Sequential sampling from memory underlies perceptual decisions unyoked from actions

Author List: Prayshita Sharma[1*], Michael N. Shadlen[1,2,3], S. Shushruth[4,5]

Contact: shushruth@pitt.edu (SS), shadlen@columbia.edu (MNS)

Author Affiliations:

[1]: Zuckerman Mind Brain Behavior Institute, Department of Neuroscience, [2]: Howard Hughes Medical Institute [3]: Kavli Institute; Columbia University, 612 West 130th Street, New York, NY 10027, USA

[4]: Department of Neuroscience, University of Pittsburgh; [5]: Center for Neural Basis of Cognition; 4400 Fifth Avenue, Pittsburgh, PA 15213, USA

[*] Current address: Program in Computational Neuroscience, University of Chicago

Abstract

Perceptual decision-making refers to the class of decisions in which sensory evidence is used to categorize percepts and guide actions. Conventionally, categorical decisions are thought to precede motor actions. However, recent studies in nonhuman primates challenge this assumption – when perceptual decisions were uncoupled from the actions they bear upon, animals postponed the decisions until relevant response options were revealed. To determine whether this postponement stems from cognitive limitations unique to nonhuman primates, we conducted a similar experiment with human subjects. Naive subjects viewed a random-dot motion (RDM) stimulus that was difficult to categorize. After a delay period following the RDM, two choice targets were presented and subjects decided which target lay closer to the perceived motion direction. Decision accuracy varied across subjects, reflecting individual differences in ability to integrate motion evidence. Notably, subjects with higher decision accuracy showed prolonged deliberation after choice-target presentation. Furthermore, the time they took to report their decisions depended on the strength of the motion evidence. This pattern of accuracy and decision reporting time could be accounted for by a bounded diffusion model in which subjects sequentially sample stored sensory information from memory during the target selection phase. When the RDM was challenging to categorize, the subsequent appearance of the targets provided a framework to interrogate stored evidence and render a decision. Our results reveal a strategic feature of working memory of retaining information based on its future utility. This observation opens new avenues for investigating how memory and decision-making interact.

Introduction

Perceptual decisions intuitively feel like they precede and are separated from the actions they bear upon. For instance, a soccer goalkeeper might decide a shot is headed to their right (decide motion as "rightward") and execute a dive in that direction (choose an action). But neurophysiological recordings in both animals and humans indicate that the accumulation of sensory evidence towards a decision transpires in the same neurons involved in action planning.[1–5] This overlap suggests that perceptual decisions are embodied in terms of the motor actions that a percept affords.[6–8]

In behavioral tasks commonly used to study perceptual decision-making in the laboratory, the actions associated with decision outcomes are usually prespecified. It has been suggested that decisions are only embodied in terms of actions when such decision-to-action mapping is known in advance. In tasks in which decision-making is uncoupled from the actions they bear upon, "action-independent" decision signals have been reported in humans,[9–11] monkeys[12–21] and rodents.[22,23] However most of these studies still confined the subjects to choose between two possible actions for reporting their decision – primarily randomizing the mapping between the stimulus type and reporting action across trials. Thus the degree of flexibility of the mapping between the decision and action uncovered by these studies is unclear. Further, in many of these studies, the stimulus that was being decided upon was unambiguous. Thus it is difficult to ascertain the process by which the decision was formed.

A recent study in macaques,[24] addressed these two issues. Monkeys were trained to associate two directions of stochastic random dot motion (RDM) stimuli with choice-targets of two colors. Importantly, the colored choice targets appeared following a delay after the RDM was extinguished at unpredictable locations. Thus the monkeys had to learn to be highly flexible in mapping decisions to actions. And because of the stochastic nature of the RDM, the animals had to integrate motion evidence over time to arrive at a decision – and this deliberation would serve as a signature of the decision making process. Surprisingly, this study found that monkeys, instead of integrating evidence towards a decision when the RDM was shown, postponed it until after the choice targets were shown. Further, activity of neurons in the sensorimotor association area LIP represented decision formation during this action selection epoch. These results suggested that the monkeys were storing sensory information during RDM viewing and retrieving it from memory to evaluate it in the context of available responses.

The postponement of evidence accumulation could arise from an inability of monkeys to effectively categorize the stimulus, possibly due to their limited conceptual understanding of direction. We hypothesized

that when confronted with stimuli that are similarly difficult to categorize, humans also resort to a strategy similar to that used by monkeys. To test this, we designed a decision-making task similar to that in.[24] Human subjects estimated the net direction of an RDM which varied over 360° across trials. After a delay period following the RDM, two choice targets were shown. Subjects indicated their decision by choosing the target closest to their perceived motion direction.

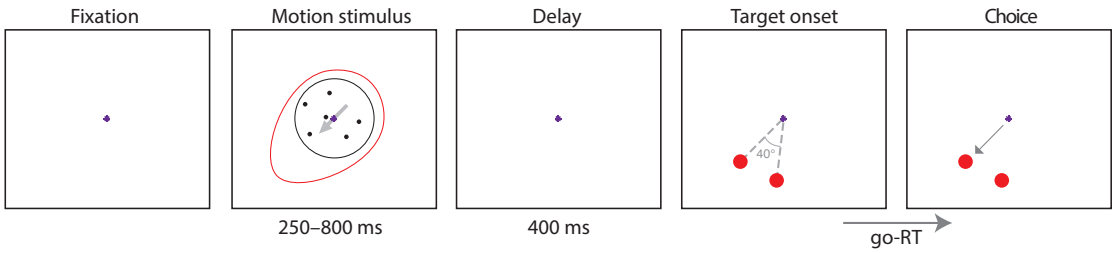

Figure 1: **Direction-decision task**. After subjects acquire fixation, a random dot motion stimulus is presented. The direction of motion of the coherent dots is drawn from a von Mises distribution (denoted by the red oval - not visible to the subject). Across trials, the mean of the distribution varies randomly between 0°-350° (in 10° increments). This is followed by a short delay period. Two targets are then presented equidistant from the fixation point. One target is in the direction of the mean of the von Mises and the other, 40° away. The subjects report their choice by an eye movement to one of the two targets.

The decision accuracy varied across the six subjects, reflecting differences in their ability to integrate motion evidence. Notably, subjects with higher decision accuracy showed prolonged deliberation after choice-target presentation, and the time they took to report their decisions depended on the strength of the motion evidence. We found that this pattern of accuracy and decision reporting time can be explained by a model in which subjects sequentially sample stored information from memory while choosing the targets.[24–27] When the stimulus was hard to categorize, the appearance of the targets provided a framework to interrogate the stored evidence and render a decision. Our results show that working memory retains sensory details strategically, based on their anticipated future use.

Results

Six naive human subjects performed a direction discrimination task (Figure 1). They were first presented a random-dot motion (RDM) stimulus whose dominant direction varied between $0° - 350°$. After a 400 ms delay following stimulus offset, two targets appeared equidistant from fixation – one aligned with the motion direction and the other offset by $\pm 40°$. subjects were instructed to choose the target aligned with the motion direction. The difficulty of direction discrimination varied across trials as noise was introduced to both motion direction and fraction of coherently moving dots (see Materials and Methods).

Subjects exhibit deliberation during action selection

All six subjects found the task challenging. Unlike standard RDM tasks where subjects rarely make errors at high coherence (*lapses*), all subjects in this task showed lapses at 64% coherence trials (Figure 2). Since, to correctly discern the net direction of motion in this task, one needs to integrate motion information over time,[28,29] the presence of lapses underscores the demand the task placed on effective integration of motion evidence. Subjects varied notably in their sensitivity to motion coherence – those with fewer lapses exhibited higher sensitivity to motion strength. This suggests that subjects varied in their ability to integrate motion evidence over time.

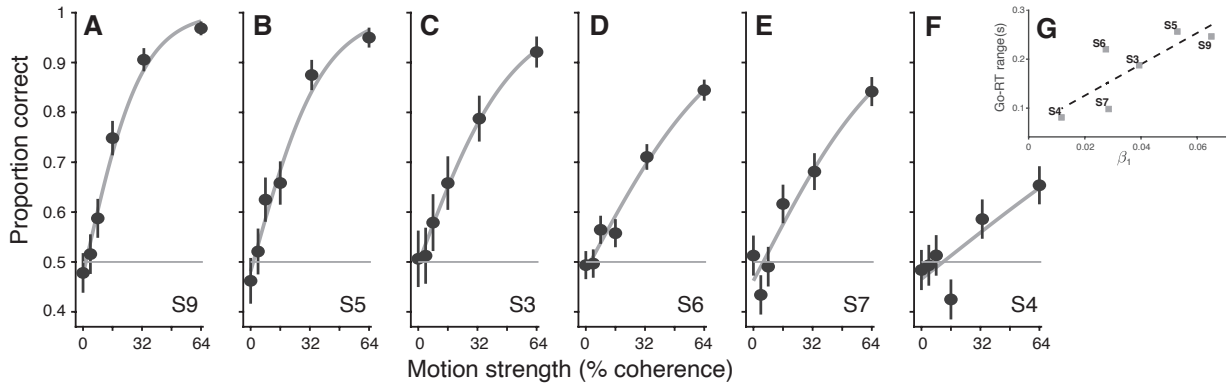

Figure 2: **Decision Accuracy**. **(A-F)** The proportion of correct choices is plotted as a function of motion coherence for individual subjects. Solid lines are fits to a logistic model (Equation 1). The subjects are in the order of decreasing sensitivity (β_1 from logistic fits). **(G)** Correlation between β_1 and range of go-RT across the six subjects.

The variability across subjects in the ability to integrate motion information could have arisen in two ways. One possibility is variability in perceptual sensitivity to motion stimuli during the viewing phase, a hypothesis partially supported by logistic regression coefficients. Intriguingly, recent studies in monkeys suggest another possibility[20,24] – when motion evidence is weak, the subjects may store the motion infor-

mation in memory and later, once the targets are presented, use the location of the targets as spatial reference to integrate the stored motion information to decide which target to choose.

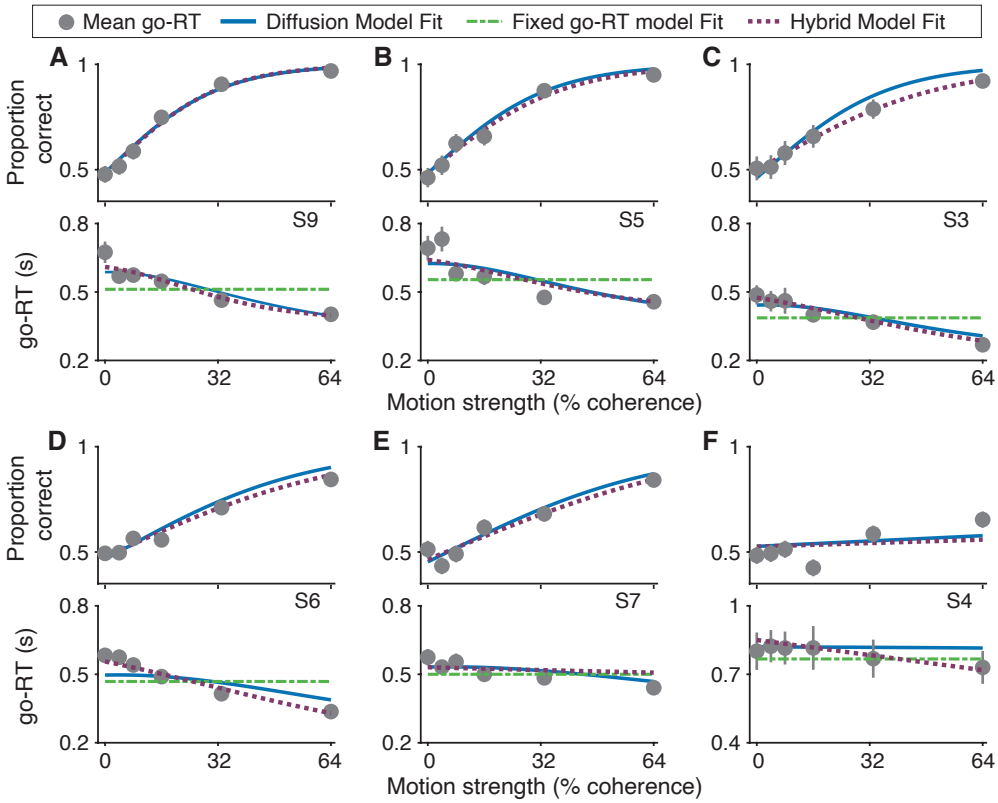

Figure 3: **Model fits for decision accuracy and go-RT**. For each subject, the proportion of correct choices (*top*) and go-RTs (*bottom*) are plotted as a function of motion strength. Solid lines are fits to various models indicated in the legend. Subjects are ordered as in Figure 2.

In monkeys, a signature of evidence integration from memory was prolongation of the time between target onset and decision report (go-reaction time, go-RT, Figure 1). Consistent with this, the accuracy of our subjects' decisions (slope of logistic fit in Figure 2, Equation 1) was correlated with the range of go-RT between the easiest and the hardest decisions ($p = 0.047$, Pearson's correlation, Figure 2G). Further, subjects with high accuracy also showed a systematic dependence of go-RT on motion coherence (Figure 3), mirroring patterns observed in monkeys.[24] This coherence-dependent increase in go-RT strongly suggests that human subjects also deliberate about stored motion evidence after the targets appear.

Drift-diffusion models account for deliberation during action selection

We tested whether prolonged go-RTs enhanced decision accuracy by modeling subjects' choice and go-RT data using a diffusion-to-bound (DtB) framework. In DtB models, sensory evidence is accumulated as a

decision variable and a choice results when the decision variable reaches one of two boundaries. Typically, reaction times in a standard RDM task correspond directly to evidence accumulation duration, providing a powerful mechanistic link between choice accuracy and RT. In our task, if subjects integrated evidence after targets appeared, a DtB model would similarly link choices and prolonged go-RTs.

Indeed, DtB models provided robust fits to individual subject's choice data and go-RT distributions (Figure 3, blue lines). The model's performance was especially strong for subjects showing pronounced go-RT dependence on coherence, who also exhibited higher decision accuracy. We compared these fits to an alternative model that assumes subjects form an abstract decision during motion viewing and quickly convert that decision into a choice when the targets are shown (*fixed go-RT model*, Equation 3). In this model, go-RT is independent of motion coherence and go-RT variability is solely attributed to motor noise. Model comparisons using Bayesian Information Criterion (BIC) strongly favored the DtB model for all subjects (Figure 4A). This model comparison provides support for decision deliberation during action selection.

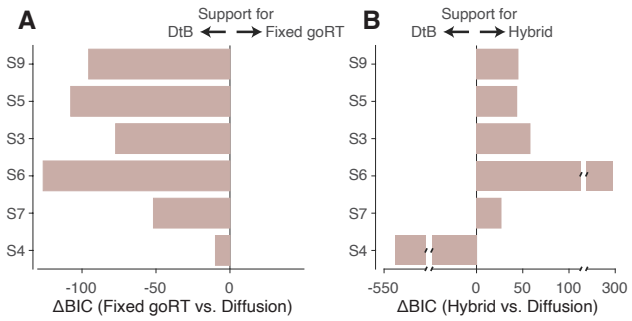

Figure 4: **Model comparisions**. ΔBIC for comparing diffusion model to either **(A)** the fixed goRT model or **(B)** the hybrid model. Each bar represents individual subjects, with negative values indicating support for diffusion model. Subjects are ordered as in Figure 2.

To explore individual differences in strategy further, we analyzed model fits for each subject across different coherence conditions Figure 5. For most subjects, the DtB model outperformed the fixed go-RT model primarily at lower coherence conditions. This led us to consider a hybrid, two strategy model. In this model, subjects make an abstract decisions when motion evidence is strong but resort to evidence integration from memory of the stimulus when motion evidence is ambiguous. The contributions of DtB vs. fixed go-RT model to the go-RT distributions were fit per individual subject with a scaling factor (α, Equation 4). This two-strategy model (purple dotted line in Figure 3 and Figure 5) provided superior fits over the diffusion model for most subjects, except subject S4, who exhibited the lowest decision accuracy (Figure 4B).

These results demonstrate a strategic use of memory during decision-making, with subjects storing either an abstract estimate of motion direction (when evidence is strong) or the motion evidence itself (when

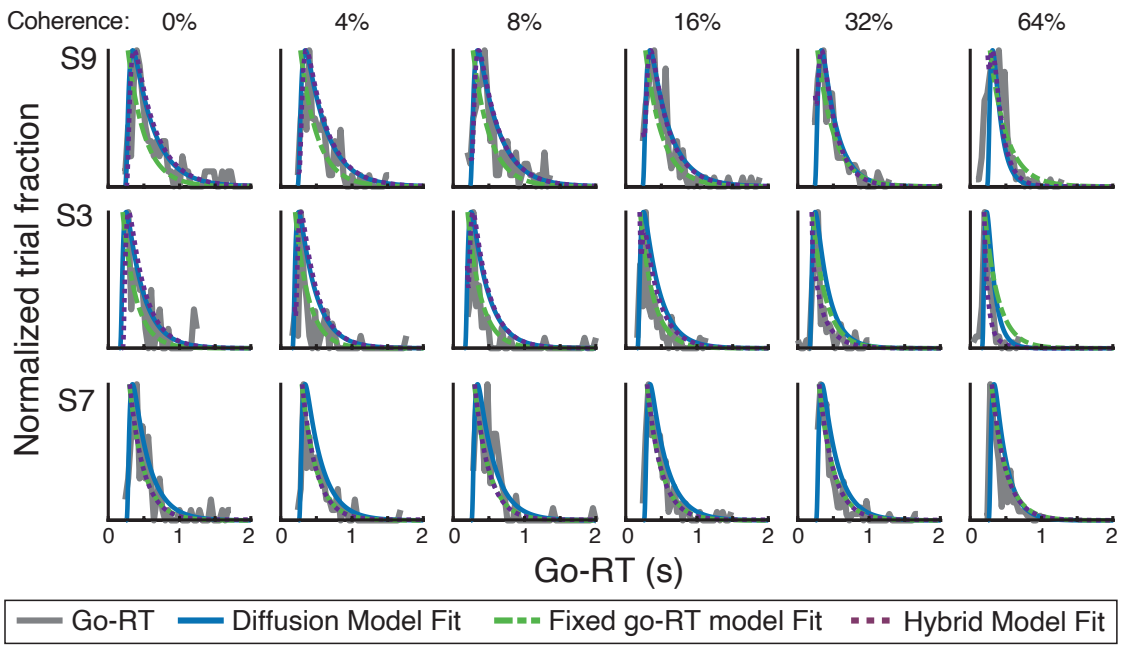

Figure 5: **Distributions of go-RTs and model fits**. For three example subjects, the distribution of go-RTs for correct choices are plotted at different coherences (gray lines). Superimposed are the fits to the three models indicated in the legend.

ambiguous), enabling flexible deliberation once targets are revealed. The α values of individual subjects provided insight into how different individuals weighted fast vs. deliberative decisions as a function of coherence (Table 1), underscoring individual differences in memory utilization and decision-making approaches.

Motion information is held in working memory

The RDM stimulus is noisy and stochastic. How can subjects store such sensory information over hundreds of milliseconds? One possibility is that this information is held in iconic memory, which is considered a property of sensory systems.[30] While iconic memory is high capacity, it is also labile and decays rapidly within a second.[31] For intermediate-term storage, some aspects of iconic memory are thought to be transferred to working memory, but this storage is known to be capacity limited.

To test whether the stimulus information driving decisions is held in working or iconic memory, we re-tested three proficient subjects in a modified task version, where the wait duration on each trial could be either 400 or 1200 ms. We focused on lower coherence trials, where decisions relied more heavily on memory sampling. The decision accuracy of all three subjects remained statistically indistinguishable even with the longer 1200 ms delay ($p = 0.28, 0.65, 0.63$ for subjects S9, S5 and S3, respectively. $\mathcal{H}_0$: $\beta_3 \neq 0$ in

Equation 5). The persistence of motion information in memory for over a second indicates that it is held in working memory.

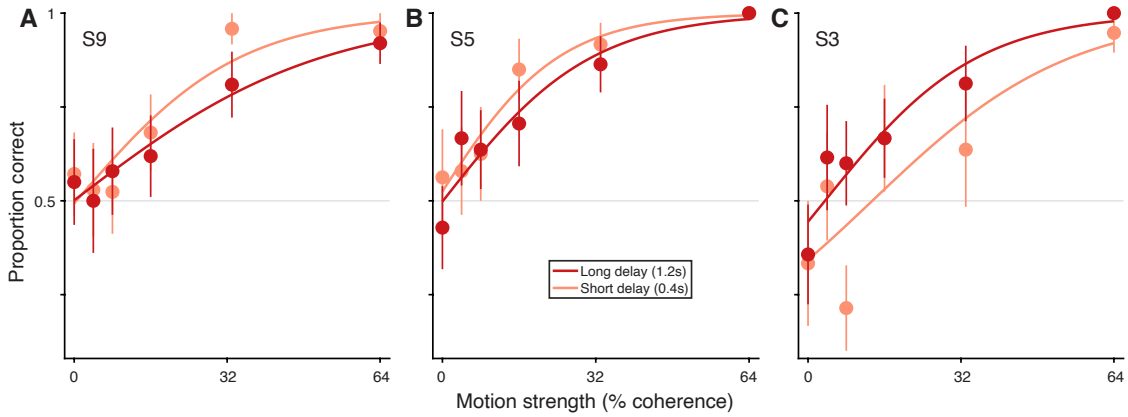

Figure 6: **Decision accuracy at different memory delays**. Proportion of correct choices as a function of motion coherence is plotted for three subjects who performed the task at two different wait durations. Solid lines are fits to a logistic model (Equation 1).

	DtB			Fixed go-RT		Hybrid		
	$\kappa\ (coh^{-1}\ s^{-1})$	B	$T_{nd}\ (s)$	$u\ (s)$	$T_{nd}\ (s)$	κ	s	$T_{nd}\ (s)$
S9	5.30	0.57	0.23	0.24	0.28	5.37	1.00	0.24
S5	5.08	0.55	0.28	0.23	0.33	4.16	0.63	0.35
S3	5.32	0.50	0.16	0.19	0.20	3.70	1.00	0.19
S6	2.91	0.59	0.10	0.31	0.17	2.14	0.64	0.24
S7	3.07	0.50	0.25	0.21	0.30	1.28	0.03	0.30
S4	0.19	0.79	0.14	0.50	0.27	0.09	0.11	0.62

Table 1: Model fit parameters for individual subjects.

Discussion

The study of perceptual decision making has offered a window into cognition by revealing the processes through which sensory information is deliberated upon to guide motor actions.[32] A salient result from this line of research is that the accumulation of sensory evidence for decisions is instantiated by neurons associated with motor planning.[33–36] This observation has led to the proposal that perceptual decision-making is embodied as a choice between potential actions.[6,37] However, this framework typically applies when actions for reporting decisions are specified in advance. The current study demonstrates that decision-making can remain embodied even when response actions are specified post-decision. Specifically, when perceptual information is ambiguous and requires temporal integration, subjects can maintain the information in working memory and strategically delay evidence accumulation until the appropriate response actions are presented. We discuss the relevance of our results to the concept of embodied cognition and to our understanding of working memory.

Implications for embodied cognition

The concept of embodied perceptual decision-making has been widely debated.[8,38] Decision related signals have been reported in humans and animals making perceptual decisions without explicit knowledge of decision-action mapping.[9–11,14–19,22,23] However most of these studies were structured to randomize between two available decision-to-action mappings. This leaves open the possibility that subjects made provisional motor decisions and adjusted them when the stimulus response associations were revealed. Our task overcomes this limitation by making it difficult for the subjects to prepare a motor response during stimulus viewing.

Prior studies have shown that, in tasks similar to the one in the current study,[20,24] nonhuman primates postpone decision-making until the decision-action mapping is revealed. Our results show that humans also postpone decision formation until action selection, as evidenced by prolonged go-reaction times that scale with motion strength. This finding corroborates previous human studies. In tasks with similar ambiguity as ours,[39] subjects show deliberation before action selection, but do not in tasks with limited stimulus-action mapping ambiguity.[40,41] Our results reinforce the view that, despite humans' capacity for abstract cognition, the organization of perceptual knowledge fundamentally serves potential actions.[42–44] Thus, when faced with perceptual stimuli that resist easy categorization, humans appear to default to an embodied strategy, using action-oriented frameworks to guide decision formation.

Working memory representations of sensory information

Given the RDM stimulus is noisy and stochastic, it would seem that the memory requirements that can support protracted integration of such evidence are daunting. This information could reside in iconic short term memory which is a high capacity memory buffer.[30] It has been demonstrated that such memory can be formed strategically in anticipation of operations that may be required.[45,46] However, iconic memory is highly labile and decays rapidly.[31] Indeed, our modified experiment with extended delay duration showed that stimulus information is held for longer than a second, suggesting the involvement of the working memory system.

Working memory is classically thought to be of limited capacity,[47] although more recent work has revealed its more dynamic and adaptive properties.[48,49] In RDM tasks, it is possible to strategically store limited samples of evidence to support good accuracy,[24,29,50] making working memory a feasible site of storage. An emerging perspective is to consider the purpose of working memory as not mere retention of information, but to make information readily available for cognitive computations[51] such as attention[52] and decision-making.[53,54] A recent study demonstrated that human subjects can adeptly integrate information from working memory to drive decisions.[55] Our results add to this growing body of evidence that working memory storage is a forward looking process – flexibly adapting based on expected future needs.

In closing, our study underscores the remarkable adaptability of embodied cognition strategies, even under conditions of abstract decision-making. It is noteworthy that, despite recent advances, artificial intelligence systems remain incapable of similarly flexible, action-oriented representations, underscoring a fundamental gap between biological and artificial cognition.[56] Our findings advocate for continued exploration of how action affordances can still underlie the remarkable flexibility of our higher cognition.

Materials and Methods

Subjects

Six adult subjects (three males and three females) participated in the experiment after providing informed written consent. All the subjects were naive to the hypothesis of the experiment and five out of the six subjects had no previous experience with random dot direction discrimination tasks. The experiments were approved by the Institutional Review Board of Columbia University (IRB #AAAL0658).

The number of subjects was limited due to the demanding nature of the task, which required individual subjects to perform $>$1000 trials of challenging perceptual decision-making over two sessions. All model fitting and key analyses are performed at the within-subject level. This approach enables us to characterize each individual's decision-making strategy independently, without relying on population averages. Importantly, all six subjects exhibited the core phenomenon of interest, with inter-individual variability primarily in model parameter estimates. This level of replication is consistent with recent similar studies employing bounded evidence accumulation models for perceptual decision-making.[57]

Apparatus

Subjects were seated in a comfortable chair in a semi-dark room, with their chin and forehead stabilized on a tower mounted on a table. They viewed visual stimuli on a ViewPixx monitor (60 Hz refresh rate, 68 cm viewing distance). Their eye movements were recorded at 1 kHz with a non-invasive infrared eye-tracking device (Eyelink 1000, SR Research Ltd., Ontario, Canada). The temporal precision of the visual stimuli was controlled by PsychToolBox (www.psychtoolbox.org) run on a Macintosh computer.

Behavioral tasks

Subjects made decisions about the net direction of stochastic random-dot motion (RDM) stimuli across multiple trials (Figure 1). Each trial started after the subject fixated on a circular fixation point (FP) on the screen. After a variable delay ($400 - 800$ ms, drawn from a truncated exponential distribution), the RDM stimulus was displayed in a circular aperture of radius 5° visual angle around the FP. The RDM stimulus was based on previous studies,[33] but modified to increase the difficulty of direction estimation. On each trial, a motion direction $\theta \in \{0, 10, 20, ..., 350\}$ and a motion strength $C \in \{0, 0.04, 0.08, 0.16, 0.33, 0.64\}$ were randomly chosen. The first three frames of the stimulus consisted of white dots randomly plotted at a density of $16.7\ \mathrm{dots{\cdot}deg^{-2}{\cdot}s^{-1}}$. From the fourth frame, a fraction of dots C from three frames before were

randomly chosen to be 'signal dots'. Each signal dot was displaced in a direction randomly sampled from a von Mises distribution centered at θ. The remaining dots were replotted at random locations. The stimulus was presented for a variable duration drawn from a truncated exponential distribution (range 250–800 ms, mean 350 ms). 400 ms after the cessation of the stimulus, the FP was extinguished and two circular targets were presented at an eccentricity of 6° visual angle from the center, one in the direction θ ('correct' target) and another at $\theta \pm 40^\circ$ ('incorrect' target). Subjects reported their decision by making an eye movement to the target closest to their perceived direction of motion. We refer to the time between target presentation and decision report as go-reaction time (*go-RT*). To ensure that subjects were motivated to engage with this challenging task, we offered them a performance-based monetary bonus.

Analysis

The accuracy of the subjects' decisions (Figure 2) were fit with a logistic model of the following form:

$$P_{\text{right}} = \lambda + (1 - 2\lambda)\left[1 + \exp(-(\beta_0 + \beta_1 C)\right]^{-1} \tag{1}$$

where λ (lapse rate, i.e. errors at highest coherence), β_0 (bias) and β_1 (sensitivity) are fit parameters.

To assess the correlation between β_1 and go-RT across subjects, we computed the metric *go-RT range* as the difference in mean go-RT between the lowest and highest coherence condition for each subject.

Model fitting

To investigate the relation between subject's choices and go-RTs, we fit the distribution of go-RTs with a variety of computational models. Each model provided predicted go-RT probability densities for each coherence level. The models were fit by maximizing the log likelihood of the observed go-RT distributions given the distributions from each model. For models that also provided predictions of choice distributions, fitting was performed by jointly maximizing the log likelihood of both choice and go-RT distributions under the model.

Drift-diffusion model

We first fit choice accuracy and go-RTs of individual subjects with diffusion-to-bound models (DtB).[26] Traditionally, for direction discrimination tasks, perceptual samples of evidence are considered to be accumulated during RDM viewing. In our adaptation of the model, the samples of evidence are instead presumed to be stored in memory during the RDM viewing epoch. When the target locations are revealed, these samples in memory are integrated to decide which target to choose. The evidence from memory at each time

step is assumed to arise from a normal distribution with variance Δt and mean $\kappa * C * \Delta t$, where C is the motion coherence, and κ is a scaling parameter. The samples of instantaneous evidence are assumed to be independent and this evidence is accumulated as a decision variable (DV), until the integrated evidence reaches an upper or lower bound ($\pm B$) which determines the subject's choice. The go-RT would be the time taken to reach the bound, together with a non-decision time (T_{nd}) to account for sensory and motor delays.

To capture both correct and error go-RTs, we allowed the decision bound (B) to collapse over time:[58]

$$B = \begin{cases} B_0 \times \exp\left(-a\left(t - B_{\text{del}}\right)\right) & \text{if } t \geq B_{\text{del}} \\ B_0 & \text{otherwise} \end{cases} \tag{2}$$

where B_0 is the initial bound height, a is the rate of collapse and B_{del} is the delay to onset of collapse.

We fit the DtB model to the choice and go-RT data using a maximum likelihood procedure. The go-RT and decision accuracy for a given set of parameters were computed from numerical solutions to Fokker-Planck equations.[59,60]

Fixed go-RT model

We considered an alternative model in which subjects reach a decision during RDM viewing or delay epoch, and report their decision after target onset (after sensory and motor delays). This model assumes that the mean go-RTs are invariant to the strength of motion (*Fixed go-RT model*).

The stochasticity of go-RTs was modeled as an exponential distribution:

$$P_{frt}(t) = \frac{e^{-t/u}}{u} \tag{3}$$

where t represents time following target onset and a sensorimotor latency, and u is the mean go-RT. Note that the fixed go-RT model does not directly predict choice distributions, as it assumes choices and go-RTs are independent.

Hybrid Model

We formulated a hybrid model to capture the possibility that subjects' switch between decision-making during RDM and delayed integration based on the reliability of motion evidence on each trial. The contributions of the diffusion model and fixed go-RT model to the go-RT distribution are captured by a coherence dependent scaling factor, α, that is fit to each subject. The go-RT probability distribution in the model for coherence C is:

$$P(t \mid C) \;=\; \alpha(C)P_{frt}(t \mid C) + [1-\alpha(C)]P_{dtb}(t \mid C) \tag{4}$$

where $P_{frt}(t \mid C)$ and $P_{dtb}(t \mid C)$ are, respectively, go-RT probabilities from the fixed go-RT model and the bounded drift diffusion model, and $\alpha(C) \in [0,1]$ is the fractional contribution of the fixed go-RT model.

To model the increasing contribution of the fixed go-RT model as a function of motion strength, we parameterized the scaling factor as a linear function of coherence: $\alpha(C) = (1-s) + s\,C, \quad s \in [0,1]$. Here, the parameter s governs how strongly the fast-strategy is favored as coherence increases. At $s = 0$, $\alpha(C) = 1$ and the model reduces to a pure fixed go-RT strategy; at $s < 1$, the contribution of the fixed go-RT model increases linearly with coherence.

This hybrid formulation provides a flexible yet parsimonious account of how decision strategy can vary with stimulus strength: the slope parameter s capturing the shift from decisions during RDM viewing to integration from memory at different levels of motion strength.

Comparison between models

We used Bayesian Information Criterion (BIC) to adjudicate between the drift-diffusion, fixed go-RT and hybrid models. Since the fixed go-RT model can only explain go-RTs but not choice, the comparison between drift-diffusion and fixed go-RT models were made solely from fitting go-RTs. For comparing the drift-diffusion to hybrid models, we used the complete fits to both choice and go-RT distributions.

Effects of prolonging delay epoch

In a second experiment conducted on a subset of three subjects in separate sessions, on 50% of the trials, the time between RDM cessation and target onset was extended from 400 ms to 1200 ms. To test whether the duration of the delay significantly affected the slope of the logistic fits, we included an interaction term in the logistic regression model in Equation 1 as follows:

$$P_{correct}(C,D) = \lambda + (1-2\lambda)\left[1+\exp(-(\beta_0 + \beta_1 C + \beta_2 D + \beta_3 (C \times D)))\right]^{-1} \tag{5}$$

where β_2 represents the main effect of delay duration D (coded as 0 for 400 ms and 1 for 1200 ms), and β_3 captures the interaction between coherence and delay duration. The significance of the interaction effect was tested by evaluating whether β_3 was significantly different from zero.

Data availability

Behavioral data and code to generate the figures will be uploaded to a publicly available repository on acceptance of the manuscript.

Author Contributions

Conceptualization: SS, MNS

Formal Analysis: PS, SS

Funding Acquisition: MNS, SS

Investigation: PS

Methodology: SS, PS

Software: PS, SS, MNS

Supervision: SS, MNS

Writing - Original Draft Preparation: SS, PS

Writing - Review & Editing: SS, PS, MNS

Acknowledgements

We thank Anne Loffler for help with online psychophysics testing that generated pilot data for this project.

Funding Information

The research was supported by the Howard Hughes Medical Institute (MNS) and an R21 grant from the NIH National Institute on Aging (MNS and SS, 1R21AG067108)

References

[1] Shadlen MN, Newsome WT. Motion perception: seeing and deciding [Journal Article]. Proceedings of the National Academy of Sciences of the United States of America. 1996;93(2):628-33. Available from: http://www.ncbi.nlm.nih.gov/pubmed/8570606.

[2] Donner TH, Siegel M, Fries P, Engel AK. Buildup of choice-predictive activity in human motor cortex during perceptual decision making. Current Biology. 2009;19(18):1581-5.

[3] Selen LPJ, Shadlen MN, Wolpert DM. Deliberation in the Motor System: Reflex Gains Track Evolving Evidence Leading to a Decision. Journal of Neuroscience. 2012 Feb;32(7):2276-86. Available from: http://www.jneurosci.org/cgi/content/abstract/32/7/2276.

[4] Hanks TD, Summerfield C. Perceptual Decision Making in Rodents, Monkeys, and Humans. Neuron. 2017 Jan;93(1):15-31. Available from: http://linkinghub.elsevier.com/retrieve/pii/S0896627316309424.

[5] Gallivan JP, Chapman CS, Wolpert DM, Flanagan JR. Decision-making in sensorimotor control. Nature Reviews Neuroscience. 2018 Sep;19(9):519-34. Publisher: Nature Publishing Group. Available from: http://www.nature.com/articles/s41583-018-0045-9.

[6] Shadlen MN, Kiani R, Hanks TD, Churchland AK. In: Neurobiology of decision making: An intentional framework; 2008. p. 71-101.

[7] Cisek P, Kalaska JF. Neural mechanisms for interacting with a world full of action choices [Journal Article]. Annu Rev Neurosci. 2010;33:269-98. Available from: https://www.ncbi.nlm.nih.gov/pubmed/20345247.

[8] Wispinski NJ, Gallivan JP, Chapman CS. Models, movements, and minds: bridging the gap between decision making and action. Annals of the New York Academy of Sciences. 2020;1464(1):30-51. Available from: https://onlinelibrary.wiley.com/doi/abs/10.1111/nyas.13973.

[9] Filimon F, Philiastides MG, Nelson JD, Kloosterman NA, Heekeren HR. How Embodied Is Perceptual Decision Making? Evidence for Separate Processing of Perceptual and Motor Decisions. Journal of Neuroscience. 2013 Jan;33(5):2121-36. Available from: http://www.jneurosci.org/content/33/5/2121.abstract.

[10] Gherman S, Markowitz N, Tostaeva G, Espinal E, Mehta AD, O'Connell RG, et al. Intracranial electroencephalography reveals effector-independent evidence accumulation dynamics in multiple human brain regions. Nature Human Behaviour. 2024 Apr;8(4):758-70. Publisher: Nature Publishing Group. Available from: https://www.nature.com/articles/s41562-024-01824-9.

[11] O'Connell RG, Dockree PM, Kelly SP. A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. Nature neuroscience. 2012 Oct;15(12):1729-35. Publisher: Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved. Available from: http://dx.doi.org/10.1038/nn.3248.

[12] Freedman DJ, Riesenhuber M, Poggio T, Miller EK. Categorical representation of visual stimuli in the primate prefrontal cortex [Journal Article]. Science. 2001;291(5502):312-6. Available from: https://www.ncbi.nlm.nih.gov/pubmed/11209083.

[13] Gold JI, Shadlen MN. The influence of behavioral context on the representation of a perceptual decision in developing oculomotor commands [Journal Article]. The Journal of neuroscience. 2003;23(2):632-51. Available from: http://www.ncbi.nlm.nih.gov/pubmed/12533623.

[14] Freedman DJ, Assad JA. Experience-dependent representation of visual categories in parietal cortex [Journal Article]. Nature. 2006;443(7107):85-8. Available from: http://www.ncbi.nlm.nih.gov/pubmed/16936716.

[15] Genovesio A, Tsujimoto S, Wise SP. Feature- and order-based timing representations in the frontal cortex [Journal Article]. Neuron. 2009;63(2):254-66. Available from: http://www.ncbi.nlm.nih.gov/pubmed/19640483.

[16] Bennur S, Gold JI. Distinct representations of a perceptual decision and the associated oculomotor plan in the monkey lateral intraparietal area [Journal Article]. J Neurosci. 2011;31(3):913-21. Available from: http://www.ncbi.nlm.nih.gov/pubmed/21248116.

[17] Goodwin SJ, Blackman RK, Sakellaridi S, Chafee MV. Executive control over cognition: stronger and earlier rule-based modulation of spatial category signals in prefrontal cortex relative to parietal cortex [Journal Article]. J Neurosci. 2012;32(10):3499-515. Available from: https://www.ncbi.nlm.nih.gov/pubmed/22399773.

[18] Quinn KR, Seillier L, Butts DA, Nienborg H. Decision-related feedback in visual cortex lacks spatial selectivity. Nature Communications. 2021;12(1):1-11.

[19] Horwitz GD, Batista AP, Newsome WT. Representation of an abstract perceptual decision in macaque superior colliculus. Journal of neurophysiology. 2004;91(5):2281-96.

[20] Wang M, Montanede C, Chandrasekaran C, Peixoto D, Shenoy KV, Kalaska JF. Macaque dorsal premotor cortex exhibits decision-related activity only when specific stimulus-response associations are known [Journal Article]. Nat Commun. 2019;10(1):1793. Available from: https://www.ncbi.nlm.nih.gov/pubmed/30996222.

[21] Charlton J, Goris R. Abstract deliberation by visuomotor neurons in prefrontal cortex. Nature Neurosci. 2024 Apr:1-9. Available from: https://www.nature.com/articles/s41593-024-01635-1.

[22] Wu Z, Litwin-Kumar A, Shamash P, Taylor A, Axel R, Shadlen MN. Context-Dependent Decision Making in a Premotor Circuit [Journal Article]. Neuron. 2020;106(2):316-28 e6. Available from: https://www.ncbi.nlm.nih.gov/pubmed/32105611.

[23] Pagan M, Tang VD, Aoi MC, Pillow JW, Mante V, Sussillo D, et al. Individual variability of neural computations underlying flexible decisions. Nature. 2025 Mar;639(8054):421-9. Publisher: Nature Publishing Group. Available from: https://www.nature.com/articles/s41586-024-08433-6.

[24] Shushruth S, Zylberberg A, Shadlen MN. Sequential sampling from memory underlies action selection during abstract decision-making. Current Biology. 2022 Mar;0(0). Publisher: Elsevier. Available from: http://www.cell.com/article/S0960982222004055/fulltext.

[25] Ratcliff R, Rouder JN. Modeling response times for two-choice decisions [Journal Article]. Psychological science. 1998;9(5):347-56.

[26] Shadlen MN, Hanks TD, Churchland AK, Kiani R, Yang T. The speed and accuracy of a simple perceptual decision: A mathematical primer. Bayesian Brain: Probabilistic Approaches to Neural Coding, ed K Doya et al. 2006:209-37.

[27] Shadlen MN, Kiani R. Decision making as a window on cognition [Journal Article]. Neuron. 2013;80(3):791-806. Available from: http://www.ncbi.nlm.nih.gov/pubmed/24183028.

[28] Kiani R, Hanks TD, Shadlen MN. Bounded integration in parietal cortex underlies decisions even when viewing duration is dictated by the environment [Journal Article]. The Journal of neuroscience. 2008;28(12):3017-29. Available from: http://www.ncbi.nlm.nih.gov/pubmed/18354005.

[29] Stine GM, Zylberberg A, Ditterich J, Shadlen MN. Differentiating between integration and non-integration strategies in perceptual decision making [Journal Article]. Elife. 2020;9. Available from: https://www.ncbi.nlm.nih.gov/pubmed/32338595.

[30] Sperling G. The information available in brief visual presentations. Psychological Monographs: General and Applied. 1960;74(11):1-29.

[31] Graziano M, Sigman M. The dynamics of sensory buffers: Geometric, spatial, and experience-dependent shaping of iconic memory. Journal of vision. 2008;8(5):9-9.

[32] Kiani R, Corthell L, Shadlen MN. Choice certainty is informed by both evidence and decision time. Neuron. 2014;84(6):1329-42.

[33] Roitman JD, Shadlen MN. Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task [Journal Article]. The Journal of neuroscience. 2002;22(21):9475-89. Available from: http://www.ncbi.nlm.nih.gov/pubmed/12417672.

[34] Ding L, Gold JI. Caudate encodes multiple computations for perceptual decisions [Journal Article]. J Neurosci. 2010;30(47):15747-59. Available from: https://www.ncbi.nlm.nih.gov/pubmed/21106814.

[35] Ding L, Gold JI. Neural correlates of perceptual decision making before, during, and after decision commitment in monkey frontal eye field [Journal Article]. Cereb Cortex. 2012;22(5):1052-67. Available from: http://www.ncbi.nlm.nih.gov/pubmed/21765183.

[36] de Lafuente V, Jazayeri M, Shadlen MN. Representation of accumulating evidence for a decision in two parietal areas [Journal Article]. J Neurosci. 2015;35(10):4306-18. Available from: https://www.ncbi.nlm.nih.gov/pubmed/25762677.

[37] Cisek P. Cortical mechanisms of action selection: the affordance competition hypothesis [Journal Article]. Philos Trans R Soc Lond B Biol Sci. 2007;362(1485):1585-99. Available from: http://www.ncbi.nlm.nih.gov/pubmed/17428779.

[38] Cisek P, Pastor-Bernier A. On the challenges and mechanisms of embodied decisions. Philosophical transactions of the Royal Society B: Biological sciences. 2014 Nov;369(1655). Available from: http://www.ncbi.nlm.nih.gov/pubmed/25267821.

[39] Bang D, Fleming SM. Distinct encoding of decision confidence in human medial prefrontal cortex. Proceedings of the National Academy of Sciences. 2018;115(23):6082-7.

[40] Twomey DM, Kelly SP, O'Connell RG. Abstract and Effector-Selective Decision Signals Exhibit Qualitatively Distinct Dynamics before Delayed Perceptual Reports [Journal Article]. J Neurosci. 2016;36(28):7346-52. Available from: https://www.ncbi.nlm.nih.gov/pubmed/27413146.

[41] Coallier É, Kalaska JF. Reach target selection in humans using ambiguous decision cues containing variable amounts of conflicting sensory evidence supporting each target choice. Journal of neurophysiology. 2014;112(11):2916-38.

[42] Gibson JJ. The ecological approach to visual perception; 1979.

[43] Merleau-Ponty M. Phenomenology of Perception. Routledge; 1962.

[44] Clark A. Being there: Putting brain, body, and world together again. MIT Press; 1997.

[45] Gegenfurtner KR, Sperling G. Information transfer in iconic memory experiments. Journal of Experimental Psychology: Human Perception and Performance. 1993;19(4):845.

[46] Sperling G, Weichselgartner E. Episodic theory of the dynamics of spatial attention. Psychological review. 1995;102(3):503.

[47] Luck SJ, Vogel EK. The capacity of visual working memory for features and conjunctions. Nature. 1997 Nov;390(6657):279-81. Number: 6657 Publisher: Nature Publishing Group. Available from: https://www.nature.com/articles/36846.

[48] Ma WJ, Husain M, Bays PM. Changing concepts of working memory. Nature Neuroscience. 2014 Mar;17(3):347-56. Number: 3 Publisher: Nature Publishing Group. Available from: https://www.nature.com/articles/nn.3655.

[49] Buschman TJ, Miller EK. Working memory is complex and dynamic, like your thoughts. Journal of cognitive neuroscience. 2022;35(1):17-23.

[50] Kang YH, Loffler A, Jeurissen D, Zylberberg A, Wolpert DM, Shadlen MN. Multiple decisions about one object involve parallel sensory acquisition but time-multiplexed evidence incorporation [Journal Article]. Elife. 2021;10. Available from: https://www.ncbi.nlm.nih.gov/pubmed/33688829.

[51] van Ede F, Chekroud SR, Stokes MG, Nobre AC. Concurrent visual and motor selection during visual working memory guided action. Nature Neuroscience. 2019 Mar;22(3):477-83. Number: 3 Publisher: Nature Publishing Group. Available from: https://www.nature.com/articles/s41593-018-0335-6.

[52] van Ede F, Nobre AC. Turning Attention Inside Out: How Working Memory Serves Behavior. Annual Review of Psychology. 2023 Jan;74:137-65.

[53] Shadlen MN, Shohamy D. Decision Making and Sequential Sampling from Memory. Neuron. 2016 Jun;90(5):927-39. Publisher: Elsevier. Available from: http://linkinghub.elsevier.com/retrieve/pii/S0896627316301234.

[54] Pearson B, Raskevicius J, Bays PM, Pertzov Y, Husain M. Working memory retrieval as a decision process. Journal of vision. 2014 Jan;14(2). Available from: http://www.ncbi.nlm.nih.gov/pubmed/24492597.

[55] van Ede F, Nobre AC. A neural decision signal during internal sampling from working memory in humans. Journal of Neuroscience. 2024;44(19).

[56] Bennett MS. A brief history of intelligence: evolution, AI, and the five breakthroughs that made our brains. HarperCollins; 2023.

[57] Kira S, Zylberberg A, Shadlen MN. Incorporation of a cost of deliberation time in perceptual decision making. Journal of Neuroscience. 2025.

[58] Drugowitsch J, Moreno-Bote R, Churchland AK, Shadlen MN, Pouget A. The Cost of Accumulating Evidence in Perceptual Decision Making. J Neurosci. 2012;32(11):3612-28.

[59] Chang JS, Cooper G. A practical difference scheme for Fokker-Planck equations. Journal of Computational Physics. 1970;6(1):1-16.

[60] Kiani R, Shadlen MN. Representation of confidence associated with a decision by neurons in the parietal cortex. Science. 2009;324(5928):759-64.