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A proposed common neural mechanism for categorization and perceptual decisions

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One of the most fascinating issues in neuroscience is how the brain makes decisions. Recent evidence points to the parietal cortex as an important locus for certain kinds of decisions. Because parietal neurons are also involved in movements, it has been proposed that decisions are encoded in an intentional, action-based framework based on the movements used to report decisions. An alternative or complementary view is that decisions represent more abstract information not linked to movements *per se*. Parallel experiments on categorization suggest that parietal neurons can indeed represent abstract categorical outcomes that are not linked to movements. This could provide a unified or complementary view of how the brain decides and categorizes.

A critical question in neuroscience is how the brain makes decisions. 'Decision' implies (i) presentation of an input or offers and (ii) a choice among alternative outcomes. Classes of decisions can be distinguished on the basis of the form of the input or the outcome. Economic decisions involve choosing among alternative offers that provide different returns or utilities[1,2]. Perceptual decisions entail monitoring (often imprecise) sensory evidence to detect or identify sensory stimuli or to choose appropriate actions on the basis of those stimuli[3]. Other decisions reflect rules or algorithms that map inputs to actions[4]. These different types of decisions are not mutually exclusive; for example, deciding on a course of action for a hospitalized patient involves integration of imperfect diagnostic tests (evidence), differential diagnoses (algorithms or rules and quality-of-life considerations (value or utility).

Whatever distinctions we might draw between classes of decisions—perceptual, economic or rule-based—decisions often have discrete or categorical outcomes: we choose between one entrée or another on a menu; we discern whether an object moves to the right or left; we classify an animal as predator or prey. In this view, a common engine for decision making could be one that drives the system from a state of ambiguity toward a discrete state that defines the outcome.

Brain mechanisms for decision making

There are well developed theories for decision making stretching back decades to centuries, but only recently have neuroscientists begun to

chip away at the biological basis of decisions[5]. In a long-standing model for perceptual decisions, introduced by Newsome and colleagues[6], monkeys are presented with a noisy motion stimulus and report the perceived direction of the stimulus by making a saccadic eye movement toward one target or another. The motion stimulus consists of a dense patch of randomly arrayed dots, with some proportion of the dots moving coherently in one direction (signal) and the other dots meandering in random directions (noise). The animal typically chooses between two opposite directions of motion, with the difficulty of the direction discrimination depending on the proportion of dots that moves coherently.

The use of visual motion as input and saccades as output were astute choices given that the neural circuits underlying motion perception and saccade generation are among the best understood in the primate brain[7,8]. Neural circuits for motion processing and saccades converge in the posterior parietal cortex, making it a part of the brain where decisions linking motion to eye movement could be played out. One part of the parietal cortex, the lateral intraparietal area (LIP), is of particular interest. LIP has direct projections to eye movement–related areas, such as the superior colliculus and frontal cortex[9], but it also receives inputs from visual cortical areas of the dorsal and ventral visual streams[10,11]. LIP neurons have spatially defined receptive fields (RFs) and are usually activated by visual stimuli in the RF, but they are also activated when the animal makes saccades, or plans to make a saccade, to the RF location. Although there has been vigorous debate about whether activity in LIP specifies an intention to move the eyes[12] or rather encodes the general salience of the RF location[13], there is consensus that LIP neurons provide spatial information about the location demarked by their RFs[14].

Using the noisy motion decision paradigm, Shadlen and colleagues have proposed an intriguing model whereby sensory evidence accumulates in the LIP, drifting toward a system threshold that when exceeded drives the eye movement toward the appropriate saccade target[3]. LIP neurons commonly show a ramp-like increase in activity during the noisy motion presentation, with the rate of increase affected by variations in the strength of the noisy motion stimulus, as if LIP neurons are integrating signals from direction-selective neurons in lower visual areas[15–17].

Proposed intentional framework for decisions

The fact that the decision could be played out in a cortical area that is intimately associated with saccadic eye movements led Shadlen and colleagues to hypothesize that there is a fundamentally "intentional" framework for decision making[18,19]. In a strong version of this view, at a mechanistic level, decisions are indivisible from the way they are reported. For example, a decision reported by an eye movement might

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be mediated by an eye movement–related area such as LIP, but the same type of decision reported by an arm movement might be mediated by an arm movement–related area, such as the parietal reach region. From an evolutionary perspective, the intentional framework could have developed by the decision circuitry incorporating into established sensorimotor networks[19]. The intentional framework may also extend to other types of decisions; for example, Glimcher and colleagues have proposed a similar action-based framework to describe parietal activity related to economic decisions[20].

Because decisions are typically manifested through actions, it is tempting to assume that many decisions are played out in an intentional framework. For example, when we turn a car right or left at a fork in the road, we might assume that the decision is mediated by the brain's motor system, perhaps as a competition between motor ensembles that rotate the steering wheel either clockwise or counterclockwise. But an alternative view is that decisions are represented independently from the way the subject reports the decision. In the example of turning a car left or right, the decision might instead be mediated in a perceptual space, perhaps on the basis of discriminating a road sign or landmark, and then mapped onto the appropriate motor pattern. Thus, even if a decision is signaled by only one possible set of movements, the decision need not be mediated in an intentional framework. Extending this view to the classic noisy motion, perceptual decision task, the decision could be captured by neurons that signal the perceived direction of the motion rather than the upcoming saccade direction. The decision would still have to be translated into an appropriate eye movement, but that translation might be akin to a rule-based mapping once the direction had been decided. From a computational perspective, both intentional and 'nonintentional' frameworks would seem to have certain advantages. For example, the intentional framework might allow for a more rapid response to a stimulus, because decisions are embodied directly in brain structures that drive movement. A nonintentional framework might be more flexible in terms of response. The two views could also be complementary. For example, when the movement is predetermined, it might be efficient to represent the decision in an area that drives the movement, but when the response is not yet determined, the perceptual decision must be buffered in some non-movement-related coordinate frame.

A critical limitation in evaluating the intentional framework hypothesis is that, in nearly every neurophysiological study on perceptual decisions in LIP, each perceived direction of motion has been uniquely mapped onto one direction of saccade. Typically, one direction of motion is reported by a saccade to a target placed at the neuron's RF location whereas the other direction is reported by a saccade to a location far away from the RF location. This experimental design complicates interpretation of an intentional framework, because it is difficult to determine whether decision-related activity in LIP represents a decision about the direction of stimulus motion or the predetermined motor response that is used to report the decision. Moreover, even if there are report-independent signals about the direction of stimulus motion rather than the motor response, they might be swamped by motor-related signals that are the outcome of the decision process.

Brain mechanisms for categorization

A seemingly distinct line of research could address this issue. In several experiments, we trained animals in a delayed match-to-sample paradigm. Animals compared a visual stimulus to a second stimulus, which appeared after a delay and which could not be predicted. For example, we trained monkeys in a direction-categorization task in which they learned to group directions of motion into two 180°-wide categories separated by an arbitrary category boundary[21]. The task was based on

similar categorization tasks that have been used to study neurons in the prefrontal cortex and elsewhere[22,23]. In each trial of the direction-categorization task, the animals were shown a brief burst of motion in 1 of 12 directions (the sample) placed in the RF of the neuron under study; this was followed by a delay in which nothing was shown in the RF, and then by a second burst of motion (the test) in the RF with the direction chosen at random from the 12 possible directions of motion. If the sample and test stimulus were from the same learned category, then the animals reported the match by releasing a touch bar; if the two directions were from different categories, the animals had to continue holding the touch bar. In this way neural signals before the onset of the test stimulus were dissociated from the form of the report, because at those times the animals did not know yet whether they would release the touch bar. Moreover, both sample and test stimuli were placed in the same location in visual space, the RF of the neuron under study, so even if the animals were planning an eye movement to the stimulus, that movement would always be to the same location, and thus should not cause differences in neuronal firing.

Using this task, we found that LIP neurons had direction-selective responses, but those responses tended to reflect the learned direction categories. Average spike rates were much more similar within a category than between categories, and many neurons had an almost binary response pattern that mirrored the monkeys' learned binary classification of the stimuli. These category-selective signals were prevalent during the sample-stimulus interval and the delay period, and could even persist into the test period, at which time the monkey had to use remembered information about the sample category to respond appropriately to the test stimulus. Critically, the directional signals were independent of the animal's report because of the dissociation of match or non-match from direction of motion. Similar match–non-match experiments have been used previously to examine categorical signals in prefrontal cortical neurons[22].

We interpreted these signals as related to representing the learned categories, but in previous studies we have also observed potentially related signals in different contexts. Using a delayed match-to-sample design, we have found that LIP neurons represent the perceived direction of a motion stimulus in which the direction is perceptually ambiguous[24]. We have also found color-selective responses in the LIP when animals use color to guide an upcoming (not predetermined) saccade[25]. In all cases we have used a delayed task design that dissociates the decision and the motor response to ensure that the neuronal signals are independent of the movement the animal uses to make its report.

Relationship between categorization and decisions

Although we labeled signals according to the attributes of the sensory stimuli we used (direction, color, and so on), the common denominator might be that they represent a categorical outcome, that is, decision A versus decision B. Given that these signals were evoked by different tasks with different stimuli (and different types of motor responses), the categorical signals might be generic rather than signaling any particular visual attribute. This generic view is supported by our preliminary observation of categorical signals for nonmotion visual stimuli. In monkeys trained to associate pairs of unrelated, arbitrarily chosen static shapes, we find that the firing of LIP neurons reflects those learned pair associations: neurons tend to fire at similar rates for pairs of shapes that have been associated but fire at different rates for pairs of shapes that have not been associated. Moreover, in animals trained to carry out both the pair-associate task and the direction-categorization task, the same LIP neurons tend to encode both types of categories (J.K. Fitzgerald, J.A. Assad & D.J. Freedman, *Soc. Neurosci. Abstr.*, 711.6, 2008). These data suggest that categorical representations in LIP are

generic. Other groups have also reported categorical signals in LIP that are independent of planned movements or visuospatial factors, such as cognitive set signals related to the particular rule required to carry out a task[26,27].

A generic categorical representation is reminiscent of the report-independent perceptual decision signals that we hypothesized above. According to one version of the intentional framework hypothesis, report-independent decision signals could be present in higher-association cortices, such as prefrontal cortex, but not in parietal cortex[19]. On the contrary, we found report-independent signals in parietal cortex that seem to be at least as strong, if not stronger, than those in prefrontal cortex. The finding of report-independent decision or category signals in parietal cortex does not necessarily rule out the possibility that some decisions could be carried out in an intentional framework, but it minimally suggests that the intentional framework cannot be universal. This places an additional burden on researchers to demonstrate that the intentional framework is not a consequence or artifact of the constraints of previous experimental designs.

Potential limitations to his interpretation

There are some important differences between our experiments and the previous perceptual decision experiments that make it difficult to compare the results directly. Shadlen and colleagues used eye movements as a report whereas we used hand movements, and they presented a range of stimulus strengths, including stimuli near perceptual threshold, whereas we used more suprathreshold stimuli. However, recent work by Bennur and Gold[28] could bridge the gap. Bennur and Gold used the classic noisy motion stimuli and had the animals report the direction with a saccade, but in some trials the animals did not know where the saccade targets would appear until after the motion stimulus had been presented. In this case, saccade planning must be delayed, yet the authors found signals in LIP neurons related to the perceived direction of motion. These could be taken as report-independent perceptual decision signals, but at that point 'perceptual decision' and 'categorical' signals begin to sound closely aligned, if not interchangeable. Notably, Bennur and Gold also found signals related to perceived direction in trials in which the saccade targets were presented simultaneously with the motion stimulus. The results suggest that abstract, categorical signals are present even in the classic noisy motion, eye movement–based perceptual decision task, and that the signals can be present even when the decision could be formulated in a movement-based framework.

Another difference between the experiments is that Shadlen and colleagues generally placed their noisy motion stimulus at the fovea, away from the location of the RF, whereas we placed our motion stimuli within the RF. However, we also found direction-categorization signals even when stimuli were placed in the opposite hemifield from the RF (albeit weaker signals than when the stimuli were presented in the RF)[29], and Bennur and Gold found report-independent perceptual decision signals with motion stimuli placed at the fovea, outside the RF[28]. These observations suggest that the categorization or decision signals are not necessarily encoded with respect to the spatial framework defined by the RFs of LIP neurons.

In our match-to-category experiment, we also included a delay between when we presented the sample stimulus and when the animal could plan its movement, whereas in the experiments of Shadlen *et al.* the animals could, in principle, plan an eye movement right away. Abstract categorical signals might be computed only when movements have not yet been specified, but not otherwise. In this view the two models could be complementary. However, at present there is no evidence that categorical signals are not computed in all cases, even when movements are prespecified. To the contrary, Bennur and Gold

found categorical signals even when saccade targets were presented simultaneously with the noisy motion stimuli[28].

At this point, our working hypothesis is that perceptual decision and categorical signals are one and the same, but critical comparisons and questions need to be addressed. For one, it would be very useful to compare the signals head-to-head in the same animals. Animals could be trained to carry out the classic noisy motion, perceptual decision task interleaved with our direction-category task to investigate whether individual LIP neurons are selective for direction in the same way in both tasks.

We also do not know the full extent of categorical or decision signals in the brain, although they are certainly not confined to parietal cortex. Categorical signals have been reported in monkey lateral prefrontal cortex[22], and in the frontal eye fields[30] in experiments designed to eliminate movement confounds. Human imaging studies have also identified a network of frontoparietal areas that provide decision-related signals that are independent of effectors[31].

Another limitation of our hypothesis is that we have not considered decisions regarding which effector to use, for example the choice between moving eyes or hands to a target. These decisions might be naturally formulated in an intentional framework. We have also only considered decisions with discrete outcomes, but other decisions can have continuous outcomes, such as the decision of how fast to run at the start of a race or how much salt to add to a recipe. It is not clear that continuous decision outcomes could be represented in a categorical framework, or whether parietal neurons could represent continuously valued outcomes.

We also need to distinguish the decision process itself from the outcome of that process. Categorical signals in LIP could be viewed as the outcome of the decision process, but there is separate evidence that LIP neurons participate in the decision itself. For example, in the classic noisy motion experiments, the rate of rise of the ramp-like increase in activity of LIP neurons depends on the coherence of the motion, even if the monkey arrives at the same decision outcome (reports the same direction of motion)[16]. Thus our contention is not that LIP neurons are not involved in the decision process, but rather that the involvement of LIP neurons in decisions is not restricted to an intentional framework.

Decisions, categories and spatial selectivity

A final outstanding issue is how to reconcile decision and categorization signals with the classic spatial selectivity of LIP neurons. For example, in the experiments of Shadlen and colleagues, the moving dots were always placed at the fovea, but saccade targets were typically placed at eccentric locations not overlapping with the fovea. If LIP neurons integrate directional inputs from lower visual areas, there has always been a question of how directional neurons with foveal RFs (for example, in the middle temporal area, area MT) communicate with LIP neurons with eccentric RFs that might be reading out the motion input. Neurons in earlier cortical areas, such as V1, V2 and MT, are more likely to be interconnected if their RFs overlap than if their RFs do not overlap. If the same principle applies to inputs to LIP, then the circuit-level basis by which LIP neurons read out directional information from neurons with non-overlapping RFs could be complicated. In our experiments, the motion stimulus was placed at the RF location. However, when there is strong nonspatial modulation within the RF, such as category signals, it would seem that the modulation could interfere with downstream brain areas trying to read out spatial information from LIP. A related issue is that our experiment does not address how an abstract categorical or decision signal is translated into an appropriate movement. However, in our new framework, perhaps this problem could be approached as a sensory-motor transformation rather than a decision process. These

are important issues to be examined in future work. Perhaps an even more general framework could be realized for parietal cortex that ties together visual space as well as decisions and categories.

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

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1. Glimcher, P.W. & Rustichini, A. Neuroeconomics: the consilience of brain and decision. *Science* **306**, 447–452 (2004).
2. Padoa-Schioppa, C. Neurobiology of economic choice: a good-based model. *Annu. Rev. Neurosci.* (in the press).
3. Gold, J.I. & Shadlen, M.N. The neural basis of decision making. *Annu. Rev. Neurosci.* **30**, 535–574 (2007).
4. Miller, E.K., Nieder, A., Freedman, D.J. & Wallis, J.D. Neural correlates of categories and concepts. *Curr. Opin. Neurobiol.* **13**, 198–203 (2003).
5. Glimcher, P.W. *Decisions, Uncertainty, and the Brain: the Science of Neuroeconomics* (MIT Press, 2003).
6. Newsome, W.T., Britten, K.H. & Movshon, J.A. Neuronal correlates of a perceptual decision. *Nature* **341**, 52–54 (1989).
7. Maunsell, J.H. & Newsome, W.T. Visual processing in monkey extrastriate cortex. *Annu. Rev. Neurosci.* **10**, 363–401 (1987).
8. Johnston, K. & Everling, S. Neurophysiology and neuroanatomy of reflexive and voluntary saccades in non-human primates. *Brain Cogn.* **68**, 271–283 (2008).
9. Andersen, R.A., Brotchie, P.R. & Mazzoni, P. Evidence for the lateral intraparietal area as the parietal eye field. *Curr. Opin. Neurobiol.* **2**, 840–846 (1992).
10. Blatt, G.J., Andersen, R.A. & Stoner, G.R. Visual receptive field organization and cortico-cortical connections of the lateral intraparietal area (area LIP) in the macaque. *J. Comp. Neurol.* **299**, 421–445 (1990).
11. Lewis, J.W. & Van Essen, D.C. Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *J. Comp. Neurol.* **428**, 112–137 (2000).
12. Snyder, L.H., Batista, A.P. & Andersen, R.A. Intention-related activity in the posterior parietal cortex: a review. *Vision Res.* **40**, 1433–1441 (2000).
13. Goldberg, M.E., Bisley, J.W., Powell, K.D. & Gottlieb, J. Saccades, salience and attention: the role of the lateral intraparietal area in visual behavior. *Prog. Brain Res.* **155**, 157–175 (2006).
14. Bisley, J.W. & Goldberg, M.E. Attention, intention, and priority in the parietal lobe. *Annu. Rev. Neurosci.* **33**, 1–21 (2010).
15. Shadlen, M.N. & Newsome, W.T. Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. *J. Neurophysiol.* **86**, 1916–1936 (2001).
16. Roitman, J.D. & Shadlen, M.N. Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. *J. Neurosci.* **22**, 9475–9489 (2002).
17. Huk, A.C. & Shadlen, M.N. Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. *J. Neurosci.* **25**, 10420–10436 (2005).
18. Gold, J.I. & Shadlen, M.N. The influence of behavioral context on the representation of a perceptual decision in developing oculomotor commands. *J. Neurosci.* **23**, 632–651 (2003).
19. Shadlen, M.N., Kiani, R., Hanks, T.D. & Churchland, A.K. Neurobiology of decision making: an intentional framework. in *Better Than Conscious? Decision Making, the Human Mind, and Implications for Institutions* (Engel, C. & Singer, W., eds.) 71–102 (MIT Press, 2008).
20. Kable, J.W. & Glimcher, P.W. The neurobiology of decision: consensus and controversy. *Neuron* **63**, 733–745 (2009).
21. Freedman, D.J. & Assad, J.A. Experience-dependent representation of visual categories in parietal cortex. *Nature* **443**, 85–88 (2006).
22. Freedman, D.J., Riesenhuber, M., Poggio, T. & Miller, E.K. Categorical representation of visual stimuli in the primate prefrontal cortex. *Science* **291**, 312–316 (2001).
23. Freedman, D.J., Riesenhuber, M., Poggio, T. & Miller, E.K. A comparison of primate prefrontal and inferior temporal cortices during visual categorization. *J. Neurosci.* **23**, 5235–5246 (2003).
24. Williams, Z.M., Elfar, J.C., Eskandar, E.N., Toth, L.J. & Assad, J.A. Parietal activity and the perceived direction of ambiguous apparent motion. *Nat. Neurosci.* **6**, 616–623 (2003).
25. Toth, L.J. & Assad, J.A. Dynamic coding of behaviourally relevant stimuli in parietal cortex. *Nature* **415**, 165–168 (2002).
26. Stoet, G. & Snyder, L.H. Single neurons in posterior parietal cortex of monkeys encode cognitive set. *Neuron* **42**, 1003–1012 (2004).
27. Gottlieb, J. From thought to action: the parietal cortex as a bridge between perception, action, and cognition. *Neuron* **53**, 9–16 (2007).
28. Bennur, S. & Gold, J.I. Distinct representations of a perceptual decision and the associated oculomotor plan in monkey area LIP. *J. Neurosci.* (in the press).
29. Freedman, D.J. & Assad, J.A. Distinct encoding of spatial and nonspatial visual information in parietal cortex. *J. Neurosci.* **29**, 5671–5680 (2009).
30. Ferrera, V.P., Yanike, M. & Cassanello, C. Frontal eye field neurons signal changes in decision criteria. *Nat. Neurosci.* **12**, 1458–1462 (2009).
31. Wunderlich, K., Rangel, A. & O'Doherty, J.P. Neural computations underlying action-based decision making in the human brain. *Proc. Natl. Acad. Sci. USA* **106**, 17199–17204 (2009).