

Consciousness as a Decision to Engage

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Abstract Consciousness encompasses a variety of functions and properties, such as awakening, awareness, and subjective aspects of both perception and volition (e.g., qualia and authorship, respectively). It remains to be seen whether these diverse functions are related to one another through common neural mechanisms, and if so how. Here, we advance the thesis that the neural mechanisms that give rise to conscious states share features with neural mechanisms that underlie simpler forms of decisions. The neurobiology of decision-making provides detailed insight into how the brain deliberates and reasons from evidence to make choices. The underlying mechanisms, mainly studied in animals, could support a variety of complex cognitive functions that probably operate independently of many aspects of consciousness. For example, many complex decisions in humans rely upon wakefulness but not upon awareness or authorship. In animal studies, decisions are typically embodied: they can be described as selection among possible actions. By substituting “circuits” for “actions” in the preceding phrase, we generalize from “deciding to do” to “deciding to consider” or, more generally, “deciding to decide to. . .” This is an appealing notion from the perspective of brain evolution, because it allows us to recognize ideation as an elaboration of a simpler sensory-motor design. We propose that many of the functions of consciousness are simply ways of engaging the environment. Thus consciousness might be mediated by (non-conscious) decisions to engage, as in awakening, or to engage in a certain way, as when attaching narrative to action. Although the neural mechanisms underlying “decisions to engage” are unknown, they are likely to involve intralaminar (and matrix) thalamus and processes that “decide” to turn other circuits on. This idea invites an analogy between the functions of brain regions that project to

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27 matrix thalamus, including the “default system”, and the role of parietal cortex in
28 perceptual decisions. While highly speculative, we think “decision to engage”
29 provides a biologically plausible and computationally coherent hypothesis about
30 the neural correlates of consciousness.

31 1 Introduction

32 At the time of this writing, it seems safe to state that neuroscience has thus far failed
33 to provide an answer to the question of how the brain gives rise to consciousness
34 and conscious awareness. Although this essay does not provide an answer to this
35 question, we hope it will give some indication of how to go about finding one. Our
36 goal is to identify a framework for addressing at least some of the problems
37 that arise. There may be a kernel of a theory of consciousness here, but we do not
38 believe it is coherent – yet. If we are correct, and the neurobiology of decision-
39 making is closely tied to the neurobiology of consciousness, there will be plenty of
40 facts that will help to shape such a theory.

41 Our perspective brings together several ideas that might seem separate: the
42 neurology of arousal and its disorders (Laureys 2006; Laureys et al. 2004; Posner
43 et al. 2007), the neurobiology of decision making (Gold and Shadlen 2007), the
44 default system (Raichle and Snyder 2007; Raichle et al. 2001), non-conscious
45 cognition (e.g., Dijksterhuis et al. 2006; Kouider and Dehaene 2007), a bit of
46 philosophy (Merleau-Ponty 1962), and emerging ideas about intralaminar and
47 matrix thalamus (Jones 2001; Schiff 2010).

48 It may be useful to consider two broad characterizations. One is from the
49 perspective of neurology, which tends to view the phenomenon as intrinsically
50 linked to arousal. Consciousness refers to a state of wakefulness with organized
51 interaction with the environment, where organized implies behavior more complex
52 than a reflex. Consciousness is absent in sleep, coma, general anesthesia and
53 generalized seizures. It is evanescent in stupor, perhaps less so in obtundation,
54 and latent in the minimally conscious state. It is present – although one might say it
55 is impaired – in confusion states with diverse forms and etiologies (delirium, toxic/
56 infection, paraneoplastic, and psychiatric¹). We will refer to this characterization as
57 N-consciousness (for neurology).

58 The other characterization is from the philosophy of mind, which identifies a
59 collection of mental phenomena sharing subjective, personal features. These include
60 perceptual awareness, self-awareness, volition with awareness (i.e., authorship),
61 a sense of free will, a sense of what it is like to be, a capacity to report narrative,
62 introspection, and so on. Even this incomplete list portrays the daunting topic that

¹We lack strong convictions about whether fugue states and disorders of thought, such as schizophrenia, belong in this list. We suspect these disorders will involve distinct mechanisms, which are not of the type discussed here.

makes consciousness so mysterious and special. We might argue about whether animals possess such capacities, but no one doubts that they have wakefulness and even states of confusion. We will refer to this characterization as P-consciousness (for philosophy).²

These conceptual perspectives lack obvious intersection, yet our central thesis is that similar neural mechanisms, computations and structures underlie many if not all of these forms of consciousness. The common feature is a decision to engage (Shadlen and Kiani 2007). Waking from sleep is a decision to engage the environment, and acting with awareness of purpose (authorship or will) involves a decision to engage a form of narrative associated with potential reportability. Thus we propose that neural mechanisms that give rise to conscious states share features with neural mechanisms that underlie simpler forms of decisions.

There is one important assumption that deserves mention at the outset. It is that a great portion of higher cognitive processing occurs without P-consciousness, that is, without awareness and without a capacity to report. We cascade actions, juggle tasks, maintain goals and highly structured cognitive sets, interact socially, navigate in artificial environments with objects that are not part of our bodies, and so on, often without the aid of P-consciousness. The topic of non-conscious processing is difficult to study, but there are some tantalizing and beautiful studies (e.g., Christoff et al. 2009; Dehaene et al. 2006; Kouider and Dehaene 2007; Lau and Passingham 2007). What seems remarkably obvious to a neurologist is that patients with disorders of higher brain function (i.e., cognitive loss) tend to miss mainly the features of their mental lives that live below the radar of consciousness. It appears that the conscious acts survive. Indeed patients exploit P-consciousness to rescue cognitive functions, much like the deliberate coping movements that are so common in the partially paralyzed.

We will return to this point, because we suspect that the neural mechanisms that give rise to decisions to engage (in certain ways) also play a role in these non-conscious functions. They too make use of decisions to engage in certain *other* ways.

2 Why View Consciousness as a Decision to Engage in a Certain Way?

There are at least two reasons to adopt this perspective. First, the formulation is already consistent with at least some aspects of both N- and P-consciousness. This is almost a matter of definition for N-consciousness. Disorders on the spectrum of coma-to-wakefulness are distinguished by a threshold for processing an external cue, such as a sound or tactile force, to engage the environment in a certain way. Reflexive withdrawal is a way that does not require consciousness. Just about

²Not to be confused with Ned Block's "phenomenal" consciousness (Block 2005).

100 anything sustained, organized and not pathologically stereotyped³ is evidence for
101 wakefulness, hence N-consciousness.

102 In sleep, our brains monitor the auditory environment for the sounds that should or
103 should not alert us, what psychologists call a “Go vs. No-go” decision. For example,
104 our brains choose “No-go” for unimportant sounds, like the rustling or snoring of
105 a partner, the music or television that was on when we fell asleep, neighbors, car and
106 train sounds, crickets at night and much birdsong at dawn. Our brains choose “Go”
107 when a fire alarm rings, a child cries, or birds call at the right time or in some complex
108 combination with other sounds at roughly the right time. Many a sleep-deprived
109 mother will respond to the baby’s cry but not to the tornado alarm.

110 Some features of P-consciousness clearly involve decision processes. Consider
111 the spectacular demonstrations of so-called change blindness (Rensink 2000; Simons
112 and Chabris 1999). In one famous example, a gorilla walks through a small group of
113 students who are throwing and catching balls. Viewers who are instructed to count
114 the throws of the students wearing white shirts, say, often fail to see the gorilla. They
115 lack awareness of the gorilla, even when he faces the camera and beats his chest. This
116 is not because the eye and visual cortex have failed to represent the gorilla. It is
117 because the brain is engaged in a demanding task. A non-conscious process has
118 decided to ignore rather than explore data in visual cortex corresponding to the
119 gorilla. It has decided to engage the counting problem more fully. This is an example
120 of an exploration vs. exploitation decision (Cohen et al. 2007).

121 Our view is that consciousness is mediated by decisions to engage, but not all
122 decisions to engage require or imply consciousness. Again, this is based on the
123 conviction that many sophisticated cognitive functions transpire without the aid of
124 P-consciousness. Presumably such processes also involve exploration-exploitation
125 decisions, to pick just one example of a decision to engage. Thus, we view conscious-
126 ness as a decision to engage *in a certain way*, or set of ways. These certain ways are
127 likely to touch on a capacity to report, to attach narrative with episodic context (e.g.,
128 before and after, place and situation). As a field, we lack an understanding of the
129 circuits that mediate these “certain ways.” But we suspect they are not qualitatively
130 different from brain circuits involved in other behaviors, which are better understood.

131 The link between consciousness and decision-making provides an opportunity
132 to ground consciousness in neurobiology. Over the past 15 years, the neural
133 mechanisms underlying simple decisions have begun to be elucidated. These
134 include simple perceptual decisions (Gold and Shadlen 2007; Romo and Salinas
135 2003; Schall 2001; Uchida et al. 2006) and value-based and social decisions
136 (Glimcher 2003a, b; McCoy and Platt 2005; Sugrue et al. 2005). Some of the key
137 principles are explained in the next section. The connection to decision making
138 inspires hypotheses and guides the study of neural mechanism. It grounds the
139 enterprise, simplifies it in some ways, and exposes deficiencies in the current
140 emphasis on neural correlates of consciousness. That said, it offers more promise
141 than substance.

³Certain stereotyped movements occur in persistent vegetative states, whereas others are hallmarks of epileptic seizures.

3 Neural Mechanisms of Decision Making

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The remainder of this essay has a dual purpose. The first is to provide a highly selective review of some essential principles of the neuroscience of decision making – just enough detail to support the contention that there is real neuroscience here. At the very least, we wish to reassure the reader that, by tying consciousness to the neurobiology of decision-making, we are not simply relegating consciousness to another mysterious function. We do not pretend that decision making is a mature field, however. The principles and even the “facts” are not fixed, and where they appear to be so, they may be less general than we would like to believe. The second purpose is to expose tentative extensions to what is known and even more tentative connections to other areas of neuroscience. These comprise the short sections below, which describe the “intentional framework” and the problem of circuit selection.

Figures 1 and 2 show two types of tasks used in our laboratory for the study of decision making. The first is a simple perceptual decision. A monkey (or human) views a movie consisting of dynamic random dots and must decide whether the net direction of motion is to the left or right. Most of the decisions are very difficult because the stimulus consists mainly of dots appearing only briefly at random locations within the display aperture. Only a small fraction of the dots undergo displacement and then only to disappear. This fraction, termed the *percent coherence*, controls the difficulty of the discrimination. There is no actual motion to track in such a display: no dots traverse the display over extended time. The decision-maker must accumulate brief pieces of momentary evidence bearing on the two alternative hypotheses. In this sense, this simple task has more in common with cognitive decisions than with problems in perception, which rarely involve accumulation over time of independent samples of momentary evidence.

The random-dot motion task is useful for the study of decision making because so much is known about the neurobiology. Neurons in the visual cortex extract and represent the momentary evidence. Such direction-selective neurons respond to light when it is presented in a part of the visual field, termed the receptive field. The designation “direction selective” implies that the neuron responds more when motion is in one direction than in the opposite direction. Different neurons prefer different directions. The neurons that are most informative for this task are in a part of the visual cortex called MT/V5.⁴ Properties of these neurons are summarized in a recent review (Born and Bradley 2005).

Four features of the MT neurons are important. (1) The intensity of the neural response, measured as a firing rate (spikes per second), is stronger when the random dot motion is in the neuron’s preferred direction and when the percent coherence is greater. (2) There is a response even when the stimulus is purely random dots, without any net motion, termed 0% coherence. (3) The response itself is noisy, meaning that an estimate of the firing rate over a brief epoch, even from hundreds of

⁴MT stands for middle temporal, the name of the sulcus in the new world monkey where the area was first discovered (Allman and Kaas 1971).

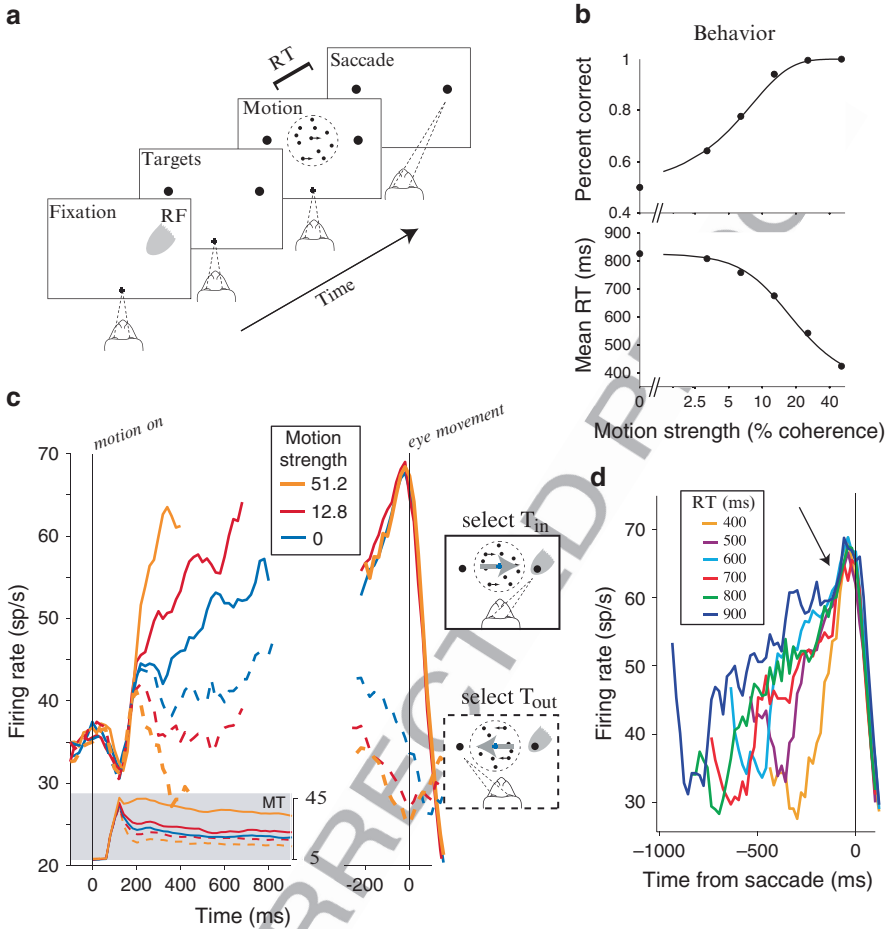


Fig. 1 Neural mechanism of a decision about direction of motion. **(a)** Choice-reaction time version of the direction discrimination task. The subject views a patch of dynamic random dots and decides the net direction of motion. The decision is indicated by an eye movement to a peripheral target. The subject controls the viewing duration by terminating each trial with an eye movement whenever ready. The *gray patch* shows the location of the response field (RF) of an LIP neuron. **(b)** Effect of stimulus difficulty on choice accuracy and decision time. Solid curves are fits of a *bounded drift-diffusion* model, which accounts simultaneously for choice and decision time. **(c)** Response of LIP neurons during decision formation. Average firing rate from 54 LIP neurons is shown for three levels of difficulty. Responses are grouped by motion strength and direction of choice, as indicated. *Left graph*: The responses are aligned to onset of random-dot motion and truncated at the median reaction time. These responses accompany decision formation. *Shaded inset* shows average responses from direction-selective neurons in area MT to motion in their preferred and anti-preferred directions (*solid* and *dashed traces*, respectively). After a transient, MT neurons respond at a nearly constant rate. The LIP firing rates approximate the integral of a difference in firing rates between MT neurons with opposite direction preferences. *Right graph*: The responses are aligned to the eye movement. For T_{in} choices (*solid curves*), all trials reach a stereotyped firing rate before saccade initiation. We think this level represents a threshold or bound, which is sensed by other brain regions to terminate the decision. **(d)** Responses grouped by reaction time. Only T_{in} choices are shown. *Arrow* shows that the stereotyped firing rate occurs ~70 ms before saccade initiation (adapted with permission from Gold and Shadlen 2007; Roitman and Shadlen 2002; Shadlen et al. 2006)

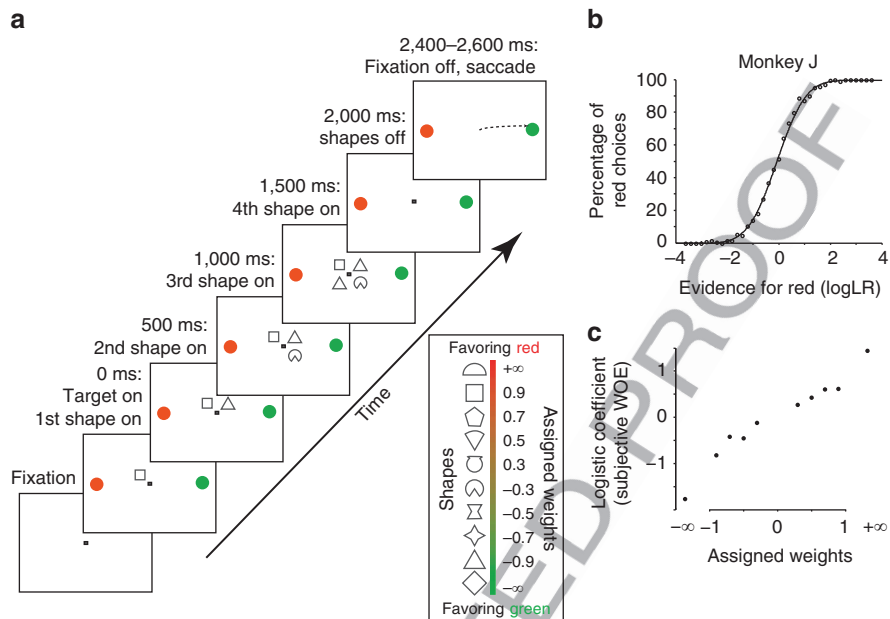


Fig. 2 Probabilistic categorization task. **(a)** Task sequence. Four shapes are presented sequentially on the computer monitor near the center of gaze. After a brief delay period, the monkey makes an eye movement (saccade) to either the *red* or *green* choice target. During neural recording, one of the choice targets was in the response field of the neuron. The shapes are selected randomly in each trial from a larger set of ten (*inset*). The reward is determined probabilistically by summing the weights associated with the four shapes. The sum is the logarithm of the odds that the *red* target will be the one rewarded on that trial. **(b)** Performance. The fraction of *red* choices is plotted as a function of the logLR conferred by the four shapes in favor of red. Curves are logistic fits to the data. Only trials that have probabilistic reward ($P \neq 1$ or 0) are included in this graph. **(c)** Effect of individual shapes on choice. The leverage of each of the *ten* shapes on the probability of a *red* choice was inferred using logistic regression, which is the contribution that the shape has on the \log_{10} of the odds of a red choice. These values are plotted as a function of the assigned weights. Movie example trials from the experiment, along with neural recordings, can be viewed at <http://www.nature.com/nature/journal/v447/n7148/supinfo/nature05852.html> (adapted with permission from Yang and Shadlen 2007)

neurons, is highly variable. (4) The neurons respond to the visual information with 182 short latency and they stop responding when the stimulus is not present. The 183 importance of features 1 and 2 is that the evidence these neurons provide for 184 decision making is graded. The importance of feature 3 is that the evidence is 185 unreliable. Indeed it is possible for the left-preferring neurons to respond more than 186 the right-preferring neurons, even when the motion is rightward, and thus lead to an 187 error of perception. The fourth feature indicates that there is no build up or 188 accumulation and no memory of the past. When the motion is on, the neuron 189 responds at a constant (albeit noisy) rate (see Fig. 1c, gray inset). These are neurons 190 that keep up with a changing world. 191

192 In short, the MT neurons supply the momentary evidence to the decision. The
193 better the evidence, the more likely the decision will be correct and the faster it will
194 complete. But the MT responses do not represent the decision outcome or its
195 formation. They do not represent the state of the decision once it is made or the
196 accumulation of evidence leading to this state.⁵ If the monkey must hold its decision
197 in working memory after the stimulus has been turned off, the MT neurons are no
198 longer informative, yet the decisions are unaffected.

199 Neurons in the association cortex are different. Their responses can linger for
200 seconds, even tens of seconds. Like visual neurons, they respond only under the right
201 conditions, and the intensity of their firing rates represent an amount of something,
202 but it is often difficult to say what. That depends on what kind of information
203 they receive and to what kinds of neurons they project. For neurons in the lateral
204 intraparietal cortex (area LIP), the input is from visual cortex and the output is mainly
205 to structures that control eye movements or the focus of spatial attention (Andersen
206 1995; Andersen and Buneo 2002; Bracewell et al. 1996; Colby and Goldberg 1999;
207 Mazzoni et al. 1996). LIP neurons are well positioned to convert the stream of
208 momentary evidence, ascribed to MT neurons, into a quantity that is used to make
209 the decision—termed a decision variable—and to represent its outcome.

210 Neurons in LIP have spatially selective persistent neural activity. Like MT
211 neurons, there are restricted regions of the visual field that support responses and
212 other regions that do not. We use the term *response field* (instead of receptive field)
213 because the LIP response is affected both by visual targets and a plan to make an
214 eye movement or shift attention to that location. In contrast to MT, the responses of
215 LIP neurons persist in the absence of continuous visual stimulation. And while they
216 are associated with a plan to make an eye movement, they do not obligate an
217 immediate movement.

218 We believe such selective persistent activity holds the key to understanding
219 higher cognitive function, its emergence in evolution and its impairment in disease,
220 because our most cherished mental functions require that neural computations can
221 transpire a time frame that is (1) not governed by immediate change in the
222 environment and (2) not tied to immediate change in body musculature. Such
223 *freedom from immediacy* probably arose as the cortical mantle expanded, thereby
224 inserting contingency into the basic sensory-motor design. We will return to this
225 theme below.

226 LIP neurons contribute to decision formation on the task illustrated in Fig. 1a.
227 During decision formation, the firing rate of these neurons represents the accu-
228 mulation of momentary evidence in the visual cortex. As shown in Fig. 1c, the
229 accumulation rises or falls depending on the direction and strength of the
230 motion. These averages belie the tremendous variability in firing rate from
231 trial to trial. On a single trial, the firing rate would resemble the path of a particle
232 undergoing drift-diffusion or biased random walk. On each trial, the LIP firing

⁵We are ignoring the small modulation of sensory neurons associated with choice (Britten et al. 1996; Celebrini and Newsome 1994). In some settings, part of this modulation could represent the outcome of the choice (Krug 2004; Nienborg and Cumming 2009).

rate represents the running accumulation of the momentary evidence they receive from the neurons in MT. Since this momentary evidence is variable, the accumulation resembles Brownian motion of a particle, hence the analogy to diffusion and random walks (Churchland et al. 2011).

When the firing rates of LIP neurons reach a critical level, the decision process halts (Fig. 1d). If the task is set up to study both choice and reaction time, then the stopping time results in a behavioral outcome – the reaction time (Fig. 1b). If the stimulus is presented for a long time, or if the experimenter imposes a delay period after turning off the motion stimulus (i.e., a memory-delay), then there is no direct behavioral manifestation of the stopping, but we have shown that it occurs (Kiani et al. 2008). The brain reaches a commitment and ignores additional evidence.

If, during the delay period, the monkey is allowed an opportunity to opt out of the left-right task to obtain a small but certain reward, it does so when it is less likely to choose the correct motion direction. Even for repetitions of identical stimuli, monkeys opt out when they are more likely to make an error. Importantly, the firing rate of LIP neurons is nearer the neutral level when the monkey chooses this low confidence option. The firing rates encode a degree of confidence, that is, the probability of answering correctly (Kiani and Shadlen 2009). These and other observations suggest that the firing rates of neurons like those in LIP do not represent quantities associated with stimuli or actions per se, but are best articulated using the language of probability, value, utility, and costs – terms associated with decision theory.

Such neural computations are key components of any conscious decision or plan of action, although we can say little about the monkeys' state of awareness in our experiments. The confidence study shows that the brain computes quantities that support a form of meta-cognitive reasoning about the degree of certainty in a decision, but the observation does not imply that the monkey is aware of the process (but see Hampton 2001; Kornell et al. 2007; Smith et al. 2003). That said, the process that transpires once the sure-target option is made available resembles a decision to report about the state of another mental process – here, the decision that occurred a second or so ago during stimulus viewing. Again, we do not believe it is possible to ascertain whether this decision to engage the sure-target in this way is associated with awareness. A more rewarding speculation is that the mechanism exposed in these experiments resembles the ones in our own brains when we engage in a way that we experience as being consciously aware. Using this idea, we can exploit animal models of cognition to study the neural mechanisms of human consciousness. We need not resolve the question of “what it is like” to be a monkey (Nagel 1974).

Another experimental observation that supports the representation of probabilities by LIP neurons comes from the probabilistic categorization task shown in Fig. 2 (Yang and Shadlen 2007). In this task, the monkey must decide between a red and a green target. One or the other will render a reward on a random half of trials. On any one trial, however, the probability of “reward at red” is governed by a set of four shapes, shown sequentially on the video monitor. These shapes are drawn randomly (with replacement) from a larger set of ten, half of which support

278 “reward at red” by varying degrees. The other half support “reward at green” by the
279 same varying degrees. The experiment tests whether the monkey can reason from
280 the probabilistic evidence and make the better choice, based on the four random
281 shapes shown on any one trial. This task is quite challenging. Although there is a
282 better choice on any one trial, there is no guarantee that selecting it will lead to
283 reward, because the reward is ultimately rendered probabilistically. After training,
284 however, monkeys learn this task (Fig. 2b) and that some shapes are more reliable
285 predictors than others (Fig. 2c).

286 The neural responses from this task are best appreciated by viewing movies from
287 the experiment.⁶ They show the same type of LIP neuron studied in the motion
288 experiment. Here, the red or the green choice target is in the neuron’s response field.
289 What is immediately evident in the movies is that the neuron performs a running sum
290 of the positive and negative support from the shapes. A more quantitative analysis
291 reveals that the firing rate is proportional to the logarithm of the ratio of probabilities
292 (the log-likelihood ratio or log-odds ratio), which is an intuitive solution. If the
293 probabilities are equal, then the ratio is 1 and $\log(1) = 0$. If the probability favors the
294 target in the response field, then the ratio exceeds 1 and the log is positive, whereas if
295 the probability favors the other target, then the ratio is less than one and the log is
296 negative. Moreover, if the neural response represents a logarithm of a probability
297 ratio based on the first shape shown in the trials, then when a second shape arrives, it
298 is sensible to simply increment or decrement the response by the new log-likelihood
299 ratio. That is what you can hear in the audio track of the movies.

300 This brief survey exposes four principles of neural function in the service of
301 decision-making. (1) The response can evolve gradually in time to represent the
302 accumulation of evidence from multiple sources in time. (2) The mechanism
303 includes a termination rule, that is, a criterion for finishing the decision. This
304 might be based on the amount of evidence, the passage of time as in a deadline,
305 or a computation involving value, costs and so on. (3) The computations bear
306 resemblance to probabilistic inference. The general importance here is that it allows
307 neurons to use spike rate to represent intensities that are loosely coupled to “degree
308 of belief in...” or “likelihood that...” or “expected loss if...” (4) The neurons
309 associated with decision formation defy classification as sensory or motor. They are
310 influenced by sensory stimuli and their responses probably influence motor func-
311 tion, but they respond without sensory input and they do not obligate a movement.
312 They lie at the nexus of sensory processing and motor planning.

313 **4 Intentional Framework and Circuit Selection**

314 The fourth principle brings us back to the main focus of the essay. It inspires most if
315 not all of the studies of decision-making in our lab, and it helps us see beyond this
316 one brain area. We assume that area LIP is not particularly special. We observe

⁶<http://www.nature.com/nature/journal/v447/n7148/supinfo/nature05852.html>

decision-related activity in LIP because the monkeys are trained to communicate 317
their decisions with an eye movement. LIP is well suited for decision making 318
these tasks because it receives input from visual cortex and because its main output 319
targets are structures that control eye movements. Unless LIP is special, it seems 320
likely that decision formation will be evident in other structures that are tied to 321
intention or planned actions, or more generally to the selection of neural circuitry 322
that controls a behavior. We refer to this architecture as an intentional framework, 323
to contrast it with the more representational framework (Shadlen et al. 2008). 324

There is some support for this idea. The parietal areas that neighbor LIP receive 325
mainly visual information, but they target premotor cortical areas devoted to other 326
motor functions. For example, the medial intraparietal area (MIP) projects to 327
regions that control reaches to targets, and the anterior intraparietal area (AIP) 328
projects to regions that control hand posture during grasp. It is tempting to speculate 329
that these areas do something very much like LIP. They operate on the stream of 330
activity from the visual cortex and construe it as evidence in support of a proposi- 331
tion. For LIP, the proposition is not really about direction of motion but ultimately 332
about which eye movement to make. Indeed, it is already known that MIP behaves 333
similarly to LIP when the monkey communicates its decision by touching a spot on 334
a touch-screen device (Andersen and Buneo 2002; de Lafuente et al. 2009; 335
Scherberger and Andersen 2007; Snyder et al. 2000). For AIP, the stream of activity 336
bears on geometry (Janssen et al. 2008), but it is perhaps more apt to describe the 337
responses in terms of a possible grasp posture (Cisek 2007). 338

An obvious shortcoming of the intentional view is that it would appear to relegate 339
all of ideation to motor planning. A natural objection to the preceding paragraphs 340
is as follows. The monkey may be deciding about where to move its eyes, but I, as 341
a human, decide about the motion, independently of what action or word I would 342
use to communicate my decision, indeed whether I communicate it at all. 343

We agree that ideation does not necessitate action. Nonetheless, we believe the 344
essential features of abstract ideation are visible in the sensory-motor decision 345
mechanisms we study. Figure 3 illustrates a simple “abstract” decision. The subject 346
decides the direction of motion without knowledge of the motor response required 347
to indicate an answer. In the epoch during motion viewing and the onset of the 348
colored choice targets, the monkey forms and remembers a decision about motion, 349
not about the next action. Neural circuits devoted to planning a particular action do 350
not reflect accumulating evidence (Gold and Shadlen 2003, 2007). Instead, the 351
brain must decide on a plan to make another decision: to make an eye movement to 352
one or another target based on color. The key to abstraction is to view decision 353
making not as information bearing on an action but on the selection of circuitry that 354
mediates another decision. 355

Indeed, the larger cortical mantle might support higher cognitive function in 356
humans by allowing us to make decisions about decisions about decisions about . . . 357
decisions to do something. It is not hard to see the elements of symbol manipulation 358
in the example of Fig. 3. By cascading association areas that do not project to motor 359
structures but instead to other association areas, we can imagine the basis of much 360
more complexity. For example, we can appreciate the layers in performing an 361

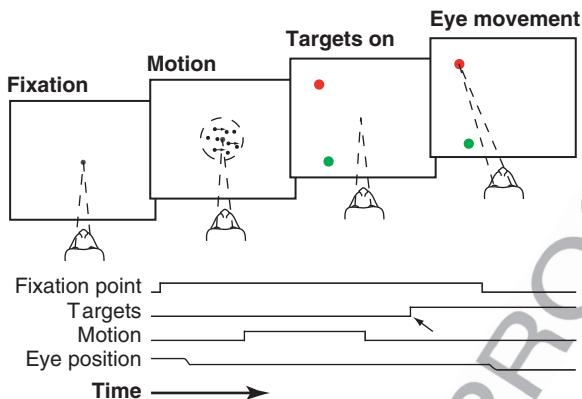


Fig. 3 A direction discrimination task used to separate abstract decision making from motor planning. The subject must decide the net direction of dynamic random dot motion: *left* or *right*. Decision formation occurs before the targets are displayed at unpredictable locations. The monkey chooses *red* (or *green*) for *right* (or *left*). Before the targets are turned on (*small arrow*), the monkey must commit to a proposition that is more abstract than a plan to move the eyes (adapted with permission from Gold and Shadlen 2003)

362 action to achieve a goal, in imitation of another's actions, in construing from
 363 another's action the goal that led to the other's action, in mirroring this goal –
 364 steps toward a neurobiology of “theory of mind.”

365 The intentional framework has much in its favor. This is not the place to expound
 366 all of its virtues, but as this meeting takes place in Paris, it is a pleasure to mention
 367 that the framework was anticipated in the writings of Maurice Merleau-Ponty.
 368 He regarded vision not as inference on visual impressions (representation) but as
 369 answers to more purposeful interrogations of the environment (Merleau-Ponty
 370 1962). The panorama to the blind man is not the sequence of vibrations from the
 371 stick to the hand but answers to questions about obstacles, the ground surface, steps,
 372 cliffs, walls and so on.

373 Much of the motivation behind many mainstream theories of perception and
 374 consciousness in neuroscience is driven by over-enthusiasm for the representational
 375 framework. It leads to bizarre solutions that elevate agnostic representations of
 376 information to the status of perception and awareness by oscillating it, synchronizing
 377 it or enhancing its power spectrum in some frequency band.⁷ Even if such
 378 measurements were to occur reliably with the phenomena they supposedly explain,
 379 by what mechanism do they arise? What brain structure *decides* to wiggle some part
 380 of the representation and thus render it available for conscious awareness?

⁷The change blindness demonstrations underscore the inadequacy of neural representation to explain perception. The unseen object (e.g., the gorilla among the ball players) is represented in visual cortex with greater amplitude than many low-contrast but highly visible objects.

5 Circuit Selection and Configuration

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The action of neurons in LIP is not to move body parts but to influence other neurons in the brain. LIP influences eye movements by guiding the selection of circuits in the frontal eye field and superior colliculus. Some other brain structure probably makes a decision that the context is befitting and selects the appropriate LIP circuits to construe evidence from visual cortex as bearing on the salience of potential saccade targets (and not other items present in the visual field). Indeed the circuit must also be configured so that the evidence is compared in a sensible way (e.g., rightward direction sensors from part A of the visual field provide support for LIP neurons that represent part B of the visual field).⁸

The mechanism underlying circuit selection is unknown. We believe it is among the most important problems in systems neuroscience, in part because of its connection to the neurobiology of consciousness. A decision to engage is simply that: evaluation of evidence leading to turning on another circuit and configuring the flow of information – for example, so that the new spot of activity in the primary visual cortex gets inspected and identified as a gorilla (or not).

The idea is not that all such operations lead to conscious awareness but rather that the ones that do so use this mechanism to engage particular circuits. A wide variety of cognitive functions requires that one operation, naturally construed as a decision, leads to the activation of one or more of a larger set of circuits. We believe this can occur without consciousness and does not necessarily lead to conscious awareness, as in the perceptual decision tasks, when contextual information induces clusters of neurons in LIP to represent the integrated evidence from the visual cortex. In this view, the N-conscious processes are those that allow the brain to make more non-conscious decisions about what else to engage, whereas the P-conscious processes are decisions to engage in certain ways, most prominently for communicating, pointing to another – that is to say, reporting.

6 Some Candidate Structures for Decisions to Engage

408

Several brain structures emerge as potential targets of inquiry. When we consider areas of the brain that are involved in arousal, the midbrain reticular formation and the intralaminar nuclei are at the top of the list. These are the sites that Schiff and colleagues targeted in their successful restoration of consciousness to a severely impaired patient (Schiff 2010; Schiff et al. 2007). It is now recognized that intralaminar nuclei make different types of connections with the cortex than the rest of the thalamus. Instead of targeting layer IV, they target superficial layers and tend to arborize more extensively. This pattern is also evident in a class of neurons

⁸For present purposes, we are lumping circuit selection and configuration. It is the former that has the clearer connection to decisions to engage.

417 outside the intralaminar nuclei that share certain molecular markers. These neurons
418 and the intralaminar nuclei comprise the thalamic matrix (Jones 2001). One
419 intriguing idea is that these matrix neurons play a role in cortical circuit selection.
420 Support for this view might be adduced from a recent paper from M. Sherman and
421 colleagues (Theyel et al. 2009).

422 Other cortical areas are likely to play a role in circuit selection. As mentioned
423 above, such decisions about *what to make decisions about* need not invoke
424 P-consciousness. Presumably executive control arises in a variety of contexts that
425 contribute to both conscious and nonconscious cognition (e.g., Del Cul et al. 2009;
426 Miller 2000). Some cortical areas that are part of a default network, however, seem
427 to play a role in monitoring the world exactly when we are not engaged (Christoff
428 et al. 2009; Raichle and Snyder 2007; Raichle et al. 2001). They seem poised to
429 make decisions about whether or not to engage, and perhaps it is a large enough
430 system to support decisions to engage in certain ways. One consideration that plays
431 a role in our thinking about cortical control is the constraint on wiring. It simply is
432 not the case that a central structure can address the entire cortex, and we do not
433 know of a switchboard in the brain, although matrix thalamus comes closest.

434 Language areas seem like obvious candidate structures for decisions to engage in
435 a narrative way. Such areas might be targets of circuit selection or they might
436 participate in decisions to engage for possible reporting or attaching narrative.
437 A more inchoate expression of such functionality might reside in the association
438 auditory cortex. Consider the prominence of audition in the examples mentioned
439 earlier concerning arousal! It is intriguing that the evolution of auditory association
440 cortex might parallel the capacities we invoke when we engage in the ways that
441 touch on P-consciousness: attaching narrative, episodic/declarative context,
442 pointing out a visual object to another individual.

443 The following coincidence may be of interest to some readers. Rhesus monkeys
444 are notoriously difficult to train on high-level auditory tasks. They can localize and
445 recognize calls, but we have had little success training them to make the kinds of
446 arbitrary associations that are exemplified in the tasks described above. A monkey
447 can make an eye movement to the location of a hidden speaker, but we have found it
448 difficult to train monkeys to decide about the duration of intervals between clicks
449 and indicate a choice with an eye movement.⁹ There may be many reasons for
450 this, including our own ineptitude, but many researchers in the field are struck by
451 the lack of auditory aptitude of macaques (Fritz et al. 2005). Coincidentally,
452 monkeys seem to possess little parietal cortex devoted primarily to audition.
453 Earlier, we mentioned three areas along the intraparietal sulcus that are devoted
454 to vision-action associations but can be co-opted for more abstract visual perceptual
455 decisions. These are somatosensory areas rostral to the sulcus. But as one moves
456 toward the auditory cortex, the sulcus disappears. There is auditory input to parietal
457 regions that are classically identified as visual association areas, whereas the
458 remaining regions, near the temporo-parietal junction, project to the most rostral

⁹We have published and are now conducting several timing tasks, which are easier for humans when using sounds. Monkeys are far more proficient using intervals between visual cues.

pole of the prefrontal cortex (Kaas and Hackett 2000; Kaas et al. 1999; Poremba 459
and Mishkin 2007; Poremba et al. 2003). 460

If the evolution of auditory association cortex remains delayed in the hominid 461
branch of *primata*, maybe we can begin to recognize why language developed late 462
and only in one hemisphere. And since there is no way to close our ears, perhaps we 463
had to have more elaborate systems of decisions to engage based on stimulation. 464
Perhaps our brains exploit this capacity to engage other systems. These are a few 465
highly speculative justifications for the view that auditory association cortex and its 466
thalamic targets might play a privileged role in decisions to engage. This is 467
obviously not the only path to P-consciousness, but it may be one that is highly 468
developed. And this is not to say that hearing must be intact to use this neural 469
substrate (e.g., in deafness). 470

7 Limitations and Dividends of the Idea 471

The main shortcomings of the decision to engage idea are (1) it lacks a known 472
mechanism, (2) it is probably involved in non-conscious as well as conscious 473
processes, (3) its parallel “intentional” architecture fails to capture the unity of 474
experience captured by conscious awareness, and (4) it does not explain the 475
subjective “what it is like to be...” aspects of consciousness, including *qualia*. 476
This is not a complete list, but it is enough to have a stab at. 477

- (1) The mysterious step in the “decision to engage” is the mechanism underlying 478
circuit selection. It is poorly understood in the simplest of perceptual decisions. 479
That said, it is a mechanism, and the notion that it can be studied in simpler 480
contexts is a dividend of the theory. We do not know how LIP “selects” neurons 481
in the frontal eye field or superior colliculus, when a decision about motion 482
leads to an eye movement, but the question is tractable. A decision to engage 483
links neural mechanisms mediating N- and P-consciousness to the neurobiology 484
of decision making. Put more bluntly, it is a testable idea about a mechanism. 485
It does not assert that a mysterious function adds an incantation – be it 486
synchrony or oscillations or power in a range of frequencies – to a representa- 487
tion, thus rendering it available to awareness. Even if rendering to awareness 488
were marked by such an “incantation,” one would ask about the mechanisms in 489
the brain that led to its application. If the answer is, “a decision to activate 490
via matrix thalamus a set of cortical circuits that decide to use vision,” we 491
would recognize a mechanism with similarities to others we are beginning 492
to understand. 493
- (2) Admittedly, decisions to engage are also shared by the organized behaviors that 494
neither require nor reach the level of consciousness. We speculate that the 495
difference is partially due to the brain structures that initiate the decision to 496
engage (and perhaps whether such initiation is programmed by a conscious or 497
unconscious mental process). Regardless of how the process is initiated, the 498

499 shared mechanism of decision-to-engage provides an opportunity to study
500 consciousness. If we can understand how a decision about a simple sensory
501 stimulus (e.g., noisy motion) leads to the selection of a motor circuit (e.g., in the
502 frontal eye field and/or superior colliculus to plan or initiate an eye movement),
503 we will have taken a step toward understanding a mechanism that could also
504 engage other circuits that lead to exploration, pointing out to another being,
505 communicating and attaching narrative.

506 (3) Decisions to engage in particular ways conform to a brain organization that
507 lacks a central executive or global workspace with access to all functions. This
508 may be limiting, or simply wrong, were it to turn out that such a central,
509 integrative, organizing structure exists. Yet, we cannot think of a brain structure
510 that could qualify as such a structure. Brain regions that project broadly (e.g.,
511 the locus coeruleus) lack the computational capacity – or even representational
512 capacity – to serve as a central workspace for consciousness. We do not pretend
513 to understand how a parallel architecture can support the unity of our experi-
514 ence, but we suspect it can be accounted for by a parallel organization viewed in
515 the intentional framework. If perception is not so much a declaration of labels
516 but answers to questions, posed serially or in parallel, about a place or time or
517 relationship of places and times, then those answers have unity arising from
518 the “aboutness” of the intention. Von Helmholtz held such an intentional view
519 of space perception (von Helmholtz 1925). Merleau-Ponty expresses this view
520 in the *Phenomenology of Perception* (Merleau-Ponty 1962).

521 (4) The mechanism alone fails to address the distinction between the personal,
522 subjective aspects of consciousness – what is it like to be me; how do I
523 experience red, love, sorrow, etc.; ownership of my feelings, perceptions and
524 acts – from other less subjective aspects of awareness and agency. We surmise
525 that these are different ways of engaging that involve different brain structures.
526 We suspect that different ways of engaging the world have attributes that can
527 facilitate or prevent subjective narratives and/or qualia. Qualia might arise
528 when we engage in ways that involve social and communicative components,
529 attach narrative context with declarative attributes (e.g., before, after, where,
530 what else is present) and sensorimotor contingencies (O’Regan and Noë 2001).
531 The subjective aspects of conscious experience are multi-faceted and complex,
532 hence unlikely to be explained by a single process. The decision to engage is the
533 first building block of a subjective conscious experience, not the entirety of it.

534 The main dividend to the notion of consciousness as a decision to engage is that
535 it offers a glimpse of an actual neural mechanism that can be studied in a variety of
536 contexts and model systems. If we wake up to sounds through a decision to engage,
537 or if we decide to engage a distant object with a decision to report, say, via pointing
538 to another, we can bring to bear what is already known about the neurobiology of
539 perceptual decisions. We can ask whether the bounded accumulation of evidence
540 in the posterior cingulate cortex (PCC), to choose one interesting example, leads
541 to the activation of another cortical area, via intralaminar and matrix thalamus,

and whether this occurs once a threshold or bound is achieved by the firing rate of neurons in PCC. 542 543

Such consideration of putative mechanism contrasts with the traditional quest for a neural correlate of consciousness (NCC), which may well mark the presence of consciousness but which fails to explain its derivation. That said, our hypothesis is compatible with popular ideas about the NCC. If it so happens that power in a range of frequencies measured in local field potentials is a signature of conscious processing, then one ought to ask what is the mechanism that causes this physiological change. It could be the case that when matrix thalamus activates cortex, it leads to changes in the cortical microcircuit that are associated with increased power in the gamma band of frequencies measured in the LFP. We are not invested in this view but mention it as testimony to the compatibility of “decisions to engage” with existing theories and observations. 544 545 546 547 548 549 550 551 552 553 554

8 Concluding Remarks 555

The concept of a decision to engage links the neurobiology of consciousness to the field of decision making. It has the virtue of tying together characterizations of consciousness employed in clinical neurology with the phenomenology that we associate with the mind’s most precious pursuits. It may guide future experiments and, if correct, it would render broad areas of systems, cellular and molecular neuroscience relevant to the study of consciousness. 556 557 558 559 560 561

References 562

Allman JM, Kaas JH (1971) A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Res* 31:85–105 563 564

Andersen RA (1995) Encoding of intention and spatial location in the posterior parietal cortex. *Cereb Cortex* 5:457–469 565 566

Andersen RA, Buneo CA (2002) Intentional maps in posterior parietal cortex. *Annu Rev Neurosci* 25:189–220 567 568

Block N (2005) Two neural correlates of consciousness. *Trends Cogn Sci* 9:46–52 569

Born RT, Bradley DC (2005) Structure and function of visual area MT. *Annu Rev Neurosci* 28:157–89 570 571

Bracewell RM, Mazzone P, Barash S, Andersen RA (1996) Motor intention activity in the macaque’s lateral intraparietal area. II. Changes of motor plan. *J Neurophysiol* 76:1457–1464 572 573

Britten KH, Newsome WT, Shadlen MN, Celebrini S, Movshon JA (1996) A relationship between behavioral choice and the visual responses of neurons in macaque mt. *Vis Neurosci* 13:87–100 574 575

Celebrini S, Newsome WT (1994) Neuronal and psychophysical sensitivity to motion signals in extrastriate area mst of the macaque monkey. *J Neurosci* 14:4109–4124 576 577

Christoff K, Gordon AM, Smallwood J, Smith R, Schooler JW (2009) Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. *Proc Natl Acad Sci USA* 106:8719–8724 578 579 580

- 581 Churchland AK, Kiani R, Chaudhuri R, Wang XJ, Pouget A, Shadlen MN (2011) Variance as a
582 Signature of Neural Computations during Decision Making. *Neuron* 69:818–831
- 583 Cisek P (2007) Cortical mechanisms of action selection: the affordance competition hypothesis.
584 *Phil Trans R Soc B Biol Sci* 362:1585–1599
- 585 Cohen JD, McClure SM, Yu AJ (2007) Should I stay or should I go? How the human brain
586 manages the trade-off between exploitation and exploration. *Phil Trans R Soc B Biol Sci* 362:
587 933–942
- 588 Colby CL, Goldberg ME (1999) Space and attention in parietal cortex. *Annu Rev Neurosci* 22:
589 319–349
- 590 de Lafuente V, Jazayeri M, Shadlen MN (2009) Decision related activity in areas lip and mip during
591 reaches and saccades. *Neurosci Mtg Planner*, vol 652.9. Society for Neuroscience, Chicago, IL
- 592 Dehaene S, Changeux JP, Naccache L, Sackur J, Sergent C (2006) Conscious, preconscious, and
593 subliminal processing: a testable taxonomy. *Trends Cogn Sci* 10:204–211
- 594 Del Cul A, Dehaene S, Reyes P, Bravo E, Slachevsky A (2009) Causal role of prefrontal cortex in
595 the threshold for access to consciousness. *Brain* 132:2531–2540
- 596 Dijksterhuis A, Bos MW, Nordgren LF, van Baaren RB (2006) On making the right choice: the
597 deliberation-without-attention effect. *Science* 311:1005–1007
- 598 Fritz J, Mishkin M, Saunders RC (2005) In search of an auditory engram. *Proc Natl Acad Sci USA*
599 102:9359–9364
- 600 Glimcher P (2003a) The neurobiology of visual-saccadic decision making. *Annu Rev Neurosci*
601 26:133–179
- 602 Glimcher P (2003b) Decisions, uncertainty, and the brain: the science of neuroeconomics. MIT,
603 Cambridge, MA
- 604 Gold JI, Shadlen MN (2003) The influence of behavioral context on the representation of
605 a perceptual decision in developing oculomotor commands. *J Neurosci* 23:632–651
- 606 Gold JI, Shadlen MN (2007) The neural basis of decision making. *Annu Rev Neurosci* 30:
607 535–574
- 608 Hampton RR (2001) Rhesus monkeys know when they remember. *Proc Natl Acad Sci USA*
609 98:5359–5362
- 610 Janssen P, Srivastava S, Omblet S, Orban GA (2008) Coding of shape and position in macaque
611 lateral intraparietal area. *J Neurosci* 28:6679–6690
- 612 Jones EG (2001) The thalamic matrix and thalamocortical synchrony. *Trends Neurosci*
613 24:595–601
- 614 Kaas JH, Hackett TA (2000) Subdivisions of auditory cortex and processing streams in primates.
615 *Proc Natl Acad Sci USA* 97:11793–11799
- 616 Kaas JH, Hackett TA, Tramo MJ (1999) Auditory processing in primate cerebral cortex. *Curr Opin*
617 *Neurobiol* 9:164–170
- 618 Kiani R, Shadlen MN (2009) Representation of confidence associated with a decision by neurons
619 in the parietal cortex. *Science* 324:759–764
- 620 Kiani R, Hanks TD, Shadlen MN (2008) Bounded integration in parietal cortex underlies decisions
621 even when viewing duration is dictated by the environment. *J Neurosci* 28:3017–3029
- 622 Kornell N, Son LK, Terrace HS (2007) Transfer of metacognitive skills and hint seeking in
623 monkeys. *Psychol Sci* 18:64–71
- 624 Kouider S, Dehaene S (2007) Levels of processing during non-conscious perception: a critical
625 review of visual masking. *Phil Trans R Soc Lond B Biol Sci* 362:857–875
- 626 Krug K (2004) A common neuronal code for perceptual processes in visual cortex? Comparing
627 choice and attentional correlates in V5/MT. *Phil Trans R Soc Lond B Biol Sci* 359:929–941
- 628 Lau HC, Passingham RE (2007) Unconscious activation of the cognitive control system in the
629 human prefrontal cortex. *J Neurosci* 27:5805–5811
- 630 Laureys S (2006) Tracking the recovery of consciousness from coma. *J Clin Invest* 116:1823–1825
- 631 Laureys S, Owen AM, Schiff ND (2004) Brain function in coma, vegetative state, and related
632 disorders. *Lancet Neurol* 3:537–546

- Mazzoni P, Bracewell RM, Barash S, Andersen RA (1996) Motor intention activity in the macaque's lateral intraparietal area. I. Dissociation of motor plan from sensory mechanisms and behavioral modulations. *J Neurophysiol* 76:1439–1456 633
- McCoy AN, Platt ML (2005) Expectations and outcomes: decision-making in the primate brain. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 191:201–211 636
- Merleau-Ponty M (1962) *Phenomenology of perception*. Routledge and Kegan Paul, London 638
- Miller EK (2000) The prefrontal cortex and cognitive control. *Nat Rev Neurosci* 1:59–65 639
- Nagel T (1974) What is it like to be a bat? *Phil Rev* 83:435–450 640
- Nienborg H, Cumming BG (2009) Decision-related activity in sensory neurons reflects more than a neuron's causal effect. *Nature* 459:89 642
- O'Regan JK, Noë A (2001) A sensorimotor account of vision and visual consciousness. *Behav Brain Sci* 24:939–973 643
- Poremba A, Mishkin M (2007) Exploring the extent and function of higher-order auditory cortex in rhesus monkeys. *Hear Res* 229:14–23 645
- Poremba A, Saunders RC, Crane AM, Cook M, Sokoloff L, Mishkin M (2003) Functional mapping of the primate auditory system. *Science* 299:568–572 648
- Posner JB, Saper CB, Schiff ND, Plum F (2007) *Plum and Posner's diagnosis of stupor and coma*. Oxford University Press, New York 649
- Raichle ME, Snyder AZ (2007) A default mode of brain function: a brief history of an evolving idea. *Neuroimage* 37:1083–1090 651
- Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL (2001) A default mode of brain function. *Proc Natl Acad Sci USA* 98:676–682 653
- Rensink RA (2000) Seeing, sensing, and scrutinizing. *Vis Res* 40:1469–1488 655
- Roitman JD, Shadlen MN (2002) Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. *J Neurosci* 22:9475–9489 656
- Romo R, Salinas E (2003) Flutter discrimination: neural codes, perception, memory and decision making. *Nat Rev Neurosci* 4:203–218 658
- Schall JD (2001) Neural basis of deciding, choosing and acting. *Nat Rev Neurosci* 2:33–42 660
- Scherberger H, Andersen RA (2007) Target selection signals for arm reaching in the posterior parietal cortex. *J Neurosci* 27:2001–2012 661
- Schiff ND (2010) Recovery of consciousness after brain injury: a mesocircuit hypothesis. *Trends Neurosci* 33:1–9 664
- Schiff ND, Giacino JT, Kalmar K, Victor JD, Baker K, Gerber M, Fritz B, Eisenberg B, Biondi T, O'Connor J, Kobylarz EJ, Farris S, Machado A, McCagg C, Plum F, Fins JJ, Rezaei AR (2007) Behavioural improvements with thalamic stimulation after severe traumatic brain injury. *Nature* 448:600–603 667
- Shadlen MN, Kiani R (2007) Neurology: an awakening. *Nature* 448:539–540 669
- Shadlen MN, Hanks TD, Churchland AK, Kiani R, Yang T (2006) The speed and accuracy of a simple perceptual decision: a mathematical primer. In: Doya K, Ishii S, Rao R, Pouget A (eds) *Bayesian brain: probabilistic approaches to neural coding*. MIT, Cambridge, pp 209–237 671
- Shadlen MN, Kiani R, Hanks TD, Churchland AK (2008) Neurobiology of decision making: an intentional framework. In: Engel C, Singer W (eds) *Better than conscious? Decision making, the human mind, and implications for institutions*. MIT, Cambridge, pp 71–102 676
- Simons DJ, Chabris CF (1999) Gorillas in our midst: sustained inattention blindness for dynamic events. *Perception* 28:1059–1074 677
- Smith JD, Shields WE, Washburn DA (2003) The comparative psychology of uncertainty monitoring and metacognition. *Behav Brain Sci* 26:317–339, discussion 340–373 679
- Snyder LH, Batista AP, Andersen RA (2000) Intention-related activity in the posterior parietal cortex: a review. *Vis Res* 40:1433–1442 681
- Sugrue LP, Corrado GS, Newsome WT (2005) Choosing the greater of two goods: neural currencies for valuation and decision making. *Nat Rev Neurosci* 6:363–375 683

- 685 Theyel BB, Llano DA, Sherman SM (2009) The corticothalamocortical circuit drives higher-order
686 cortex in the mouse. *Nat Neurosci* 13:84–88
- 687 Uchida N, Kepecs A, Mainen ZF (2006) Seeing at a glance, smelling in a whiff: rapid forms of
688 perceptual decision making. *Nat Rev Neurosci* 7:485–491
- 689 von Helmholtz HLF (1925) *Treatise on physiological optics*. Dover, New York
- 690 Yang T, Shadlen MN (2007) Probabilistic reasoning by neurons. *Nature* 447:1075–1080

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