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Making decisions through a distributed consensus

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How does the brain decide between actions? Is it through comparisons of abstract representations of outcomes or through a competition in a sensorimotor map defining the actions themselves? Here, I review strengths and limitations of both of these proposals, and suggest that decisions emerge through a distributed consensus across many levels of representation.

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Introduction

Great progress has recently been made toward understanding the neural mechanisms of decision-making [1,2,3^{••},4[•],5^{••},6,7[•],8^{••},9,10]. However, despite many reports showing how neural activity in different brain regions correlates with expected rewards, action values, and other relevant variables, there is still no agreement about the functional architecture that underlies decision-making. We have substantial data on the elements of the system, but are only beginning to glimpse its shape. Here, I focus on just one outstanding question: do we make decisions among abstract representations of outcomes, a sensorimotor space of actions, or through a distributed consensus across many levels?

Classic studies in cognitive psychology suggested the existence of a central executive system [11,12] that resides in the frontal lobes [13,14] and is separate from sensorimotor control [15,16]. However, in apparent conflict with this classic centralized view, neural activities related to decision-making are widely distributed and appear even in cortical and subcortical regions traditionally implicated in sensorimotor control [4[•],9,17–21,22[•]]. This has led to suggestions that the brain simultaneously prepares multiple actions [23,24] and decides between

them through a competition taking place within the sensorimotor system itself [1,2,3^{••},4[•],25,26].

Of course, we are capable of making decisions that have nothing to do with actions, and in such situations the decision must be abstract. That is not at question. What is at question is how we decide between actions. For example, when choosing between reaching for an apple versus an orange, the brain may compute the subjective value of each offer, pick a winner, and then prepare the appropriate reaching plan [5^{••}] (Figure 1A). Alternatively, both potential reaching actions could be simultaneously represented in the brain and compete against each other, and this competition could be biased by a variety of factors including the subjective value of each offer (Figure 1B). A third alternative is that competition occurs at multiple levels in parallel, and the final decision is achieved through a ‘distributed consensus’ [25] (Figure 1C). Distinguishing between these alternatives is not easy, and existing data are still insufficient to make any final conclusions. Nevertheless, recent experiments provide some tantalizing food for thought, and the purpose of this review is to discuss these in light of the plausible architectures shown in Figure 1. Here, I will focus primarily on neurophysiological studies in non-human primates, making the explicit assumption that the mechanisms discussed here are ones we share with our evolutionary cousins.

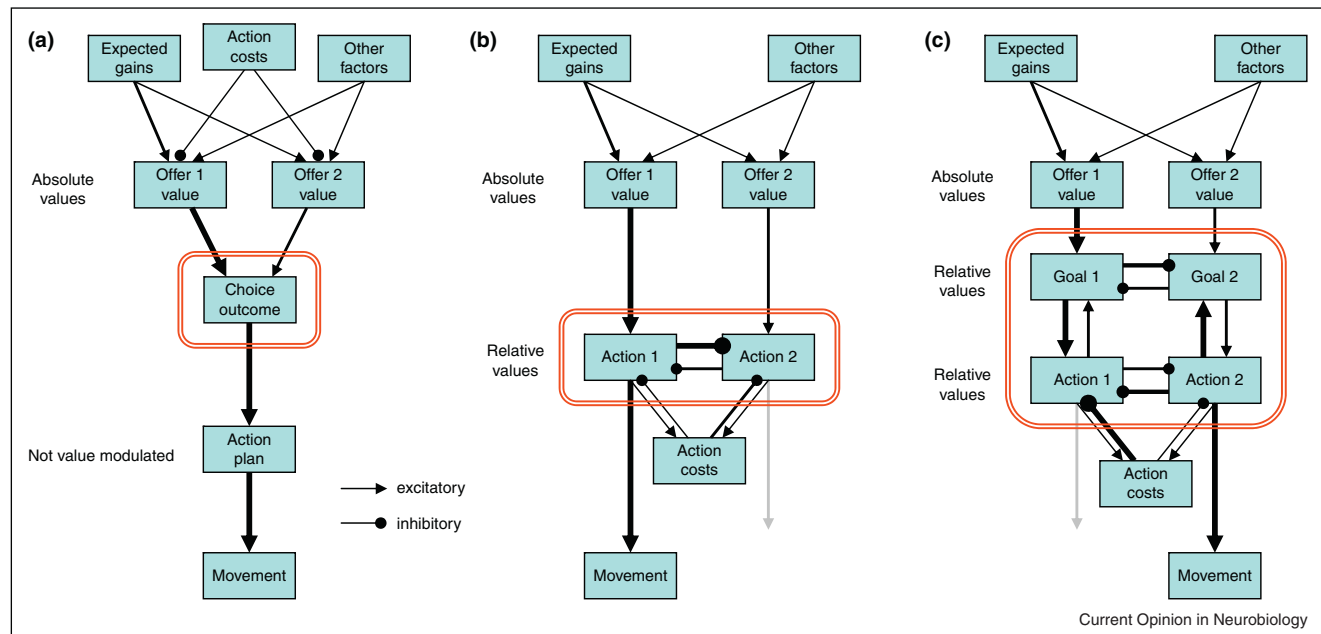
Decisions between goods

Economic theories suggest that humans make decisions between different goods by integrating all relevant factors (expected gains, potential risks, action costs, etc.) into a single variable capturing the subjective value of each offer [27]. Neurophysiological studies have suggested that this variable is encoded in the orbitofrontal cortex (OFC) and ventromedial prefrontal cortex (vmPFC) [5^{••},7[•],10,28]. In particular, neural activity in OFC correlates with the value of an option independent of other options [29], and adjusts its gain to reflect the full range of values presented in a given block of trials [30]. This is consistent with the ‘good-based model’ [5^{••}], summarized in Figure 1A. In the model, all factors relevant for a choosing an offer are integrated in the OFC and vmPFC, and these are compared and the largest one is chosen. Next, the appropriate action plan is computed to produce the required movement. This model satisfies our subjective intuition about decisions: when choosing to reach for an orange, I think about the orange and not about muscles.

However, despite the intuitive appeal of the good-based model [5^{••}], it leaves open several important questions.

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Figure 1



Three possible schemes for deciding between actions. In each, the red box emphasizes where decisions are made and arrows represent excitation and inhibition whose strength is indicated by line thickness. **(A)** A **good-based model**, in which decisions are made by comparing representations of offer values. **(B)** An **action-based model**, in which decisions are made through a biased competition between action representations. **(C)** A **distributed consensus model**, in which decisions are made through competition at multiple levels of representation. The diagram depicts a particular situation in which stimulus values favor action 1 but action costs favor action 2, and the conflict is resolved in favor of the low cost action.

First, it predicts that motor planning begins only after decisions are made. However, many studies have shown that neurons in sensorimotor regions represent multiple potential targets and actions long before the animal decides between them [4,20,21,22,24,31–35,36]. It has been argued that these representations are not ‘genuinely motor’ and instead related to attention or arousal [5,37], but that argument is difficult to reconcile with behavioral results. For example, the spatial aspects of trajectories in a variety of reach [36,38–40,41,42,43] and saccade tasks [44] are influenced by the presence of multiple potential targets (e.g. Figure 2A). A simple explanation is that the brain begins to plan the different candidate actions simultaneously before deciding between them, but does not always completely suppress unselected actions before movement onset [38,45,46].

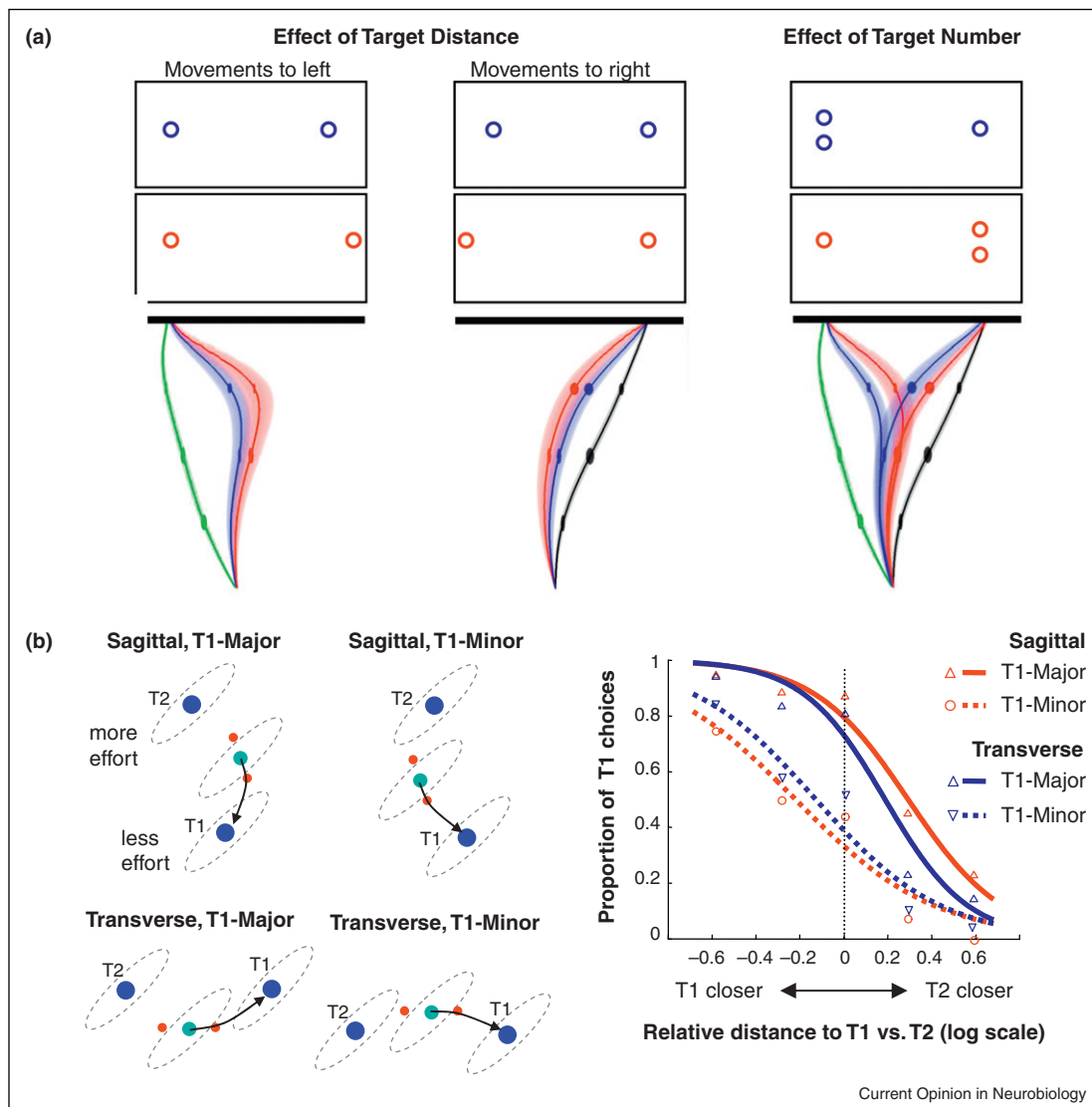
Second, it is unclear how the brain could compute action costs if it did not have at least some representation of those potential actions. Our choices are remarkably sensitive to action costs. For example, we recently showed that when humans were asked to freely choose between two reaching actions whose value was equal, they strongly preferred the one that was biomechanically easier to perform [47] (Figure 2B). Importantly, these movements had similar launching costs and differed in cost only upon approach to each target. This implies that the

brain had to have information about the future biomechanical costs of both movements, before deciding between them, in order to select the easier one. It is hard to imagine how a calculation of such subtle action costs could be accomplished without at least some representation of the actions themselves existing in the brain before the decision was made.

Third, the good-based model does not explain why neural activity in sensorimotor regions is modulated by decision variables. In particular, neural activity related to an action tends to be stronger if the action is more likely or yields higher rewards. As reviewed in detail elsewhere [1,2,3,9,19–21], such modulation has now been consistently observed in parietal, frontal, and subcortical components of both the oculomotor and skeletomotor systems, including the human primary motor cortex [48]. Recently, it was even demonstrated at the level of reflexes. Selen *et al.* [49] showed that as human subjects make perceptual judgments about visual motion direction, the gain of the mid-latency reflex of the reporting arm is stronger as the quality of visual motion increases, as if the decision process changes the arm’s preparatory state at the corticospinal level.

To be fair, the above observations do not invalidate the good-based model. The model could address all of these

Figure 2



(A) Average reach trajectories during a rapid reaching choice experiment [41*]. Left and middle: When two targets were shown (blue and red traces), reach trajectories deviated significantly from the single-target average (green or black traces) in a manner biased by target distance. Right: The bias was also affected by the number of targets on the right or left. **(B)** In this experiment [47**], subjects were asked to choose between two opposite planar reaching movements, in four configurations shown on the left. Each movement started from a central circle, passed through a 'via-point' (red) and arrived at a target (blue). In each of the configurations, the 'Major' target was placed such that the hand would arrive in it along the major axis of biomechanical mobility (dashed ellipse, not shown to subjects), which requires less effort, while arrival at the 'Minor' target would be along the minor axis, requiring more effort. The right panel shows the proportion of trials in which subjects chose target 1 as a function of the relative distance of the path to target 1 versus the path to target 2 (negative numbers mean target 1 is closer). Subjects tended to prefer shorter movements, but exhibited a strong and significant bias for the Major (lower effort) target, as evidenced by the separation of the choice preference curves when T1 was the Major (solid) or Minor (dashed) target, for both sagittal and transverse orientations.

results if it allowed the processing of potential actions before the decision, in parallel with the evaluation of goods. Such pre-emptive planning could be useful for computing action costs and for preparing the sensorimotor system for the most likely movements, but may not necessarily be causally involved in determining which decision is made. In other words, the choice could still be made among abstract representations of goods, separate

from sensorimotor control. But is such separation desirable from an ecological perspective?

Decisions between actions

The good-based model follows the classic tradition of cognitive psychology, in which the cognitive system responsible for decisions is separate from the sensorimotor systems that implement its commands [15,16]. This strict

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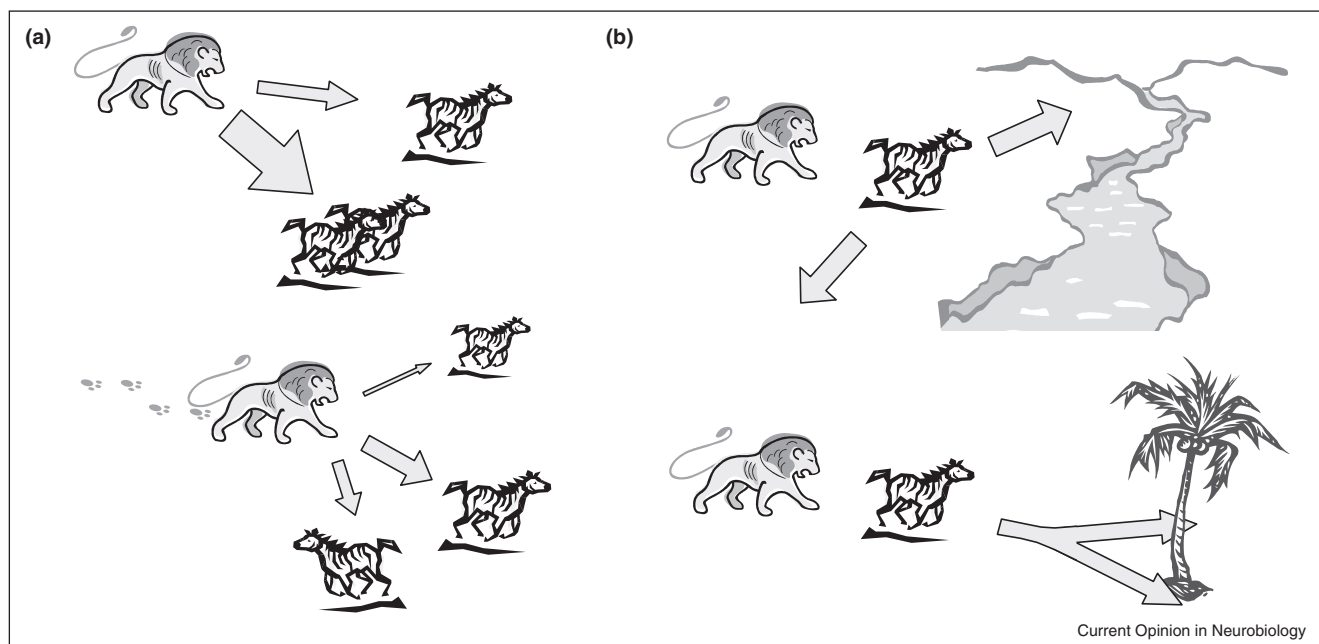
division is well-suited to the problem-solving tasks usually addressed by cognitive psychologists, in which the relevant contingencies are purely abstract. However, the brain evolved to support natural behaviors that are very different than the kinds of situations tested in psychological experiments. For example, during foraging behavior, choices between simultaneously offered goods are relatively rare and **foraging is instead dominated by sequential choices between exploiting nearby resources versus exploring elsewhere**. For such situations, classic economic policies are less effective than the context-dependent valuation policies that animals actually use [50^{••}].

In the natural environment, decisions between simultaneous options are **usually associated with particular actions**, whose metrics are specified by geometric information picked-up by the sensors. Furthermore, unlike the individual trials of psychological experiments, in which a stimulus is presented before a response, in most natural circumstances new opportunities and dangers constantly present themselves, even during ongoing actions. Consider the situations depicted in **Figure 3**. A predator may be initially faced with two potentially valuable pursuit actions, but as soon as the chase begins both the metrics of the actions themselves and estimates of their relative value will change continuously, and sometimes what was a single option can split into two (**Figure 3A**). This demands that animals engage in sensorimotor control in parallel with

evaluating alternative options. Furthermore, how decisions are made between actions is strongly dependent upon their geometric relationships. For example, consider an animal seeking to escape a predator (**Figure 3B**). If faced with two opposite escape routes it must make an immediate all-or-none decision (top). However, if potential escape routes are similar then the best strategy may be to not discard either option but mix them and delay making the choice to the last moment (bottom), when more information may be available. These are the kinds of problems for which brains have evolved, in which the spatial metrics of potential actions and the geometry of the environment are among the *most* relevant contingencies influencing what is the best choice at any given moment.

The challenges of a continuously changing environment demanded the evolution of a functional architecture in which the mechanisms specifying possible actions and those which evaluate how to select between them can operate in parallel. The ‘affordance competition hypothesis’ [3^{••},25] suggests that for visually guided behavior, multiple actions are specified in parallel as regions of activity in sensorimotor maps within fronto-parietal cortex, and engage in a competition that is biased by information from other regions. The biasing can use many sources of information, including stimulus value representations from OFC and vmPFC [5^{••},51,52^{••}], action value representations from anterior cingulate cortex

Figure 3



Schematic decision-making scenarios during natural behavior. **(A)** The environment around the lion provides information on both the spatial metrics and relative values of potential pursuit actions (arrows, with value indicated by width). During ongoing activity, this information is constantly changing and what was once a single action may sometimes split into two (bottom). **(B)** When faced with two opposite escape routes (top), the zebra must make an all-or-none decision, but when the escape routes are similar (bottom), it may mix them initially and veer toward one or the other in-flight (see **Figure 2A**).

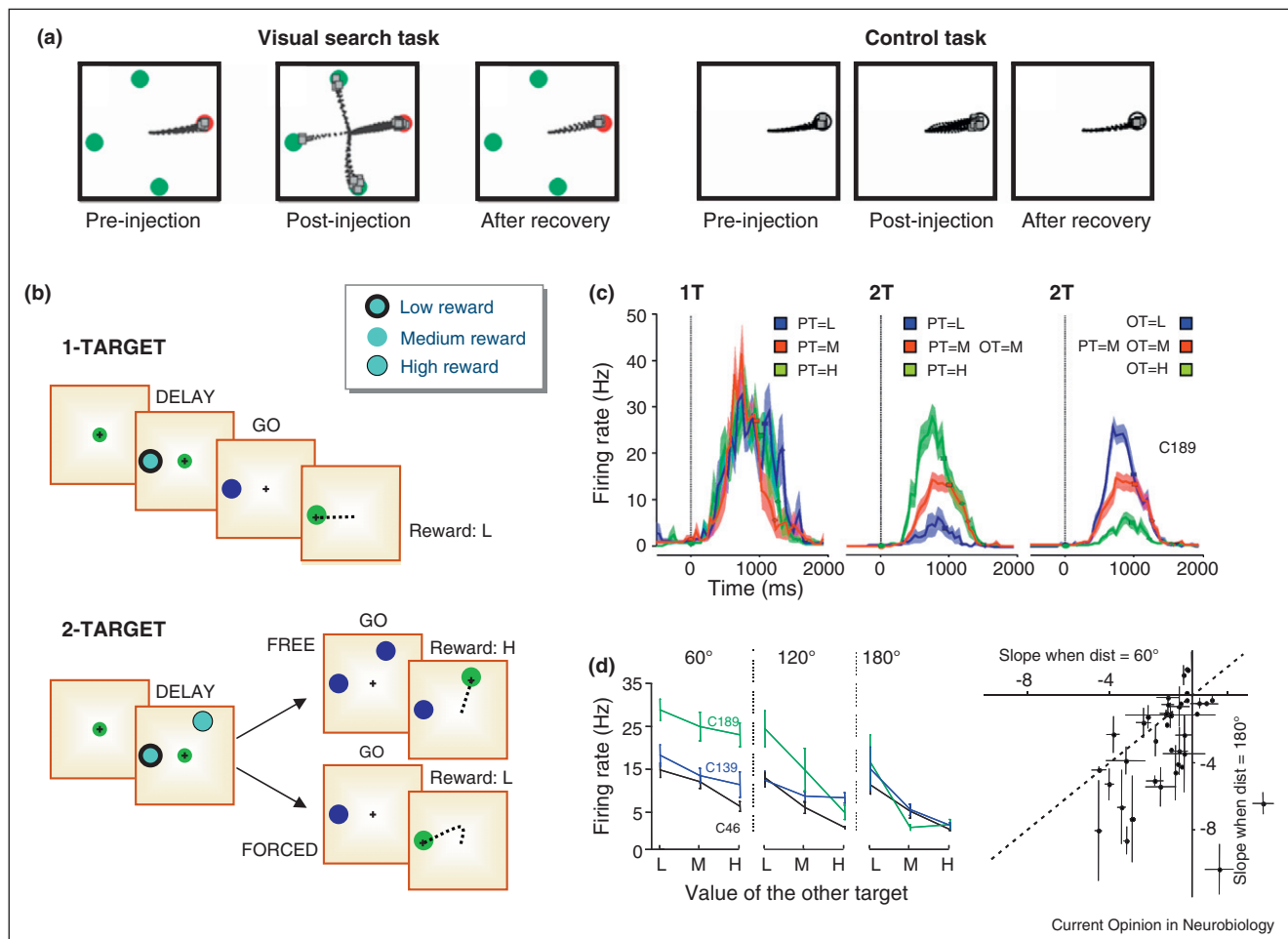
(ACC) [51,52^{**},53,54^{**}], context-dependent rule representations from lateral prefrontal cortex [6,10,55,56], and predictions of reward from the basal ganglia [57].

Figure 1B summarizes such ‘action-based’ models [45]. A common currency for computing offer values is still important, but these signals are not directly compared in the abstract space of goods. Instead, they are just one of several sources of bias influencing a competition that takes place within a representation of potential actions.

This allows action costs to be estimated and to influence decisions, and explains why neural activity in motor structures is modulated by decision variables.

How can we establish whether sensorimotor structures are causally involved in decisions? One approach is to perturb the system through microstimulation or inactivation, as done in the superior colliculus (SC) (see [4^{*}] for review). For example, McPeck and Keller [58] showed that after inactivation of the deeper intermediate layers of

Figure 4



(A) An experiment testing the effects of SC inactivation on saccade selection [58]. Left: In a saccadic visual search task, inactivation caused monkeys to make more errors when the oddball stimulus was placed in the affected location. Right: However, when a single target was present, saccades were only mildly affected. **(B)** An experiment testing the effects of sensorimotor contingencies on decision-related neural activity in PMd [62^{**}]. Monkeys were presented with one or two reach targets whose value was indicated by the border style (inset). In the two-target task, free choice and forced choice trials (in which one target disappeared at the time of the GO signal) were randomly interleaved, but here we focus only on activity before the GO. **(C)** Neural activity from a PMd cell, aligned on target onset, from trials in which a target was present in the cell's preferred direction. In the one-target (1T) task (1st column), the cell showed no modulation with the value of its 'preferred target' (PT). However, a strong modulation with PT value appeared when an 'other target' (OT) was present 120° away and medium-valued (2nd column). Conversely, if we held constant the PT value and varied the value of the other target (3rd column), activity was inversely related to OT value. In other words, the cell shows a strong modulation with *relative reward size*. **(D)** On the left is shown the mean (and s.e.) activity of three cells (C46, C149, C189) during trials in which the PT was medium-valued and the OT was low, medium, or high-valued, shown separately for trials in which the targets were 60°, 120°, and 180° apart. Note that the slope of the inverse relation to OT value was steeper as the targets were moved further apart. This suggests that when selecting between actions that are dissimilar, the gain of inhibitory interactions is stronger than when selecting between similar actions. On the right is shown a comparison of slopes with 60° versus 180° for a population of PMd cells. Dots indicate mean slope and lines indicate standard error.

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SC, monkeys performing a visual search task made fewer saccades to targets in the affected zone (Figure 4A). A control task confirmed that this was not simply a motor deficit, since saccades in a single-target control task were nearly unaffected. Carello and Krauzlis [59] presented monkeys with two potential pursuit stimuli and showed that subthreshold SC microstimulation led them to select the one contralateral to the stimulation site. Again, this was not merely a motor effect because the subsequent pursuit movements were accurate. Similar findings have been reported in cortex. For example, Schieber [60] showed that inactivation of ventral premotor cortex (PMv) caused monkeys to select ipsilateral targets during a dual target task, and Oliveira *et al.* [61] showed that TMS over left parietal cortex biased subjects' choices in a hand selection task.

Another way to test the predictions of action-based models is to analyze how the relationship between potential movements influences the decisions between them (e.g. Figure 3B). In a recent experiment [62], we trained a monkey to choose between two reach targets whose reward value was indicated by stimulus cues (Figure 4B). We found that the activity of directionally tuned cells in dorsal premotor cortex (PMd) was modulated by the relative value of potential reach targets – it increased with the value of the target in a cell's preferred direction but decreased with the value of other options (Figure 4C, 2nd and 3rd columns), and this modulation was completely absent when only a single target was present (Figure 4B, 1st column). Such relative value encoding in PMd was predicted by a model in which a competition between action representations in sensorimotor regions is biased by absolute value signals coming from elsewhere [45].

Still more important for the present discussion is another prediction made by that same model – that the strength of the competition between two targets should be greater when they are far apart than when they are close together [45]. As shown in Figure 4D, this was indeed observed. A PMd cell was inhibited by the value of targets away from its preferred direction, and the gain of this inhibition was stronger when the targets were further apart. This is consistent with the situation depicted in Figure 3B – a choice between two opposite actions must be all-or-none, requiring strong mutual inhibition, but a choice between similar actions can permit a mixture of two movements. Indeed, when targets were within 60° of each other the monkey often began reaching in-between them, consistent with earlier human data [41,42,63]. This supports the hypothesis that the decision is made within a neural representation of potential actions, which is sensitive to sensorimotor contingencies such as the spatial relationship between options. A model of purely economic choices (more juice vs. less) would not make this prediction because the angle between the reaching actions (which does not affect the costs of the actions themselves)

is a sensorimotor contingency that does not enter into the economic equation [5]. Finally, a follow-up study showed that the same PMd cells whose activity predicts choices continue to be involved during movement execution and predict when a monkey changes his mind in flight [36]. Biased competition in sensorimotor maps [45] explains all of these results as well as the distributions of reaching choices [42,63] that are difficult to explain with a purely good-based model.

Nevertheless, an action-based model obviously cannot explain how we make choices that are not about actions. When deciding on a house to buy one is presumably not planning potential movements of opening the door, but instead is considering cost, space, commuting distance, and so on. A good-based model appears to be better suited to these kinds of problems. It is possible that the brain possesses two systems: one for decisions between actions and one for more abstract choices, and neurological evidence suggests the former may involve ACC while the latter involves OFC [54]. While separate systems are a possibility, considerations of evolutionary continuity motivate us to ask how a single system could have evolved to flexibly deal with both kinds of decisions.

A distributed consensus

Brain evolution is highly conservative, and the basic anatomical features of the mammalian nervous system were established many millions of years ago. At that time, decision-making was almost exclusively about actions, and could have been supported by the kind of action-based architecture depicted in Figure 1B. But how could that architecture have evolved to handle more abstract kinds of decisions?

In the scheme depicted in Figure 1C, the competition between actions has been differentiated into two levels. Activity at the lower level represents specific movements (reach right vs. reach left) in a sensorimotor space where they compete through connections whose topology reflects the geometry of the actions themselves. Activity at the higher level represents choices in an abstract space of goals (obtain apple vs. orange) which compete through connections that reflect their behavioral relationships (choices between two apples are more similar than choices between an apple and an orange). These levels may correspond to progressively more anterior portions of frontal cortex that process progressively more abstract information [64] and are more strongly interconnected with sensory regions [7]. The linkage between the levels need not be one-to-one: a single action can lead to two goals and many actions can lead to the same goal.

Because the levels are reciprocally connected, they share the biases that may arrive from a variety of sources, and gradually arrive at a decision through a 'distributed consensus'. For example, when choosing between two

different reaching trajectories for obtaining the same piece of fruit, activity at the upper level is uniform and the decision is determined at the lower level based on action costs. By contrast, when deciding between exploiting nearby resources versus exploring elsewhere, specific actions are not explicitly defined and the decision is resolved at the higher level on the basis of available versus desired goods. Finally, when choosing between two pursuit actions (Figure 3A), one must weigh high level factors such as their value (e.g. amount of food) as well as relevant sensorimotor contingencies (e.g. distance to target). In such conditions the biases may not be in agreement, but positive feedback between layers will eventually force a choice to emerge. For example, Figure 1C depicts a situation in which stimulus values favor choice 1 but action costs favor choice 2, creating a conflict that is eventually resolved in favor of the low cost action.

There is an important distinction between mechanisms that bias us toward one choice or another, and the mechanisms by which we commit. The fact that neural activity in a brain region is modulated by decision variables does not imply its role in commitment to a choice. Indeed, a region that encodes absolute decision variables may be more involved in computing the relevant biases that influence competition elsewhere. In the circuits that determine commitment, we would instead expect activity to reflect relative decision variables resulting from inhibitory interactions [4*,45]. A prominent model suggests that while the brain is deciding between actions, commitment occurs when activity in effector-specific sensorimotor regions reaches a threshold [18,48*,65–69,70*]. That commitment to an action should depend on activity in motor-related regions makes good sense from an ecological perspective: You can covertly change your mind all you want, but once you begin to move the consequences of your actions begin to play out (opponents can predict what you're going to do, declined opportunities may be lost, etc.).

Commitment to more abstract decisions may occur at a higher level, but it may follow similar rules [26]. For example, Hayden *et al.* [71**] studied a task inspired by foraging behavior: Monkeys were faced with a decision analogous to exploiting a depleting resource in one 'patch' versus investing time to switch to a new one. It was found that on each trial, neurons in ACC fired a burst that grew as the patch was being depleted, but it was not simply related to the reward size. Rather, it was related to the monkey's exploit-versus-explore decision, reaching a threshold firing rate on the trial just before the monkey decided it was time to move on. This finding is consistent with the idea that ACC may encode higher-level aspects of an action's value [53], akin perhaps to the level of goals (Figure 1C).

The distributed consensus model can be tested using conflict tasks, in which different decision factors favor

different choices (e.g. high-reward-high-cost versus low-reward-low-cost actions). The model predicts that in such situations, regions involved in commitment (red box in Figure 1C) will always indicate the choice that is made, but they will do so with different latencies depending on how the conflict was ultimately resolved. For example, on trials in which the subject made the high-reward-high-cost choice, commitment should appear at the upper level before the lower, but the opposite should be true if the low-cost-low-reward choice won. By contrast, cells which provide the relevant biases but which lie outside of the distributed consensus circuits may not always reflect the choice that was actually made. Studying such conflict scenarios could go a long way into shedding light on the neural architecture that underlies how we commit to a choice.

Concluding remarks

Although recent studies have made impressive progress at characterizing how neural activity is related to various aspects of decision-making, we are still only beginning to understand how these pieces fit together into a functional whole. Some theories suggest that decisions (at least about action) emerge as a competition between representations of potential actions, while others propose that all decisions are made in an abstract cognitive representation. Here, I describe a multi-level model in which decisions emerge as a consensus distributed among a variety of representations, some of which are directly involved in sensorimotor control, and some which deal with more abstract aspects of behavior.

Of course, how we commit to decisions is only one of many open questions relevant for a general theory of decision-making. To date, most research has studied very constrained laboratory situations in which reward sizes and probabilities are known, responses are clearly specified, and time is broken up into a series of familiar repeating trials. These address only a small subset of the challenges animals must face to survive in their complex world. As our theories gradually expand to address that world, we should not expect them to survive for long without some major adaptations.

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36. Pastor-Bernier A, Tremblay E, Cisek P: **Dorsal premotor cortex is involved in switching motor plans.** *Front Neuroeng* 2012, **5**.
This study tested the hypothesis that the same PMd cells that initially indicate a monkey's reach decision continue to be involved in on-line processes during movement. Analyses focused on trials in which the monkey chose the more valuable of two reach targets but it disappeared at the time of the GO signal, forcing the monkey to change his mind during the reaction or movement time. Consistent with the hypothesis, cells

which showed relative value modulation before the GO signal clearly reflected when the monkey changed his mind after the more valuable target vanished.

37. Roesch MR, Olson CR: **Impact of expected reward on neuronal activity in prefrontal cortex, frontal and supplementary eye fields and premotor cortex.** *J Neurophysiol* 2003, **90**:1766–1789.

38. Tipper SP, Howard LA, Houghton G: **Behavioural consequences of selection from neural population codes.** In *Control of Cognitive Processes: Attention and Performance XVIII*. Edited by Monsell S, Driver J. Cambridge, MA: MIT Press; 2000:223–245.

39. Welsh TN, Elliott D, Weeks DJ: **Hand deviations toward distractors. Evidence for response competition.** *Exp Brain Res* 1999, **127**:207–212.

40. Song JH, Nakayama K: **Target selection in visual search as revealed by movement trajectories.** *Vision Res* 2008, **48**:853–861.

41. Chapman CS, Gallivan JP, Wood DK, Milne JL, Culham JC, Goodale MA: **Reaching for the unknown: multiple target encoding and real-time decision-making in a rapid reach task.** *Cognition* 2010, **116**:168–176.

This paper describes a set of rapid reaching experiments in which subjects are presented with one, two, or three potential targets, and the correct one is indicated at movement onset. It was observed that reaching trajectories were deviated in a manner biased by both the locations and number of targets shown.

42. Ghez C, Favilla M, Ghilardi MF, Gordon J, Bermejo R, Pullman S: **Discrete and continuous planning of hand movements and isometric force trajectories.** *Exp Brain Res* 1997, **115**:217–233.

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44. McPeck RM, Han JH, Keller EL: **Competition between saccade goals in the superior colliculus produces saccade curvature.** *J Neurophysiol* 2003, **89**:2577–2590.

45. Cisek P: **Integrated neural processes for defining potential actions and deciding between them: a computational model.** *J Neurosci* 2006, **26**:9761–9770.

46. Erlhagen W, Schöner G: **Dynamic field theory of movement preparation.** *Psychol Rev* 2002, **109**:545–572.

47. Cos I, Belanger N, Cisek P: **The influence of predicted arm biomechanics on decision-making.** *J Neurophysiol* 2011, **105**:3022–3033.

In this study, human subjects made free choices between reaching movements that had the same value but varied in path distance and biomechanical costs. A strong preference was observed for actions with lower biomechanical costs, even if their path distance was substantially longer. This implies that decisions can take biomechanical costs into account when choosing between actions. Importantly, because the movements had similar launching costs and differed only in the costs around target arrival, the observed preferences demonstrate that the brain is able to predict subtle biomechanical costs associated with candidate movements before movement onset.

48. Michelet T, Duncan GH, Cisek P: **Response competition in the primary motor cortex: corticospinal excitability reflects response replacement during simple decisions.** *J Neurophysiol* 2010, **104**:119–127.

In this experiment, single-pulse TMS was applied to M1 while human subjects performed a task testing the influence of salient distracters on finger flexion/extension choices. The muscle potentials evoked by TMS revealed that M1 initially reflected the erroneous distracter-driven movement and later switched to reflect the subjects' actual correct choice. Each subject's reaction time was well predicted by a threshold of corticospinal excitability across conditions.

49. Selen LPJ, Shadlen MN, Wolpert DM: **Deliberation in the motor system: reflex gains track evolving evidence leading to a decision.** *J Neurosci* 2012, **32**:2276–2286.

This study demonstrates that while humans make perceptual decisions that are reported using arm movements, their arm reflex gains change in parallel with the theoretical decision variable that explains their choice behavior. This suggests that decisions can spill into the motor system all the way into setting feedback gains, providing further support for the tight integration of decision-making and movement control.

50. Freidin E, Kacelnik A: **Rational choice, context dependence, and the value of information in European starlings (*Sturnus vulgaris*).** *Science* 2011, **334**:1000–1002.

The authors argue that situations in which animals choose between simultaneously available goods are much less frequent in the natural world than situations in which they must choose between what is available now versus what may be available later. Such sequential choices motivate animals to judge an offer in relation to the background context in which it is usually found. This was tested by presenting European starlings with two contexts in which they made choices between accepting or rejecting an offered stimulus: one context in which trials presented them either with a high-value stimulus A or a slightly less high-value stimulus B, and a second context in which they encountered a low-value stimulus C or a still lower-valued stimulus D. As predicted, in the rare trials that simultaneously presented stimuli B and C, the animals chose C more often than B, especially when the context was explicitly cued.

51. Wallis JD, Kennerley SW: **Contrasting reward signals in the orbitofrontal cortex and anterior cingulate cortex.** *Ann NY Acad Sci* 2011, **1239**:33–42.

52. Kennerley SW, Behrens TE, Wallis JD: **Double dissociation of value computations in orbitofrontal and anterior cingulate neurons.** *Nat Neurosci* 2011, **14**:1581–1589.

In this study, monkeys chose between pairs of stimuli associated with different probability of reward, reward amount, or action cost. In the ACC, neurons encoded reward probability during the stimulus and outcome phases with opposite slope, consistent with a reward prediction error signal. By contrast, OFC neurons encoded chosen value relative to recent history. In addition to these observations, the study raised a word of caution, demonstrating that some effects at a single-neuron level can cancel out at the population level, rendering them undetectable with methods such as fMRI.

53. Hayden BY, Platt ML: **Neurons in anterior cingulate cortex multiplex information about reward and action.** *J Neurosci* 2010, **30**:3339–3346.

54. Camille N, Tsuchida A, Fellows LK: **Double dissociation of stimulus-value and action-value learning in humans with orbitofrontal or anterior cingulate cortex damage.** *J Neurosci* 2011, **31**:15048–15052.

This paper reports that patients with damage to the OFC show deficits in learning stimulus values but not action values, while patients with dorsal ACC damage show the opposite effect. This suggests the existence of separate systems for making decisions using stimulus values versus action values, which may operate in parallel in the intact brain.

55. Tsujimoto S, Genovesio A, Wise SP: **Comparison of strategy signals in the dorsolateral and orbital prefrontal cortex.** *J Neurosci* 2011, **31**:4583–4592.

56. Wallis JD, Miller EK: **From rule to response: neuronal processes in the premotor and prefrontal cortex.** *J Neurophysiol* 2003, **90**:1790–1806.

57. Schultz W: **Neural coding of basic reward terms of animal learning theory, game theory, microeconomics and behavioural ecology.** *Curr Opin Neurobiol* 2004, **14**:139–147.

58. McPeck RM, Keller EL: **Deficits in saccade target selection after inactivation of superior colliculus.** *Nat Neurosci* 2004, **7**:757–763.

59. Carello CD, Krauzlis RJ: **Manipulating intent: evidence for a causal role of the superior colliculus in target selection.** *Neuron* 2004, **43**:575–583.

60. Schieber MH: **Inactivation of the ventral premotor cortex biases the laterality of motoric choices.** *Exp Brain Res* 2000, **130**:497–507.

61. Oliveira FT, Diedrichsen J, Verstynen T, Duque J, Ivry RB: **Transcranial magnetic stimulation of posterior parietal cortex affects decisions of hand choice.** *Proc Natl Acad Sci USA* 2010, **107**:17751–17756.

62. Pastor-Bernier A, Cisek P: **Neural correlates of biased competition in premotor cortex.** *J Neurosci* 2011, **31**:7083–7088.
- This study examined neural activity in monkey PMd as a function of rewards associated with reach targets. No cells showed any modulation with value when one target was presented, but many of the same cells were strongly modulated by relative value when two targets were present. Importantly, the inhibitory effect of a second target was stronger as the distance between targets increased, implying competition at the level of a

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sensorimotor map of actions. While the spatial distance effect appeared in PMd at the same time as directional tuning (consistent with processing along the fast dorsal visual stream), the modulatory effect of relative rewards appeared later (consistent with processing through prefrontal cortex or basal ganglia).

63. Favilla M: **Reaching movements: concurrency of continuous and discrete programming.** *Neuroreport* 1997, **8**:3973-3977.

64. Badre D, Kayser AS, D'Esposito M: **Frontal cortex and the discovery of abstract action rules.** *Neuron* 2010, **66**:315-326. This fMRI study showed that when human subjects learn a task which contains high-order structure, activity in anterior frontal cortex is stronger than in a task in which no such structure exists, and parallels the timing of behavioral performance stages during learning. The authors suggest that the more anterior regions of frontal cortex support the learning of rules at progressively higher levels of abstraction, and that in normal behavior these multiple levels all operate in parallel.

65. Hanes DP, Schall JD: **Neural control of voluntary movement initiation.** *Science* 1996, **274**:427-430.

66. Pesaran B, Nelson MJ, Andersen RA: **Free choice activates a decision circuit between frontal and parietal cortex.** *Nature* 2008, **453**:406-409.

67. Bastian A, Schöner G, Riehle A: **Preshaping and continuous evolution of motor cortical representations during movement preparation.** *Eur J Neurosci* 2003, **18**:2047-2058.

68. Lebedev MA, O'Doherty JE, Nicolelis MA: **Decoding of temporal intervals from cortical ensemble activity.** *J Neurophysiol* 2008, **99**:166-186.

69. Thura D, Cisek P: **Neural activity during adjustment of the speed-accuracy trade-off in a reach decision task [abstract].** *Neuroscience Meeting Planner* 2011, **Program No. 609.17**.

70. Bannur S, Gold JI: **Distinct representations of a perceptual decision and the associated oculomotor plan in the monkey lateral intraparietal area.** *J Neurosci* 2011, **31**:913-921.

This study examined neural activity in LIP during the well-known random dot motion discrimination task, but with an important variation. In some trials, the saccade targets for indicating each motion direction were indicated before the motion stimulus appeared, in some during motion viewing, and in some they were indicated only after the motion stimulus vanished. The neural activity of many LIP neurons showed the classic stimulus-related build-up of activity only after the targets were known, suggesting that this activity is related to motor preparation. By contrast, other LIP neurons showed activity related to the stimulus even before the target mapping was known. Although this activity did not exhibit the long build-up often ascribed to stimulus discrimination, it suggests a certain degree of abstract processing in a putatively sensorimotor brain region.

71. Hayden BY, Pearson JM, Platt ML: **Neuronal basis of sequential foraging decisions in a patchy environment.** *Nat Neurosci* 2011, **14**:933-939.

In this study, monkeys performed a saccadic task analogous to foraging in a patchy environment. On each trial, monkeys chose between two options: to 'stay in the patch' which yielded a small immediate reward whose amount decreased over time; or to 'switch to a new patch' which reset the reward value but incurred a delay. As the subjective value of switching increased relative to staying, neural activity in dorsal ACC increased and reached a threshold that predicted when the monkeys chose to switch.