range of tasks[18,19] (Fig. 2C). Indeed, there is a mathematical elegance in this approach—the process of evidence accumulation is intimately related to signal detection theory[20] and Bayesian inference,[21] and is regarded as optimal in some sense.[22]

While broadly successful, recent research shows decision making is more complex than simple evidence accumulation models can describe. Models need significant elaboration to account for very early responses,[23] the dynamic cost of accumulating evidence for a decision,[24,25] the growing urgency to make a response,[26,27] or, on the other end of the spectrum, the ability to refrain from making a decision (often accomplished via "leaky" accumulators).[28]

Regarding the two central questions of our review, bounded evidence accumulation models are largely agnostic to what exactly is being represented during

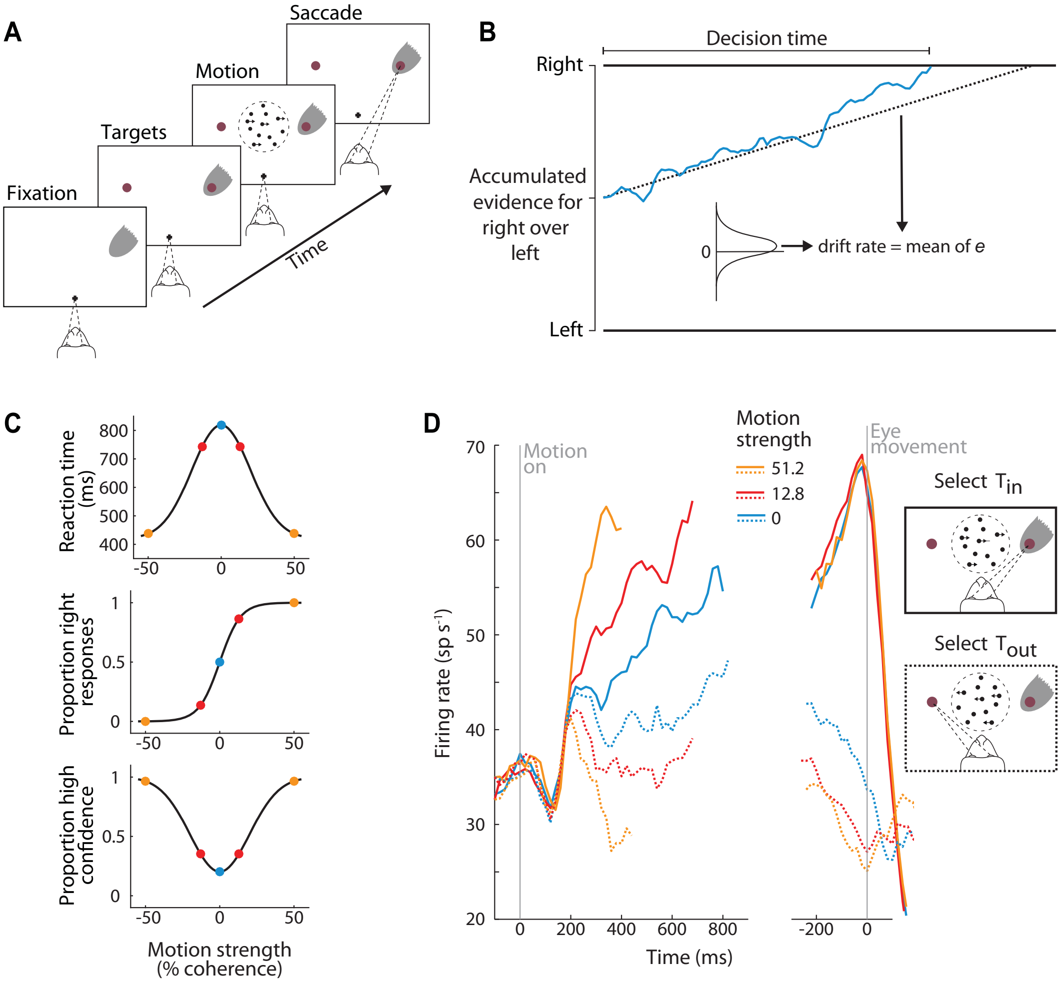

**Figure 2.** Findings from investigations on the mechanisms underlying perceptual decision making. (A) Trial structure of a typical random dot motion (RDM) task. After maintaining fixation, left and right targets appear (dark red). Animals are trained to execute a saccade to the target corresponding to the net direction of the moving dots. Moving dots appear within a central region of the screen, some of which move coherently left or right, while the remaining dots move in a random direction. Gray region indicates the receptive field of neurons typically recorded in this task. (B) Schematic of a drift-diffusion model applied to decision making on a single trial. Motion from the stimulus is sampled, and the difference in motion evidence for left and right target choices is accumulated (typically modeled as a normal distribution; see inset). When the accumulated evidence (blue trace) crosses a specified bound, the respective response is executed. (C) Example behavioral results in the RDM task. As the stimulus includes more coherently moving dots, reaction time decreases, accuracy increases, and confidence in the executed choice increases. (D) Average firing rates of recorded LIP neurons in the RDM task. Average firing rates of LIP neurons increase (or decrease) in proportion to the motion evidence favoring a saccade toward the receptive field of the recorded neuron. Average firing rates of LIP neurons reach a common firing rate "threshold" before a saccade is executed in the direction of the corresponding receptive field. Panels A, B, and D are reproduced and adapted from Ref. 12.

choice competition but are fairly committed to the position that decisions are made before movement execution (i.e., the crossing of a decision threshold). That is, evidence accumulation can as easily be applied when what is being accumulated is a representation of abstract value (good-based) as it can if what is being accumulated reflects the value of specific planned movements (action-based). However, when it comes to the timing of decisions, bounded evidence accumulation models generally assume that the decision process is complete before a movement is initiated, mirroring a serial process of perception, decision making, and finally movement planning.

### *Behavior*

Recent reviews identify the "three pillars of choice behavior" as accuracy, reaction time, and confidence,[29,30] and it is the measurement and explanation of these three outcomes across a variety of tasks that grants bounded evidence accumulation models their status as one of the best theoretical accounts of decision making. Classically, signal detection theory[20,31] can explain choice accuracy (and perhaps confidence) but not choice timing. However, evidence accumulation with recent additions can account for all three.[32] While it is beyond the scope of our review to exhaustively describe these additions, it is useful to highlight that a successful decision theory should be able to account for how accuracy, reaction time, and confidence vary as a function of decision difficulty.

In a good-based framework, decisions vary in the degree of value similarity between available choice options. Two options that have very similar value will be harder to decide between, while two options that have disparate value will result in easier decisions. Classically, easier decisions are resolved more quickly and more accurately, leading to faster reaction times and more correct responses. Conversely, hard decisions take longer to make and result in more errors.

The effects of decision difficulty are particularly evident in psychophysical tasks of perceptual discrimination like the RDM task (Fig. 2A). The decision difficulty is manipulated by changing the number of dots moving coherently from very easy (100%) to very hard ($<5\%$). The general finding in these tasks is that as coherence is reduced, accuracy decreases and reaction times get longer[33] (Fig. 2C). Similar results on accuracy and reaction time are abundant, even in the less-represented domain of decisions based on subjective value.[6,34,35]

Recent additions[30] or extensions[36] to evidence accumulation models can account for reductions in confidence with increases in decision difficulty. In a modified RDM task, in addition to the usual left and right choice options, Kiani and Shadlen presented monkeys a third "safe bet" option on some trials which gave a smaller "sure" reward. This allowed the monkeys to opt out of making a decision and instead take a small certain gain. Consistent with predictions from an evidence accumulation model when the trials were more difficult, monkeys more often opted for the safe bet.[36]

Here, we define the three key behavioral outcomes that decision-making models must account for when decision difficulty is varied: as choice options become more similar, reaction times increase, while accuracy and confidence decrease (Fig. 2C). These features are well accounted for by robust models within a bounded evidence accumulator framework or the broader good-based theory, which state how the values of options are constructed, represented, and compared in order to ultimately select an action. Of note, these are all behavioral features that occur up to and including reaction time, but not after.

### *Neural*

Strong neural evidence for both good-based competition and bounded evidence accumulation models in part affords the high status they enjoy within cognitive neuroscience and beyond.

In an exemplary group of studies, researchers recorded from the nonhuman primate (NHP) lateral intraparietal cortex (LIP), a brain area involved in oculomotor control,[37] while monkeys perform the RDM task. The neural responses are strikingly consistent with bounded evidence accumulation models[38–41] (Fig. 2D). Firing rates of LIP neurons increase (or decrease) over time proportional to the amount of motion evidence favoring a saccade into the preferred direction of the recorded neuron. When the firing rate reaches some fixed threshold, a saccade is generated in that direction. This pattern is exactly consistent with that predicted by bounded evidence accumulation models—an accumulation of evidence in favor of each option until a threshold is crossed to execute an action.

Further experiments have provided even stronger support for this hypothesis. Short pulses of background motion during the RDM task briefly enhance or suppress the increase in firing rate for neurons associated with the correct response.[42] Subthreshold stimulation of LIP neurons increases the proportion of saccades in the stimulated direction, and decreases their reaction times, as does subthreshold stimulation of the earlier motion-sensitive middle temporal visual area (MT), through which LIP receives significant input.[43] Together, this suggests that momentary motion evidence in the RDM task is computed within MT, and the accumulation of this evidence occurs downstream within LIP. Studies in humans using magnetoencephalography,[44] electroencephalography,[45] and functional magnetic resonance imaging (fMRI)[46] have also shown support for bounded evidence accumulation. While these experiments might seem to support choice selection at the level of saccades tuned to specific directions (action-based), others have argued that these patterns might instead simply reflect the motion direction of the random dot stimulus.[47] Furthermore, the idea that LIP plays a causal role in evidence accumulation is being reevaluated in light of recent experiments implementing pharmacological or optogenetic LIP inactivation, which fail to show corresponding deficits in decision making.[48–50] These challenges to LIP-based decision models give rise to the idea that perhaps options are represented and selected elsewhere in the brain, but at the same time do not invalidate the bounded evidence accumulation mechanism.

In support of a good-based decision-making model, studies have found evidence that the abstract value of available options is represented by orbitofrontal cortex (OFC) neurons integral in option selection. In a seminal experiment, NHPs made saccades to a left or right target offering different amounts of different kinds of juices, which the NHP would then receive.[1] The overwhelming majority of recorded neurons in the OFC were either sensitive to the amount of a particular type of juice offered, the type of juice the NHP was about to select, or the amount of juice the NHP was expecting to receive. In this task, the types and amounts of each juice option are sufficient for a rich representation of value, and the presence of neurons specifically encoding what option was to be chosen suggests the OFC may have a critical role in option selection. Importantly, neuronal responses were not found to vary with the spatial configuration of the options, nor with the direction of the upcoming saccade, suggesting the representations of value in the OFC were truly abstract. Other studies in NHPs have also shown little sensitivity to motor properties in OFC neurons despite significant sensitivity to aspects of subjective value.[51,52] Furthermore, while associations to specific actions are difficult to parse with human fMRI data, value signals in a wide range of tasks and contexts have likewise been reported in the OFC.[53–55]

### Discussion

The frameworks reviewed above are well supported and, as we will argue, are necessary for a complete understanding of the mechanisms underlying decision making. The bounded evidence accumulation framework provides an elegant explanation regarding how options are selected, and a good-based theory provides a convincing solution as to how value is constructed and represented in the first place. However, they share a common limitation in that they generally argue a decision is complete before a movement is initiated.

In the vast majority of tasks to which these frameworks have been applied, the decision to move (measured via reaction time) is temporally bound with the movement outcome (measured via response time; Fig. 1). That is, saccadic eye movements,[1,41] button presses,[45] and verbal responses are essentially ballistic—reaction and response time are treated as the same value. Thus, it is perhaps unsurprising that many models do not account for decision making *after* movement initiation—indeed, in most tasks, this does not even exist. However, in the real world, the execution of most decisions takes time. The temporal protraction of movement has important implications for decision making; if an animal moving through a dynamic world wants to be optimally responsive to their environment,[5] it would be maladaptive to wait for one movement to complete before initiating a new decision process. Such models may also be a byproduct of the tasks used—decisions are studied in sequential isolation, deliberately separated by intertrial intervals. However, in the real world, new decision alternatives are constantly appearing or shifting, and require constant updating. This need to account for more ecologically relevant scenarios brings us to discuss another framework—action-based models, which may be particularly suited to account for decision making after movement initiation.

## Action-based models: from reaction time to end of movement

Action-based models of decision-making state that available options are represented and selected in sensorimotor maps,[5,6,56,57] where options preserve their relative spatial relation to the deciding agent. For example, when reaching for the pitcher of iced tea or the bottle of sparkling water (Fig. 3), both candidate objects would become activated in a map (or,

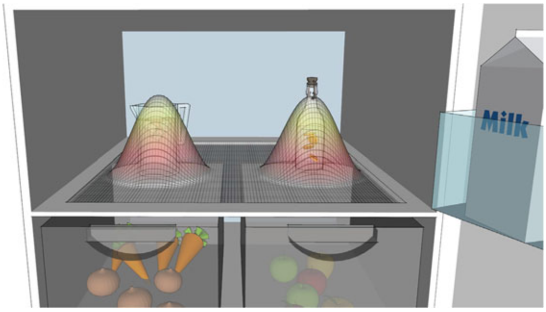

**Figure 3.** A visual depiction of how the brain might use a relevance landscape to represent the value of actions associated with real objects. Here, both a pitcher of iced tea (left) and bottle of sparkling water (right) are desirable drink options on a hot day. According to action-based models, both would have positive neural representations (e.g., hills of activity) in brain areas involved in specifying hand actions.

more likely, multiple maps) of space preserving their relationship on the refrigerator shelf. Moreover, this topographic representation, at least in some maps, would contain information about the movements associated with successfully interacting with the object—also known as the object affordance.[58] These affordance competition maps[5,59] give rise to what have been called attentional landscapes[60] or desirability density functions.[7,9,56] According to action-based models, when one object is chosen, what is being selected is not some abstract representation to which an action then needs to be planned, but rather, some aspect of the action itself. Thus, decision making from an action-based framework can be viewed as representing the value of available actions, which shifts the body through the real world as a means of traversing a landscape of behavioral relevance specified in a neural map.[7]

### Model

In contrast to good-based decision-making models, few computational models within an action-based framework have been proposed. One of the earliest computational models, aimed at explaining observed neural data, consists of layers of simulated neurons in a frontoparietal network.[61] In this model, multiple competing actions are represented in parallel at several levels of the network and compete for selection. This model, while successful at recreating observed neural patterns, does not predict any specifics of how a movement is enacted.[61] A more recent action-based computational model accounts for both neural data and observed reaching movements during decision making.[62,63] This model integrates the value of options and goal-relevant information into a dynamic neural field, which simulates the activity of hundreds of neural populations each tuned to a different direction in space. These directionally tuned neuronal populations compete, and if any population reaches a specified activity threshold, an optimal control policy[64] for reaching in that direction is activated. A weighted average of active policies then determines how the hand moves before the process is updated by a new state of the hand in space. In essence, this model specifies that value influences representations for specific actions, and that option selection, rather than being specified solely before movement, is an outcome of a process that evolves during movement.[5,59,62]

Other models have mostly ignored accounting for neural data and instead, focus on accounting for specific movement features. For example, movement trajectories toward targets and away from obstacles are strikingly similar to a model of attractors and repellers in a dynamical system.[65] Similarly, attractor landscape models provide an appealing account of how the hand (or computer mouse) moves through space in decision-making tasks.[66–68] These models show that action-based mechanisms provide many convincing frameworks to explain how animals decide when moving and move when deciding.

Regarding our two key questions, action-based models postulate that decisions are made through the competition at the level of actions and most of these models state that decisions are complete only when the movement enacting the decision is finished (cf. Ref. 69). By and large, however, these action-based models suffer the opposite problem from that of many good-based models: they rarely explain or even attempt to explain the three classic behavioral hallmarks of decision making—reaction time, accuracy, and confidence—and instead, focus almost entirely on explaining what happens after a movement has been initiated.

### Behavior

In the set of behaviors a decision theory should account for, changes of mind have emerged as a fourth alongside choice accuracy, reaction time, and confidence. A change of mind refers to the infrequent (e.g., 5%) but a reliable observation

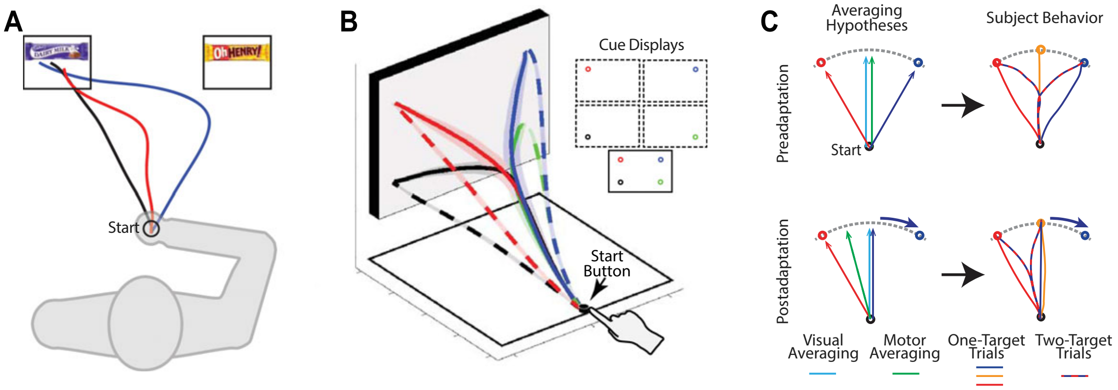

**Figure 4.** Behavioral evidence for an action-based framework of decision making. (A) When choosing between chocolate bars, participants sometimes move straight toward the chosen option (black), sometimes move on an intermediate path between options before committing (red), and sometimes move toward one option before changing their mind and switching to the other option (blue). From unpublished data. (B) In a go-before-you-know task, participants are required to initiate a reach movement toward a cue-display before the final target is revealed (after movement onset). When there is only one potential target presented (dashed traces), the hand moves straight toward its location. When four potential targets are presented (solid traces), the hand initially moves midway between all targets (spatial averaging) before correcting to the cued final target. Adapted from Ref. 84. (C) To test whether average movements (Fig. 4B) are visual (predicted, blue, left) or motor (predicted, green, left) in nature, participants were gradually adapted to visuomotor rotations, which shifted their hand from a distinct reach to a single right target (blue, top) to a central reach for a single right target (blue, bottom). When simultaneously presented with the left and right targets (dashed, right) after adaptation (bottom), participants reached in a direction that averaged between movements, not visual, directions. Adapted from Ref. 92.

that individuals will sometimes initiate an action toward one choice option, but then switch to another choice option before the action is completed (Fig. 4A).[70–73] These changes of mind are overwhelmingly corrective (i.e., they shift actions from incorrect to correct targets), indicating that they are based on a decision process that continues throughout movement[71]—something outside the scope of most good-based models.

Further evidence for the continued access to, and influence of, decision information on in-flight movements can be seen in what is a now a long list of studies showing the influence of multiple potential targets on both eye[74,75] and hand movements.[76–79] A particularly acute demonstration can be found in so-called *go-before-you-know* tasks (Fig. 4B), wherein participants are required to move before knowing which of several potential targets is the final option.[80,81] Under these conditions, participants initially execute an averaged movement between both options before ultimately selecting one. Furthermore, it has been shown that the probability,[81] number,[80,82,83] spatial arrangement,[80,84] luminance,[85] reward-association,[86,87] and symbolic representation[88] of targets all impact rapid reach trajectories.

But what exactly is the nature of option representations that give rise to this behavior according to action-based theory? Some researchers argue that curved or averaged reach trajectories reveal value represented at the level of possible states associated with movements, which then are used to optimize a single movement control policy.[89] One such model proposes that effort, accuracy, and evidence for each available option act as inputs along with the state of the arm to form a single optimal control policy.[90] Other researchers argue that these trajectories reveal the representation of multiple competing motor plans.[80,91] While distinct, both views largely acknowledge that (1) decisions move from a space with many options to an action space with only one eventual movement, (2) ultimate movement output is largely based on the optimization of a single action and not a literal average of simultaneously executed movements, and (3) that fluctuations in the value of multiple and simultaneously held motor representations can influence the single resultant movement.

Thus, one of the most pressing questions facing action-based models is What information is available in parallel motor representations? The above studies show this information reflects both bottom-up (e.g., luminance, see Ref. 85) and top-down (e.g., learned reward, see Ref. 87) factors. But are there properties about the details of the movement beyond the spatial (and usually visual) endpoint? To directly dissociate visual target from reach directions, Gallivan *et al.*[92] used a visuomotor adaptation task (Fig. 4C). Over a series of trials, a gradual, imperceptible rotation of reach direction was applied such that eventually, two targets separated visually by 30° required identical straight-ahead movements. Critically, in go-before-you-know trials toward one adapted target and one nonadapted target, the hand direction followed the motor midpoint (e.g., was shifted by the adapted target's rotation) and not the visual midpoint. Consistent with other studies,[93,94] these findings support the notion that the brain directly maps visual target locations onto associated motor representations, and uses these to compute initial movements in cases of competing targets. Such a mechanism might support the specification of initial movement directions that minimize the cost of corrected movements to the targets once selected,[90] thereby reconciling the optimization of motor goals with the averaging of motor representations.[80]

A recent study has extended these findings to a go-*after*-you-know task.[95] Here, participants viewed two targets of varying orientation and, when one of the targets was cued, were required to rapidly orient and place the tip of a handheld tool on that target. Movements toward an ambiguously oriented target (i.e., one that could equally be reached via wrist pronation or wrist supination) were biased by the noncued target, more often matching its orientation, even though it was never an explicit movement target. The fact that this "co-optimization" effect emerged in a go-*after*-you-know task suggests that multiple movements (in this case, wrist orientations) were specified in advance of target cueing. This raises the important question: Why would the brain expend its limited resources to directly map competing visual targets onto associated motor representations? According to action-based models, the preparation of multiple potential movement representations might support the rapid execution of any one of the possible movements if required (see Ref. 5). Results from the co-optimization experiments support this claim since individuals exhibited faster reaction and movement times on trials in which the co-optimized wrist posture was selected versus trials in which it was not selected.[95,96]

Action-based models are also consistent with many experiments regarding how motor-related costs factor into decision making. Cos *et al.*[97,98] provide compelling support for action-based models by showing that when individuals make free choices between two potential reaching movements, which vary in motor-related costs (e.g., energy, stability, distance, etc.), they tend to choose the movements that are biomechanically easiest[98] and simplest to control.[97] Importantly, this indicates that information about the predicted biomechanical costs of both candidate movements is available to the decision-making process. Going further, neurostimulation within 200 ms of target presentation suggests a causal role of motor cortex in these rapid, automatic predictions.[99] Other recent work further shows that the costs associated with motor control bias decision making between actions.[100–102] While the impact of motor costs on decision making is not limited to action-based models—for instance, good-based models can account for motor costs through learning or association—the representation of options in a sensorimotor space provides a convincing and direct way for motor information to influence value.

The role of biomechanical costs in decision making has also been extended to changes of mind. Studies show that when the motor costs associated with redirection are increased (through distance[103] or force fields[70]), changes of mind become more infrequent. Motor costs can even affect perceptual decision making when participants are unaware of them (i.e., when they are introduced very gradually), and these can bias verbal reports of perceptual discriminations, even when they are conveyed through a completely different effector system.[104] Together, this work indicates that the motor system, rather than merely reflecting the output of upstream perceptual processing, can itself influence perceptual processes and the transformation into decision space.

### *Neural*

Unlike the predictions from a good-based framework which argues that option selection precedes action specification,[2,105,106] neural recordings often show parallel action-based representations throughout the decision process.[59,91,107]

Several studies of neural responses have shown that before a decision is made, value is not only represented abstractly,[1] but also with associations

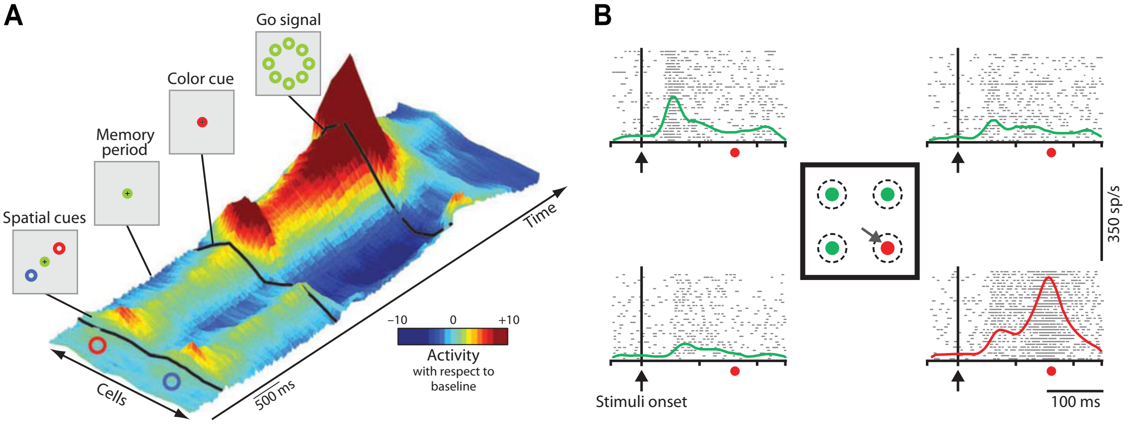

**Figure 5.** Neural evidence for the representation of competing movement options. (A) Population activity in dorsal premotor cortex while NHPs performed a delayed reaching task. Cells sorted by preferred direction along the bottom edge reveal sustained encoding of two potential reach directions when the final direction was unknown, even during a period when the potential targets were not visible. Reproduced from Ref. 59. (B) Simultaneous recordings of four superior colliculus neurons with receptive fields (dashed circles) for three distractors (green) and one target (red). Each tick represents an action potential, and each row of ticks represents one trial (31 trials total, all correct). The black arrow represents stimuli onset, and the red circle represents the average saccade latency. Spike density functions for each neuron are overlaid on each raster plot. The discriminability of target and distractor neuronal activity was found to predict performance. Adapted from Ref. 130.

to specific actions (often called action-value responses).[34] For example, studies have documented neurons whose firing rates are sensitive to the value of a leftward saccade on each trial.[41] Human fMRI, and NHP and rodent electrophysiological recordings have observed action-value responses in several brain areas including the anterior cingulate cortex,[108–110] frontal eye fields (FEFs),[111] LIP,[9,112] striatum,[113,114] basal ganglia,[115] dorsolateral prefrontal cortex,[116] superior colliculus (SC),[117–119] and the supplementary motor area.[120,121]

In a seminal study, when NHPs had to hold in mind two possible reach targets, dorsal premotor neural population activity increased in the directions of both potential targets[107] (Fig. 5A). In a more recent extension, it was shown that this activity was also evident if the possible reach directions were specified by rules, rather than spatial targets.[122] This activity reflecting multiple motor representations was observed even though the NHPs could have simply waited for the correct option to be cued before representing the single corresponding movement.

Similar neurophysiological results have also been observed in oculomotor tasks.[123–129] For example, simultaneous recordings from SC (an oculomotor structure only a few synapses removed from the eye muscles) neurons with nonoverlapping receptive fields mapped the competition between targets and distractors[130] (Fig. 5B). Specifically, the difference in simultaneous activity between target- and distractor-related neurons predicted task accuracy of the NHP. The link between multiple eye movement representations and decision making is even clearer in a study showing that subthreshold stimulation to SC neurons influenced the eventual choice.[131] These findings appear to directly refute the good-based account[2] wherein value—the determinant factor of a choice outcome—should not be altered by neural stimulation of a putative motor structure.

## *Discussion*

In many ways, action-based models are the mirror image of good-based models with the reflection point occurring at the moment of movement initiation—they are two halves of the same decision. That is, whereas good-based theories provide convincing mechanisms for decision making during reaction time but lack explanations for much of movement time behavior, action-based theories tend to lack explanatory richness for reaction time mechanisms but offer compelling explanations for behavior during movement time. This is highlighted in the key experiments discussed above. Experiments that use ballistic responses such as keypresses or eye movements, which either do not allow for or mitigate post movement decision processes, ultimately force a decision to be resolved entirely during the reaction time period. In our view, this scenario does not reflect the vast majority of evolutionarily old and ecologically valid decisions for which the primate brain is organized—for example, moving through the world when deciding where to forage. However, in the same way, experiments that force movement initiation so that decisions are resolved entirely during the movement time period are similarly lacking, and again do not reflect the majority of decisions for which the primate brain is organized. Framed this way, it should be clear that regarding the competition between choice options, there is nothing particularly special about the time of movement onset—competition occurs before and continues after movement initiation. Granted, if a movement is very brief (e.g., as in a keypress or eye movement), and reaction time and response time collapse, then the movement is the end of the decision. However, in the real world, where actions enacting a choice are often voluntary and evolve over several hundreds of milliseconds or more, decision making that was initiated when options were presented evolves through reaction time and can continue to unfold during movement. In particular, the sequential sampling of evidence for a decision after stimuli onset (good-based models), and the competition between multiple motor representations during movement (action-based models), while each with their own limitations, may reflect a continuation of the same process.

## Bringing two halves together: decision making as a continuous process

Theories of decision making that cross the boundary between reaction and movement times are beginning to be more prevalent. This shift has been necessitated, in part, by behavioral observations of competition and changes of mind during movement. In fact, a change of mind is precisely the case where a (mostly resolved) competition during reaction time leads to a movement being initiated toward one option, but then further competition during movement time leads to a revised decision. The majority of the models we review here have therefore been concerned with predicting the frequency of a change of mind given the competition evident during reaction time.

### *Model*

Computational models aimed at bridging the gap between pre- and post-movement decision making are relatively recent and comparatively rare. The most prominent of these is the changes-of-mind model (CoMM) by Resulaj *et al.*,[71] which states that decision making both before and after movement initiation is based on a single, continuous process of evidence accumulation. Like a drift-diffusion model,[17] the CoMM states that subjects base their decisions on the accumulated difference in evidence between options. When accumulated evidence crosses a decision threshold associated with one of the options, the subject initiates an "initial choice" movement straight toward that option. Unlike other bounded evidence accumulation models, however, evidence sampled just before an initial choice that has not yet been processed continues to accumulate, even during movement. If this postinitiation evidence causes the crossing of a new threshold, the subject changes their mind and begins moving straight toward the other option. This CoMM predicts and explains reaction times, accuracy, and the frequency of changes of mind. It is particularly powerful in that it can explain our flexibility to adapt actions as needed, all while preserving the elegant mathematics of an evidence accumulation process. Furthermore, a recent refinement,[73] adapting a race model,[15] is able to explain changes in confidence as well.

However, in these models, threshold crossing determines one action, and if another threshold is crossed, another action is selected. This discrete switching between actions cannot explain several highly related behavioral phenomena reviewed above which support action-based models, such as intermediate movement trajectories[80] (Fig. 4A). Other models have likewise attempted to unify decision making before and after movement initiation by associating an evidence accumulation process with aspects of movement.[90,133,134] While this method has proven successful, several important behavioral and neural phenomena remain unaccounted for.

### *Behavior*

Some of the best support for the idea that decision making is a single and continuous process that traverses stimulus presentation to movement completion comes from research that explicitly manipulates the amount of decision information prior to observable behavior (early work reviewed by Meyer *et al.*[135]). Approaches to this problem have included fitting to reaction time distributions (as in evidence accumulation models[19]), analyzing the conjunction of reaction time and kinematic parameters during response time,[136,137] or looking for evidence of motor priming.[138,139] Here, we focus on experiments that manipulate the speed–accuracy tradeoff. It is well known that increasing the speed of a movement also increases its variability,[140] and increasing the speed of a decision decreases its accuracy,[141] suggesting that by forcing participants to respond faster than is natural, they are forced to act with less accumulated evidence.

Ultimately, however, even the analysis of speed–accuracy tradeoffs is somewhat impoverished since changes in accuracy or reaction time, while intimately linked to the amount and quality of evidence accumulated, can also arise for a variety of other reasons.[142] To address this limitation, some research directly forces partial information by decoupling the stimulus cueing movement (the imperative stimulus) from the stimuli you are responding to (the test stimulus), thus varying the stimulus–response interval (SR interval, see Fig. 6). By using these timing techniques and observing changes in movements, researchers have access to a continuous measure that reflects ongoing decision making started during reaction time.[76] Adapting a rhythmic responding task,[141] Ghez *et al.* developed a *timed response task* where the imperative stimulus was the fourth of four repeated tones and the test stimuli were visual targets toward which restricted arm movement responses were required.[143] By varying the SR interval, Ghez and colleagues were able to map the evolution of this response (Fig. 6A). With less processing time (<80 ms), initial movement directions were averaged between unpredictable targets (akin to go-before-you-know tasks, see Ref. 80) but with more processing time (>200 ms), responses were more directed toward the correct target. However, these results also demonstrated that the decision between movement targets was influenced by spatial layout.[144] If targets were closer together, averaging was more evident and lasted for longer SR intervals. But, if they were further apart, intermediate movements were reduced and even eliminated[89,144] (Fig. 6A). This implies that ongoing decision making must be informed early on by the potential motor consequences for each available option.

Chapman *et al.* recently extended this technique to explore the temporal evolution of a higher order decision bias between options with positive and negative values. Participants made a rapid reach choice (average RT ∼250 ms) as soon as they heard an imperative auditory tone[87] (Fig. 6B). Approximate SR intervals ranged from –50 ms (move before test stimuli appear) to 750 milliseconds. These results showed clear evidence of the evolution of a value-based decision—reaches were more curved with less time to process targets. They also demonstrated a clear temporal advantage for processing gains relative to losses. A recent follow-up study has shown that this competition revealed through reaching is prevalent even in relatively slow, self-initiated movements.[145] Furthermore, other research shows that the instantaneous changes in movement angles can reveal how competition between options and sources of decision evidence evolves over time.[146,147] In sum, these studies are consistent with competition being initiated during reaction time, but now seeping into response time and affecting movement.

Another tool used to probe the evolving competition between options has been to force movement initiation via the startle response.[148] In general, a loud auditory tone will elicit an electromyogram (EMG) signal from upper arm muscles after ∼70 ms and an arm movement after ∼115 ms—much faster than normal reaction times. When multiple options are available for selection, the startle response reveals clear cases of the representation of multiple options at a motor level.[149,150] In another line of work, the imperative stimulus was instead a mechanical perturbation causing an elbow extension and a resulting stretch reflex, and the key dependent measure was the EMG of the resulting reflex response as participants performed the RDM task.[72] Critically, the strength of the reflex (within 75 ms) was sensitive to both the direction and strength of evidence.

Other novel techniques show just how far the competition between options during decision making flows downstream. For example, experimenters read out motor excitability during value-based decision making by applying transcranial magnetic stimulation (TMS) over the motor cortex and measuring the motor evoked potential (MEP)[151] (Fig. 6C). By varying the timing of the TMS pulse,

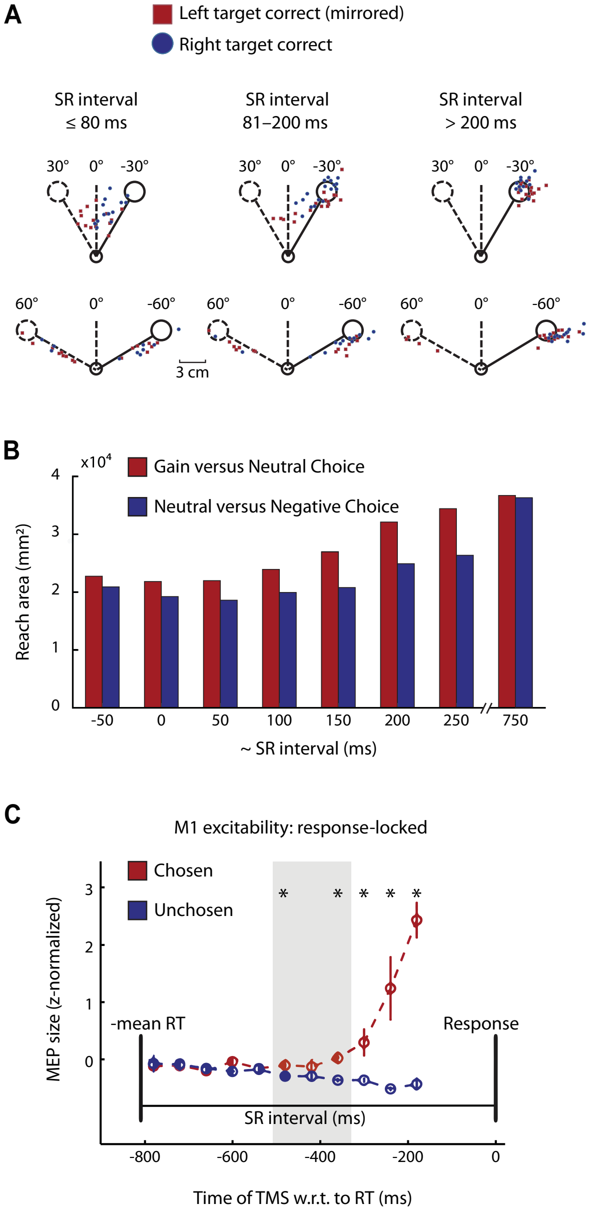

**Figure 6.** Behavioral evidence for the evolution of decision information both before and during movement. (A) Reaches toward unpredictable targets produce trajectories that average between directions when target separation is small (± 30°, top row) and the stimulus–response interval (SRI) is short (left). When the SRI is long, (right) reaches are directly toward the correct target. When target separation is large, (± 60°, bottom row), participants are forced to guess with short SRIs. Movement amplitude (not shown) was also varied, accounting for the observed undershoots. Adapted from Ref. 144. (B) Participants rapidly reached to choose positive over neutral targets (red) and neutral over negative targets (blue). Depicted is the area between reaches toward correct targets on the left and right (larger area corresponds to straighter reaches). The SRI was approximated by subtracting the average RT (~250 ms) from the test stimuli presentation time. Short SRIs led to more competition (curved reaches) and choosing positive targets showed a consistent temporal advantage (straighter reaches) except for the shortest and longest SRIs. Adapted from Ref. 87. (C) Response-locked analysis of changes in primary motor cortex (M1) excitability to transcranial magnetic stimulation (TMS) pulses, measured via normalized motor evoked potentials (MEPs) toward chosen (red) versus unchosen (blue) options. Since the MEP is not an explicit response, the term "SRI" is used, and shows that excitability rises well before response, and is significant (*) even for time windows (gray shading) which isolate decision processes. Adapted from Ref. 151.

they were able to map the evolution of motor excitability during the decision process, concluding that motor excitability scales with decision competition before an action is selected. Finally, Wood *et al.*[152] measured intramuscular EMG from pectoral muscles involved in making a reach response to visual targets. Surprisingly, there were spatially sensitive muscle responses less than 100 ms after visual onsets that responded to the luminance contrast of the stimuli. Across these three examples, we see two important points of convergence: first, the readout of the accumulation of evidence toward a decision (motion coherence, value difference, and luminance) was entirely motor (reflex gain, MEP, and muscle response) and second, these responses were graded across time, scaling with the quality of accumulated evidence.

### *Neural*

Electrophysiological studies in NHPs parallel the behavioral results above. In one study, when NHPs self-initiated an eye-movement decision during the RDM task, saccades were straight toward the chosen target (Fig. 7). In separate trials, suprathreshold stimulation applied to oculomotor regions generated saccades orthogonal to the two targets. But when the same stimulation was applied during decision making but before self-initiation of a saccade, eye movements were a mixture of the orthogonal stimulated direction and the direction of the target with more dot motion evidence. These results have been shown in both the FEF[111] and SC,[131] and strongly suggest that information about the relative desirability of an option continuously updates circuits implicated in motor processes.

More recently, Kiani *et al.*[153] recorded neural population activity from the prearcuate gyrus (a brain area involved in saccade planning[154]) while monkeys performed the RDM task (Fig. 8). By employing a sliding-temporal-window decoding approach prior to launching the decision, they were able to show that they could reliably predict the animal's decision before it was reported via a saccadic eye movement. Notably, by determining how far from the classification boundary (between choice options) the neural state is, the decoding approach can provide a moment-by-moment estimate of the competition between options. Consistent with evidence accumulation, this distance measure gradually increased from zero to large values over the course of the trial, with the rate of rise correlating to the strength of dot motion. Interestingly, however, on a minority of trials, the population response crossed from one side of the decision boundary to the other, suggesting a shift in the animal's choice from one target to the other. These internal changes of mind have the same features as their behavioral counterparts.[71] That is, they were more likely: (1) to occur earlier, rather than later; (2) for weak than strong stimuli; and (3) to shift from an incorrect to a correct choice.

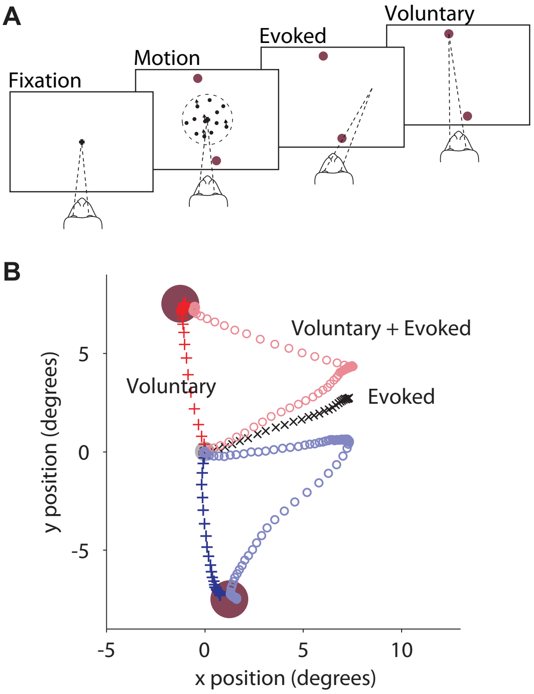

**Figure 7.** Neural evidence that decision formation and motor preparation use the same neural circuits. (A) NHPs performed the RDM task, and made saccades to the target associated with the greater net direction of dot motion (in this case, roughly up/down). (B) Voluntary saccades during this task were directly toward the target corresponding to the direction of perceived dot motion (blue and red crosses). Saccades evoked shortly after fixation using suprathreshold stimulation to FEF neurons resulted in saccades orthogonal to the two targets (black x). When suprathreshold stimulation was applied during dot motion discrimination but before a voluntary saccade, the evoked saccade deviated toward the direction with more dot motion evidence (light blue and red circles). Reproduced from Ref. 111.

Similar observations have recently been provided using a reaching task.[155] NHPs were presented with two targets along with virtual barriers that could obstruct a nearby target. By varying when the barriers appeared in a trial, a continuum of situations was constructed ranging from complete free

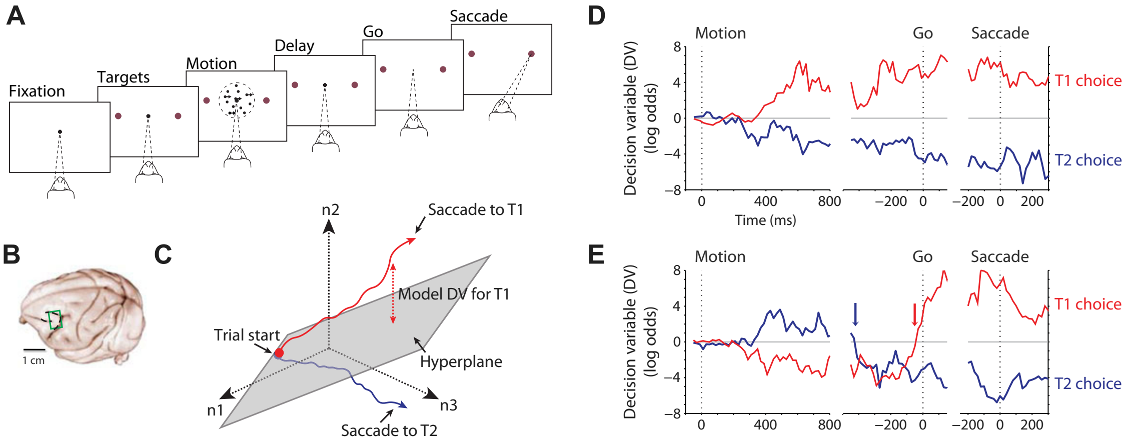

**Figure 8.** Neural evidence for changes of mind. (A) NHPs performed a delayed-response RDM task. (B) Multielectrode arrays recorded neural population activity from area 8Ar of the prearcuate gyrus. (C) The neural population response pattern at each time point can be envisioned as a point in high-dimensional space, whose axes correspond to the firing rates of individual neurons (shown for three hypothetical neurons, n1–n3). Logistic regression was used to find the hyperplane that best discriminated the neural population response patterns corresponding to leftward (T1) versus rightward (T2) choices. The distance of the population response pattern from the hyperplane, or decision variable (DV), indicates the certainty of the model's prediction about the upcoming choice. (D) Two sample trials in which the model DV maintained its sign throughout the trial, ending with T1 and T2 choices. (E) Two sample trials in which the sign of the model DV changed during the delay period (see arrows), indicative of a change in the model's predictions and suggestive of a change of mind in the animal. Adapted from Ref. 32.

choice (no barriers) to forced choice (only one target was accessible). Of particular interest were cases where a barrier changed mid-trial, making a previously inaccessible target accessible. The investigators recorded neural population activity from the dorsal premotor (PMd) and primary motor (M1) cortices and trained a decoder to categorize the two different responses on "forced choice" trials. Not only could this decoder be used to predict reach direction on "free choice" trials, but also more interestingly, on the barrier-change trials, the decoder would sometimes initially indicate one choice, and then change to the opposite choice. Notably, these neural changes of mind were primarily observed when the animal was presented with free choices, and very rarely occurred on the forced choice trials. In other reaching tasks, neural activity in the PMd appears to represent the relative desirability of multiple potential actions simultaneously.[107,156] Additionally, PMd neurons continue to be involved in action selection—if one of the potential options disappears when a "Go" signal is given, PMd activity predicts the switching of action before movement onset.[157]

Taken together, these results show at the neural level what has been shown at the behavioral level—that the competition between options continuously evolves as a single process throughout decision making. However, these neural studies have yet to show the same results during movement itself, which reveals not only the relative infancy of this research area but also the exciting opportunities to come.

## Conclusions and extensions

At the start of our review, we presented two central questions. First, given that decision making is best conceptualized as a competition between choice options, In what representational space do these options compete? Second, especially with respect to the movements required to enact a choice, When are decisions made—before movement onset or at the time of movement completion?

Given the wealth of evidence reviewed here, the answer to the second question appears to strongly favor a decision process that does not end at movement onset. Rather, a convergence of modeling, behavioral, and neural evidence indicates that decision making is a single and gradual process that begins with the presentation (or consideration) of choice options and continues throughout movement execution. This is perhaps most evident in changes of mind or tasks where choice options are not completely defined before movement. In both of these cases and many others, there is clear evidence for the continued contribution of decision making during movement.

In contrast, the first question is still very much up for debate. Here, we presented two somewhat opposing views: first, good-based theories that advocate for the competition of abstract values and, in the extreme, completely separate this value competition from movement consequences, and second, action-based theories, which argue that decisions are fundamentally sensorimotor in nature and, in the extreme, believe decisions are always the resolution of competitions between actions. One alternative to both pure good- and action-based models is a distributed consensus decision-making model.[91] According to this theory, competition occurs at multiple levels of representation, and decisions emerge as the result of reciprocal connections between these distributed competitions. This theory can explain how decisions can be made between both actions and abstract values.[131] Furthermore, recent evidence suggests that competition can indeed occur at both good- and action-based representations,[158] and that these might share strong reciprocal connections[98,104] (but see, Ref. 158).

This resolution between good- and action-based theories leaves us with a picture of decision making as a dynamic, distributed system across the brain. Most often, choice options are presented via primary sensory inputs and the resolution of a decision results in a motor response. In these situations, cascades of sensory information (usually flowing *up* from sensory to movement/planning areas) flow together with the cascades of task goals (usually flowing *down* from movement/planning to sensory areas) to shape ongoing competition.[159] This idea is consistent with continuous cortical feedback where sensory areas are updated so that behaviorally relevant stimuli receive preferential processing as early as possible. For example, the activity in the primary visual cortex (V1) of rodents,[160] NHPs,[161] and humans[162] is modulated by reward, and presents a likely candidate for the operation of selective attention.[161,163]

In this framework, since most decisions ultimately lead to actions, action-related information and neural structures are usually involved in the milieu of biasing signals. Several researchers have argued against such an architecture, as it might be unnecessarily costly for the brain to continuously transmit such information, or to update motor plans.[89,164] From these views, a single, central decision system may seem more resource efficient.[2] However, the cost of neural resources might well be worth the benefit of adaptive and flexible behavior. If decision information is constantly ready to shift our actions, we are able to efficiently adapt to changes in our environments.[91] Ultimately, from many perspectives, the main goal of information processing within the brain is to guide action.[5,58,165–168]

The flexibility of such a decision network likely gives rise to its multiple characterizations. For example, in tasks where a movement is not required, perhaps there is no need for the current decision-network configuration to include motor areas. If so, this could account for results of abstract value, divorced from movement. Similarly, in low-level perceptual decisions (e.g., RDM task) or even in nonconscious movement decisions (e.g., hand preshaping), it is not clear that abstract value is important, and there might be no need for the decision network to engage abstract value structures. Importantly, however, in all decisions, there is a requirement for the system to converge from a space of many options to a single choice, and this convergence evolves over time. Thus, more broadly, and more speculatively, it may be most accurate to say that the brain is a flexible conflict resolving machine, and decision making is one way of studying its capacities. One enticing theory that emerges from this framework is that all cognition is, at its core, reliant on the resolution of competition. We are by no means the first to articulate this kind of position,[29] and it is interesting to consider how memory recall, navigation, or even relevance determination can be conceptualized as the competition between options (with, respectively, candidate memories, possible routes, and decisions themselves being the options that are compared). This idea is not a new one and has some of its earliest origins in seminal writings of William James, who, back in 1890, wrote, “the mind is at every stage a theatre of simultaneous possibilities.”[169]

If decision making is the central function of the brain, many lines of research emerge from its study. Here, we briefly consider two lines of work that appear poised to make real progress. First, by conceptualizing decision making as an evolving process that continues throughout movement, we can better account for sequential decisions. While the vast majority of decision-making tasks study single decisions in isolation, in the real world, the enacting of one decision invariably impacts and leads to subsequent decisions. For example, a prey fleeing from a predator may initially choose to flee toward a tree, but then must decide to climb it, to hide behind it, or to keep running. These subsequent decisions are directly impacted by both the current environment and the animal's movement through it. Thus, truly sequential decision making appears to be an important next step in decision-making theories. Models like evidence accumulation can likely be extended to show how the evidence from one decision continues to affect not just the movement enacting that decision, but also remains available and biases the next decision.[170–173] Second, social signaling appears to be significantly impacted by the results of the work reviewed. If movement is the result of competition between internally represented choice options, then our movements broadcast our evolving decision process to the world. Others are able to pick up on these decision-making signals simply by observing our movements and are able to use them to guide their own actions.[174,175] This is a key aspect of body language, gesturing, and coordination, and might have been an important mechanism for the evolution of humans as a social species.

If sequential decision making and social signaling are two questions, we seem better equipped to address, countless other conundrums are enticing and unsolved. For example, How do we account for decisions that do not require an action? What competes during decisions that require the complex coordination of multiple actions and many effectors?[176] What happens during decision making to inhibit an action or to move away from an object?[177–181] And how do we decide when to begin moving? Such questions pose great challenges to current decision-making models and ultimately speak to the difficulty of using neuroscientific techniques and approaches to understand the hidden inner workings of the human mind. Fortunately, this difficulty has only added to the adventure of the expedition.

## Acknowledgments

N.J.W. was supported by awards from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Alberta Gambling Research Institute (AGRI). J.P.G was supported by NSERC Discovery Grant (RGPIN-2017-04684) and a Canadian Institutes of Health Research Grant (MOP126158). C.S.C. was supported by NSERC Discovery Grant (RGPIN-2014-05248) and a Canadian Institute for Advanced Research (CIFAR) Azrieli Global Scholar appointment.

## Competing interests

The authors declare no competing interests.

## References

1. Padoa-Schioppa, C. & J.A. Assad. 2006. Neurons in the orbitofrontal cortex encode economic value. *Nature* **441:** 223–226.
2. Padoa-Schioppa, C. 2011. Neurobiology of economic choice: a good-based model. *Annu. Rev. Neurosci.* **34:** 333–359.
3. Padoa-Schioppa, C. & K.E. Conen. 2017. Orbitofrontal cortex: a neural circuit for economic decisions. *Neuron* **96:** 736–754.
4. Levy, D.J. & P.W. Glimcher. 2012. The root of all value: a neural common currency for choice. *Curr. Opin. Neurobiol.* **22:** 1027–1038.
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. Rangel, A. & T. Hare. 2010. Neural computations associated with goal-directed choice. *Curr. Opin. Neurobiol.* **20:** 262–270.
7. Pezzulo, G. & P. Cisek. 2016. Navigating the affordance landscape: feedback control as a process model of behavior and cognition. *Trends Cogn. Sci.* **20:** 414–424.
8. Shadlen, M.N., T.D. Hanks, A.K. Churchland, *et al.* 2006. The speed and accuracy of a simple perceptual decision: a mathematical primer. In *Bayesian Brain: Probabilistic Approaches to Neural Coding*. K. Doya, S. Ishii, A. Pouget & R.P.N. Rao. Eds.: 208–237. Cambridge, MA: MIT Press.
9. Dorris, M.C. & P.W. Glimcher. 2004. Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron* **44:** 365–378.
10. Britten, K.H., M.N. Shadlen, W.T. Newsome & J.A. Movshon. 1992. The analysis of visual motion: a comparison of neuronal and psychophysical performance. *J. Neurosci.* **12:** 4745–4765.
11. Krajbich, I., C. Armel & A. Rangel. 2010. Visual fixations and the computation and comparison of value in simple choice. *Nat. Neurosci.* **13:** 1292–1298.
12. Gold, J.I. & M.N. Shadlen. 2007. The neural basis of decision making. *Annu. Rev. Neurosci.* **30:** 535–574.
13. Bogacz, R. 2007. Optimal decision-making theories: linking neurobiology with behavior. *Trends Cogn. Sci.* **11:** 118–125.
14. Shadlen, M.N. & D. Shohamy. 2016. Decision making and sequential sampling from memory. *Neuron* **90:** 927–939.

15. Smith, P.L. & D. Vickers. 1988. The accumulator model of two-choice discrimination. *J. Math. Psychol.* **32:** 135–168.
16. Link, S.W. 1975. The relative judgment theory of two choice response time. *J. Math. Psychol.* **12:** 114–135.
17. Ratcliff, R. & J.N. Rouder. 1998. Modeling response times for two-choice decisions. *Psychol. Sci.* **9:** 347–356.
18. Ratcliff, R. & P.L. Smith. 2004. A comparison of sequential sampling models for two-choice reaction time. *Psychol. Rev.* **111:** 333–367.
19. Ratcliff, R., P.L. Smith, S.D. Brown & G. McKoon. 2016. Diffusion decision model: current issues and history. *Trends Cogn. Sci.* **20:** 260–281.
20. Green, D.M. & J.A. Swets. 1988. *Signal Detection Theory and Psychophysics*. Peninsula Publications.
21. Beck, J.M. *et al.* 2008. Probabilistic population codes for Bayesian decision making. *Neuron* **60:** 1142–1152.
22. Bogacz, R., E. Brown, J. Moehlis, *et al.* 2006. The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. *Psychol. Rev.* **113:** 700–765.
23. Noorani, I. & R.H.S. Carpenter. 2016. The LATER model of reaction time and decision. *Neurosci. Biobehav. Rev.* **64:** 229–251.
24. Drugowitsch, J., R. Moreno-Bote, A.K. Churchland, *et al.* 2012. The cost of accumulating evidence in perceptual decision making. *J. Neurosci.* **32:** 3612–3628.
25. Hawkins, G.E., B.U. Forstmann, E.-J. Wagenmakers, *et al.* 2015. Revisiting the evidence for collapsing boundaries and urgency signals in perceptual decision-making. *J. Neurosci.* **35:** 2476–2484.
26. Thura, D., J. Beauregard-Racine, C.-W. Fradet & P. Cisek. 2012. Decision making by urgency gating: theory and experimental support. *J. Neurophysiol.* **108:** 2912–2930.
27. Thura, D. & P. Cisek. 2016. On the difference between evidence accumulator models and the urgency gating model. *J. Neurophysiol.* **115:** 622–623.
28. Usher, M. & J.L. McClelland. 2001. The time course of perceptual choice: the leaky, competing accumulator model. *Psychol. Rev.* **108:** 550–592.
29. Shadlen, M.N. & R. Kiani. 2013. Decision making as a window on cognition. *Neuron* **80:** 791–806.
30. Pleskac, T.J. & J.R. Busemeyer. 2010. Two-stage dynamic signal detection: a theory of choice, decision time, and confidence. *Psychol. Rev.* **117:** 864–901.
31. Macmillan, N.A. & C. Douglas Creelman. 2004. *Detection Theory: A User's Guide*. Psychology Press.
32. Kiani, R., L. Corthell & M.N. Shadlen. 2014. Choice certainty is informed by both evidence and decision time. *Neuron* **84:** 1329–1342.
33. Palmer, J., A.C. Huk & M.N. Shadlen. 2005. The effect of stimulus strength on the speed and accuracy of a perceptual decision. *J. Vis.* **5:** 376–404.
34. Sugrue, L.P., G.S. Corrado & W.T. Newsome. 2005. Choosing the greater of two goods: neural currencies for valuation and decision making. *Nat. Rev. Neurosci.* **6:** 363–375.
35. Glimcher, P.W. 2010. *Foundations of Neuroeconomic Analysis*. Oxford University Press.
36. Kiani, R. & M.N. Shadlen. 2009. Representation of confidence associated with a decision by neurons in the parietal cortex. *Science* **324:** 759–764.
37. Andersen, R.A., G.K. Essick & R.M. Siegel. 1985. Encoding of spatial location by posterior parietal neurons. *Science* **230:** 456–458.
38. Platt, M.L. & P.W. Glimcher. 1999. Neural correlates of decision variables in parietal cortex. *Nature* **400:** 233–238.
39. Shadlen, M.N. & W.T. Newsome. 1996. Motion perception: seeing and deciding. *Proc. Natl. Acad. Sci. USA* **93:** 628–633.
40. Shadlen, M.N. & W.T. Newsome. 2001. Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. *J. Neurophysiol.* **86:** 1916–1936.
41. Roitman, J.D. & M.N. Shadlen. 2002. Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. *J. Neurosci.* **22:** 9475–9489.
42. Huk, A.C. & M.N. Shadlen. 2005. Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. *J. Neurosci.* **25:** 10420–10436.
43. Hanks, T.D., J. Ditterich & M.N. Shadlen. 2006. Microstimulation of macaque area LIP affects decision-making in a motion discrimination task. *Nat. Neurosci.* **9:** 682–689.
44. Donner, T.H., M. Siegel, P. Fries & A.K. Engel. 2009. Buildup of choice-predictive activity in human motor cortex during perceptual decision making. *Curr. Biol.* **19:** 1581–1585.
45. O'Connell, R.G., P.M. Dockree & S.P. Kelly. 2012. A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. *Nat. Neurosci.* **15:** 1729–1735.
46. Krueger, P.M. *et al.* 2017. Evidence accumulation detected in BOLD signal using slow perceptual decision making. *J. Neurosci. Methods* **281:** 21–32.
47. Freedman, D.J. & J.A. Assad. 2011. A proposed common neural mechanism for categorization and perceptual decisions. *Nat. Neurosci.* **14:** 143.
48. Licata, A.M. *et al.* 2017. Posterior parietal cortex guides visual decisions in rats. *J. Neurosci.* **37:** 4954–4966.
49. Katz, L.N., J.L. Yates, J.W. Pillow & A.C. Huk. 2016. Dissociated functional significance of decision-related activity in the primate dorsal stream. *Nature* **535:** 285–288.
50. Yates, J.L., I.M. Park, L.N. Katz, *et al.* 2017. Functional dissection of signal and noise in MT and LIP during decision-making. *Nat. Neurosci.* **20:** 1285–1292.
51. Kennerley, S.W. & J.D. Wallis. 2009. Encoding of reward and space during a working memory task in the orbitofrontal cortex and anterior cingulate sulcus. *J. Neurophysiol.* **102:** 3352–3364.
52. Grattan, L.E. & P.W. Glimcher. 2014. Absence of spatial tuning in the orbitofrontal cortex. *PLoS One* **9:** e112750.
53. Plassmann, H., J. O'Doherty & A. Rangel. 2007. Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. *J. Neurosci.* **27:** 9984–9988.
54. Kable, J.W. & P.W. Glimcher. 2007. The neural correlates of subjective value during intertemporal choice. *Nat. Neurosci.* **10:** 1625–1633.
55. De Martino, B., D. Kumaran, B. Holt & R.J. Dolan. 2009. The neurobiology of reference-dependent value computation. *Neuroimage* **47:** S117.

56. Cisek, P. & A. Pastor-Bernier. 2014. On the challenges and mechanisms of embodied decisions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **369**. https://doi.org/10.1098/rstb.2013.0479.
57. Gallivan, J.P., C.S. Chapman, D.M. Wolpert & J.R. Flanagan. 2018. Decision-making in sensorimotor control. *Nat. Rev. Neurosci.* **19:** 519–534.
58. Gibson, J.J. 1986. *The Ecological Approach to Visual Perception.* Psychology Press.
59. Cisek, P. & J.F. Kalaska. 2010. Neural mechanisms for interacting with a world full of action choices. *Annu. Rev. Neurosci.* **33:** 269–298.
60. Baldauf, D. & H. Deubel. 2010. Attentional landscapes in reaching and grasping. *Vision Res.* **50:** 999–1013.
61. Cisek, P. 2006. Integrated neural processes for defining potential actions and deciding between them: a computational model. *J. Neurosci.* **26:** 9761–9770.
62. Christopoulos, V., J. Bonaiuto & R.A. Andersen. 2015. A biologically plausible computational theory for value integration and action selection in decisions with competing alternatives. *PLoS Comput. Biol.* **11:** e1004104.
63. Christopoulos, V. & P.R. Schrater. 2015. Dynamic integration of value information into a common probability currency as a theory for flexible decision making. *PLoS Comput. Biol.* **11:** e1004402.
64. Todorov, E. & M.I. Jordan. 2002. Optimal feedback control as a theory of motor coordination. *Nat. Neurosci.* **5:** 1226–1235.
65. Fajen, B.R. & W.H. Warren. 2003. Behavioral dynamics of steering, obstacle avoidance, and route selection. *J. Exp. Psychol. Hum. Percept. Perform.* **29:** 343–362.
66. Spivey, M.J. & R. Dale. 2006. Continuous dynamics in real-time cognition. *Curr. Dir. Psychol. Sci.* **15:** 207–211.
67. van der Wel, R.P., J.R. Eder, A.D. Mitchel, *et al.* 2009. Trajectories emerging from discrete versus continuous processing models in phonological competitor tasks: a commentary on Spivey, Grosjean, and Knoblich. *J. Exp. Psychol. Hum. Percept. Perform.* **35:** 588–594.
68. Zgonnikov, A., A. Aleni, P.T. Piiroinen, *et al.* 2017. Decision landscapes: visualizing mouse-tracking data. *R. Soc. Open Sci.* **4:** 170482.
69. Erlhagen, W. & G. Schöner. 2002. Dynamic field theory of movement preparation. *Psychol. Rev.* **109:** 545.
70. Burk, D., J.N. Ingram, D.W. Franklin, *et al.* 2014. Motor effort alters changes of mind in sensorimotor decision making. *PLoS One* **9:** e92681.
71. Resulaj, A., R. Kiani, D.M. Wolpert & M.N. Shadlen. 2009. Changes of mind in decision-making. *Nature* **461:** 263–266.
72. Selen, L.P.J., M.N. Shadlen & D.M. Wolpert. 2012. Deliberation in the motor system: reflex gains track evolving evidence leading to a decision. *J. Neurosci.* **32:** 2276–2286.
73. van den Berg, R. *et al.* 2016. A common mechanism underlies changes of mind about decisions and confidence. *eLife* **5:** e12192.
74. Doyle, M. & R. Walker. 2001. Curved saccade trajectories: voluntary and reflexive saccades curve away from irrelevant distractors. *Exp. Brain Res.* **139:** 333–344.
75. Ludwig, C.J.H. & I.D. Gilchrist. 2003. Target similarity affects saccade curvature away from irrelevant onsets. *Exp. Brain Res.* **152:** 60–69.
76. Song, J.-H. & K. Nakayama. 2009. Hidden cognitive states revealed in choice reaching tasks. *Trends Cogn. Sci.* **13:** 360–366.
77. Trommershäuser, J., L.T. Maloney & M.S. Landy. 2008. Decision making, movement planning and statistical decision theory. *Trends Cogn. Sci.* **12:** 291–297.
78. Welsh, T. & D. Elliott. 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.
79. Welsh, T.N., D. Elliott & D.J. Weeks. 1999. Hand deviations toward distractors. Evidence for response competition. *Exp. Brain Res.* **127:** 207–212.
80. Chapman, C.S. *et al.* 2010. Reaching for the unknown: multiple target encoding and real-time decision-making in a rapid reach task. *Cognition* **116:** 168–176.
81. Hudson, T.E., L.T. Maloney & M.S. Landy. 2007. Movement planning with probabilistic target information. *J. Neurophysiol.* **98:** 3034–3046.
82. Gallivan, J.P. *et al.* 2011. One to four, and nothing more: nonconscious parallel individuation of objects during action planning. *Psychol. Sci.* **22:** 803–811.
83. Milne, J.L. *et al.* 2013. Connecting the dots: object connectedness deceives perception but not movement planning. *Psychol. Sci.* **24:** 1456–1465.
84. Gallivan, J.P. & C.S. Chapman. 2014. Three-dimensional reach trajectories as a probe of real-time decision-making between multiple competing targets. *Front. Neurosci.* **8:** 215.
85. Wood, D.K. *et al.* 2011. Visual salience dominates early visuomotor competition in reaching behavior. *J. Vis.* **11**. https://doi.org/10.1167/11.10.16.
86. Chapman, C.S., J.P. Gallivan & J.T. Enns. 2014. Separating value from selection frequency in rapid reaching biases to visual targets. *Vis. Cogn.* **23:** 249–271.
87. Chapman, C.S., J.P. Gallivan, J.D. Wong, *et al.* 2015. The snooze of lose: rapid reaching reveals that losses are processed more slowly than gains. *J. Exp. Psychol. Gen.* **144:** 844–863.
88. Chapman, C.S. *et al.* 2014. Counting on the motor system: rapid action planning reveals the format- and magnitude-dependent extraction of numerical quantity. *J. Vis.* **14:** 30.
89. Wong, A.L. & A.M. Haith. 2017. Motor planning flexibly optimizes performance under uncertainty about task goals. *Nat. Commun.* **8:** 14624.
90. Haith, A.M., D.M. Huberdeau & J.W. Krakauer. 2015. Hedging your bets: intermediate movements as optimal behavior in the context of an incomplete decision. *PLoS Comput. Biol.* **11:** e1004171.
91. Cisek, P. 2012. Making decisions through a distributed consensus. *Curr. Opin. Neurobiol.* **22:** 927–936.
92. Gallivan, J.P., B.M. Stewart, L.A. Baugh, *et al.* 2017. Rapid automatic motor encoding of competing reach options. *Cell Rep.* **18:** 1619–1626.

93. Stewart, B.M., J.P. Gallivan, L.A. Baugh & J.R. Flanagan. 2014. Motor, not visual, encoding of potential reach targets. *Curr. Biol.* **24:** R953–R954.
94. Pearce, T.M. & D.W. Moran. 2012. Strategy-dependent encoding of planned arm movements in the dorsal premotor cortex. *Science* **337:** 984–988.
95. Gallivan, J.P., K.S. Barton, C.S. Chapman, *et al.* 2015. Action plan co-optimization reveals the parallel encoding of competing reach movements. *Nat. Commun.* **6:** 7428.
96. Gallivan, J.P., L. Logan, D.M. Wolpert & J.R. Flanagan. 2016. Parallel specification of competing sensorimotor control policies for alternative action options. *Nat. Neurosci.* **19:** 320–326.
97. Cos, I., F. Medleg & P. Cisek. 2012. The modulatory influence of end-point controllability on decisions between actions. *J. Neurophysiol.* **108:** 1764–1780.
98. Cos, I., N. Bélanger & P. Cisek. 2011. The influence of predicted arm biomechanics on decision making. *J. Neurophysiol.* **105:** 3022–3033.
99. Cos, I., J. Duque & P. Cisek. 2014. Rapid prediction of biomechanical costs during action decisions. *J. Neurophysiol.* **112:** 1256–1266.
100. Shadmehr, R., H.J. Huang & A.A. Ahmed. 2016. A representation of effort in decision-making and motor control. *Curr. Biol.* **26:** 1929–1934.
101. Morel, P., P. Ulbrich & A. Gail. 2017. What makes a reach movement effortful? Physical effort discounting supports common minimization principles in decision making and motor control. *PLoS Biol.* **15:** e2001323.
102. Manohar, S.G. *et al.* 2015. Reward pays the cost of noise reduction in motor and cognitive control. *Curr. Biol.* **25:** 1707–1716.
103. Moher, J. & J.-H. Song. 2014. Perceptual decision processes flexibly adapt to avoid change-of-mind motor costs. *J. Vis.* **14:** 1.
104. Hagura, N., P. Haggard & J. Diedrichsen. 2017. Perceptual decisions are biased by the cost to act. *eLife* **6:** e18422,.
105. Miller, G.A., E. Galanter & K.H. Pribram. 1960. *Plans and the Structure of Behavior*. Henry Holt and Company.
106. McClelland, J.L. 1979. On the time relations of mental processes: an examination of systems of processes in cascade. *Psychol. Rev.* **86:** 287–330.
107. Cisek, P. & J.F. Kalaska. 2005. Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron* **45:** 801–814.
108. Matsumoto, K. 2003. Neuronal correlates of goal-based motor selection in the prefrontal cortex. *Science* **301:** 229–232.
109. Rushworth, M., M. Walton, S. Kennerley & D. Bannerman. 2004. Action sets and decisions in the medial frontal cortex. *Trends Cogn. Sci.* **8:** 410–417.
110. Croxson, P.L., M.E. Walton, J.X. O'Reilly, *et al.* 2009. Effort-based cost–benefit valuation and the human brain. *J. Neurosci.* **29:** 4531–4541.
111. Gold, J.I. & M.N. Shadlen. 2000. Representation of a perceptual decision in developing oculomotor commands. *Nature* **404:** 390–394.
112. Louie, K., L.E. Grattan & P.W. Glimcher. 2011. Reward value-based gain control: divisive normalization in parietal cortex. *J. Neurosci.* **31:** 10627–10639.
113. Samejima, K. 2005. Representation of action-specific reward values in the striatum. *Science* **310:** 1337–1340.
114. Lau, B. & P.W. Glimcher. 2008. Value representations in the primate striatum during matching behavior. *Neuron* **58:** 451–463.
115. Hikosaka, O., K. Nakamura & H. Nakahara. 2006. Basal ganglia orient eyes to reward. *J. Neurophysiol.* **95:** 567–584.
116. Kim, S., J. Hwang & D. Lee. 2008. Prefrontal coding of temporally discounted values during intertemporal choice. *Neuron* **59:** 522.
117. Mysore, S.P. & E.I. Knudsen. 2011. The role of a midbrain network in competitive stimulus selection. *Curr. Opin. Neurobiol.* **21:** 653–660.
118. Horwitz, G.D. & W.T. Newsome. 1999. Separate signals for target selection and movement specification in the superior colliculus. *Science* **284:** 1158–1161.
119. Ikeda, T. & O. Hikosaka. 2003. Reward-dependent gain and bias of visual responses in primate superior colliculus. *Neuron* **39:** 693–700.
120. Wunderlich, K., A. Rangel & J.P. O'Doherty. 2009. Neural computations underlying action-based decision making in the human brain. *Proc. Natl. Acad. Sci. USA* **106:** 17199–17204.
121. Sohn, J.-W. & D. Lee. 2007. Order-dependent modulation of directional signals in the supplementary and presupplementary motor areas. *J. Neurosci.* **27:** 13655–13666.
122. Klaes, C., S. Westendorff, S. Chakrabarti & A. Gail. 2011. Choosing goals, not rules: deciding among rule-based action plans. *Neuron* **70:** 536–548.
123. Munoz, D.P. & R.H. Wurtz. 1995. Saccade-related activity in monkey superior colliculus. I. Characteristics of burst and buildup cells. *J. Neurophysiol.* **73:** 2313–2333.
124. Basso, M.A. & R.H. Wurtz. 1997. Modulation of neuronal activity by target uncertainty. *Nature* **389:** 66–69.
125. Platt, M.L. & P.W. Glimcher. 1997. Responses of intraparietal neurons to saccadic targets and visual distractors. *J. Neurophysiol.* **78:** 1574–1589.
126. Keller, E.L. & R.M. McPeek. 2002. Neural discharge in the superior colliculus during target search paradigms. *Ann. N.Y. Acad. Sci.* **956:** 130–142.
127. McPeek, R.M., J.H. Han & E.L. Keller. 2003. Competition between saccade goals in the superior colliculus produces saccade curvature. *J. Neurophysiol.* **89:** 2577–2590.
128. Port, N.L. & R.H. Wurtz. 2003. Sequential activity of simultaneously recorded neurons in the superior colliculus during curved saccades. *J. Neurophysiol.* **90:** 1887–1903.
129. Costello, M.G., D. Zhu, E. Salinas & T.R. Stanford. 2013. Perceptual modulation of motor—but not visual—responses in the frontal eye field during an urgent-decision task. *J. Neurosci.* **33:** 16394–16408.
130. Kim, B. & M.A. Basso. 2008. Saccade target selection in the superior colliculus: a signal detection theory approach. *J. Neurosci.* **28:** 2991–3007.
131. Thevarajah, D., A. Mikulic & M.C. Dorris. 2009. Role of the superior colliculus in choosing mixed-strategy saccades. *J. Neurosci.* **29:** 1998–2008.

132. Wunderlich, K., A. Rangel & J.P. O'Doherty. 2010. Economic choices can be made using only stimulus values. *Proc. Natl. Acad. Sci. USA* **107:** 15005–15010.
133. Friedman, J., S. Brown & M. Finkbeiner. 2013. Linking cognitive and reaching trajectories via intermittent movement control. *J. Math. Psychol.* **57:** 140–151.
134. Lepora, N.F. & G. Pezzulo. 2015. Embodied choice: how action influences perceptual decision making. *PLoS Comput. Biol.* **11:** e1004110.
135. Meyer, D.E., D.E. Irwin, A.M. Osman & J. Kounios. 1988. The dynamics of cognition and action: mental processes inferred from speed-accuracy decomposition. *Psychol. Rev.* **95:** 183–237.
136. Abrams, R.A. & D.A. Balota. 1991. Mental chronometry: beyond reaction time. *Psychol. Sci.* **2:** 153–157.
137. Balota, D.A. & R.A. Abrams. 1995. Mental chronometry: beyond onset latencies in the lexical decision task. *J. Exp. Psychol. Learn. Mem. Cogn.* **21:** 1289.
138. Rosenbaum, D.A. & S. Kornblum. 1982. A priming method for investigating the selection of motor responses. *Acta Psychol.* **51:** 223–243.
139. Bub, D.N. & M.E.J. Masson. 2012. On the dynamics of action representations evoked by names of manipulable objects. *J. Exp. Psychol. Gen.* **141:** 502–517.
140. Fitts, P.M. 1966. Cognitive aspects of information processing. 3. Set for speed versus accuracy. *J. Exp. Psychol.* **71:** 849–857.
141. Schouten, J.F. & J.A. Bekker. 1967. Reaction time and accuracy. *Acta Psychol.* **27:** 143–153.
142. Wong, A.L., J. Goldsmith, A.D. Forrence, *et al.* 2017. Reaction times can reflect habits rather than computations. *eLife* **6** https://doi.org/10.7554/eLife.28075.
143. Ghez, C., J. Gordon, M.F. Ghilardi, *et al.* 1990. Roles of proprioceptive input in the programming of arm trajectories. *Cold Spring Harb. Symp. Quant. Biol.* **55:** 837–847.
144. Ghez, C. *et al.* 1997. Discrete and continuous planning of hand movements and isometric force trajectories. *Exp. Brain Res.* **115:** 217–233.
145. Wispinski, N.J., G. Truong, T.C. Handy & C.S. Chapman. 2017. Reaching reveals that best-versus-rest processing contributes to biased decision making. *Acta Psychol.* **176:** 32–38.
146. Sullivan, N., C. Hutcherson, A. Harris & A. Rangel. 2015. Dietary self-control is related to the speed with which attributes of healthfulness and tastiness are processed. *Psychol. Sci.* **26:** 122–134.
147. Scherbaum, S., M. Dshemuchadse, R. Fischer & T. Goschke. 2010. How decisions evolve: the temporal dynamics of action selection. *Cognition* **115:** 407–416.
148. Carlsen, A.N., D. Maslovat, M.Y. Lam, *et al.* 2011. Considerations for the use of a startling acoustic stimulus in studies of motor preparation in humans. *Neurosci. Biobehav. Rev.* **35:** 366–376.
149. Carlsen, A.N. *et al.* 2009. Precues enable multiple response preprogramming: evidence from startle. *Psychophysiology* **46:** 241–251.
150. Forgaard, C.J., D. Maslovat, A.N. Carlsen & I.M. Franks. 2011. Default motor preparation under conditions of response uncertainty. *Exp. Brain Res.* **215:** 235–245.
151. Klein-Flügge, M.C. & S. Bestmann. 2012. Time-dependent changes in human corticospinal excitability reveal value-based competition for action during decision processing. *J. Neurosci.* **32:** 8373–8382.
152. Wood, D.K., C. Gu, B.D. Corneil, *et al.* 2015. Transient visual responses reset the phase of low-frequency oscillations in the skeletomotor periphery. *Eur. J. Neurosci.* **42:** 1919–1932.
153. Kiani, R., C.J. Cueva, J.B. Reppas & W.T. Newsome. 2014. Dynamics of neural population responses in prefrontal cortex indicate changes of mind on single trials. *Curr. Biol.* **24:** 1542–1547.
154. Kim, J.-N. & M.N. Shadlen. 1999. Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. *Nat. Neurosci.* **2:** 176–185.
155. Kaufman, M.T., M.M. Churchland, S.I. Ryu & K.V. Shenoy. 2015. Vacillation, indecision and hesitation in moment-by-moment decoding of monkey motor cortex. *eLife* **4:** e04677.
156. Pastor-Bernier, A. & P. Cisek. 2011. Neural correlates of biased competition in premotor cortex. *J. Neurosci.* **31:** 7083–7088.
157. Pastor-Bernier, A., E. Tremblay & P. Cisek. 2012. Dorsal premotor cortex is involved in switching motor plans. *Front. Neuroeng.* **5:** 5.
158. Chen, X. & V. Stuphorn. 2015. Sequential selection of economic good and action in medial frontal cortex of macaques during value-based decisions. *eLife* **4:** e09418.
159. Siegel, M., T.J. Buschman & E.K. Miller. 2015. Cortical information flow during flexible sensorimotor decisions. *Science*, **348:** 1352–1355.
160. Shuler, M.G. & M.F. Bear. 2006. Reward timing in the primary visual cortex. *Science* **311:** 1606–1609.
161. Stanisor, L., C. van der Togt, C.M.A. Pennartz & P.R. Roelfsema. 2013. A unified selection signal for attention and reward in primary visual cortex. *Proc. Natl. Acad. Sci. USA* **110:** 9136–9141.
162. Serences, J.T. 2008. Value-based modulations in human visual cortex. *Neuron* **60:** 1169–1181.
163. Desimone, R. & J. Duncan. 1995. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18:** 193–222.
164. Wong, A.L., A.M. Haith & J.W. Krakauer. 2015. Motor planning. *Neuroscientist* **21:** 385–398.
165. O'Regan, J.K. & A. Noë. 2001. A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* **24:** 939–973; discussion 973–1031.
166. Clark, A. 1997. The dynamical challenge. *Cogn. Sci.* **21:** 461–481.
167. Rizzolatti, G., L. Fogassi & V. Gallese. 1997. Parietal cortex: from sight to action. *Curr. Opin. Neurobiol.* **7:** 562–567.
168. Churchland, P.S., V.S. Ramachandran & T.J. Sejnowski. 1994. A critique of pure vision. In *Large-Scale Neuronal Theories of the Brain*. C. Koch & J.L. Davis, Eds.: 23–60. MIT Press.
169. James, W. 1980. *The Principles of Psychology*. Henry Holt and Company.
170. Murphy, P.R., I.H. Robertson, S. Harty & R.G. O'Connell. 2015. Neural evidence accumulation persists after choice to inform metacognitive judgments. *eLife* **4**. https://doi.org/10.7554/eLife.11946.

171. Zylberberg, A. *et al.* 2017. Serial, parallel and hierarchical decision making in primates. *eLife* **6**. https://doi.org/10.7554/eLife.17331.
172. Doll, B.B., D.A. Simon & N.D. Daw. 2012. The ubiquity of model-based reinforcement learning. *Curr. Opin. Neurobiol.* **22:** 1075–1081.
173. Urai, A.E., J.W. de Gee & T.H. Donner. 2018. Choice history biases subsequent evidence accumulation. https://doi.org/10.1101/251595.
174. Pesquita, A., C.S. Chapman & J.T. Enns. 2016. Humans are sensitive to attention control when predicting others' actions. *Proc. Natl. Acad. Sci. USA* **113:** 8669–8674.
175. Vaziri-Pashkam, M., S. Cormiea & K. Nakayama. 2017. Predicting actions from subtle preparatory movements. *Cognition* **168:** 65–75.
176. Gottlieb, J. 2012. Attention, learning, and the value of information. *Neuron* **76:** 281–295.
177. Chapman, C.S. & M.A. Goodale. 2010. Obstacle avoidance during online corrections. *J. Vis.* **10:** 17.
178. Chapman, C.S. & M.A. Goodale. 2010. Seeing all the obstacles in your way: the effect of visual feedback and visual feedback schedule on obstacle avoidance while reaching. *Exp. Brain Res.* **202:** 363–375.
179. Chapman, C.S., J.P. Gallivan, J.C. Culham & M.A. Goodale. 2011. Mental blocks: fMRI reveals top-down modulation of early visual cortex when obstacles interfere with grasp planning. *Neuropsychologia* **49:** 1703–1717.
180. Striemer, C.L., C.S. Chapman & M.A. Goodale. 2009. "Real-time" obstacle avoidance in the absence of primary visual cortex. *Proc. Natl. Acad. Sci. USA* **106:** 15996–16001.
181. Chapman, C.S. & M.A. Goodale. 2008. Missing in action: the effect of obstacle position and size on avoidance while reaching. *Exp. Brain Res.* **191:** 83–97.