

# Information processing and decision-making: evidence from the brain sciences and implications for Economics\*

Isabelle Brocas

*University of Southern California and CEPR*

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## Abstract

*This article provides a motivated summary of findings in neurobiology and assesses the potential benefits of including such findings in economic decision-making models. We emphasize that the evidence supports both ‘expected utility-like’ theory and ‘Bayesian-like’ information acquisition theory. However, we report that inferences and representations are subject to physiological limitations (or constraints) that may explain typical departures from these theories, and rationalize some behavioral biases. Hence, understanding the underlying processes that maps the formulation of a problem to a decision-maker into an actual decision may help build theories capable of predicting choice more accurately.*

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\*Correspondence address: Department of Economics, University of Southern California, 3620 S. Vermont Ave. Los Angeles, CA 90089-0253, USA, email: <brocas@usc.edu>. I am grateful to Juan D. Carrillo for very useful comments. I thank Bo Ren for research assistance.

# 1 Introduction

Economic models of decision-making rely on two important paradigms. First, decision-makers' choices can be represented by well-defined utility functions (satisfying well-defined axioms). Second, decision-makers are Bayesian processors of information. Even though these two paradigms have merits and surely account for a large proportion of observed behaviors still, various anomalies have been reported. Most of the hypotheses formulated to justify those anomalies are introspective and make implicit claims about the underlying mechanisms leading to behavior. In parallel, a myriad of experiments in neuroscience try to describe the brain processes involved in decision-making. We believe that this evidence should shed light on the fundamental causes of observed choice anomalies. The objective of this article is to provide a motivated summary of findings in neurobiology. In particular, we will disregard fMRI experiments. We are mostly interested in the following paradigm. A decision-maker (hereafter DM) faces uncertainty regarding the state of nature and collects information before making a decision. A state realizes and payoffs are obtained.

From the perspective of economists, this is a simple problem of information processing: in the first stage, DM receives a signal on the true state of nature, in the second stage he uses this information to form an updated belief, in the third stage, he makes a decision based on this belief, and in the last stage the decision is implemented and payoffs realized. Economists would further assume that the updating process is Bayesian and the decision is made by maximizing expected utility. They also would model the signal as an imperfect indicator of the true state, and assume that the information transmitted is equal to the information processed.

From the perspective of neurobiologists, this paradigm follows closely standard experimental designs: in the first stage, DM receives a stimulus, in the second stage he provides a response, and in a third stage payoffs are realized. Neurobiologists work under the assumptions that (i) the stimulus is encoded by neurons in the *sensory system* (e.g. visual and auditory systems), (ii) interpreted by the *decision system* to determine which response should be triggered and (iii) implemented by the *motor system*. However, they do not presuppose how information is processed or how decisions are made. Rather, they measure cell activity in preselected brain areas and correlate it with response.

## 2 Anatomy and Physiology

For the reader unfamiliar with brain functioning, it might be useful to start with a few words on anatomy and physiology. This description is by no means exhaustive and should

be completed by further readings.<sup>1</sup>

The human brain has a wide array of functions including functions to help us appreciate sensory inputs, originate and coordinate motor responses, control basic functions such as sleep, hunger or thirst, stock and retrieve information required to perform tasks, and guide abstract and complex decision-making. It is organized in a neural network involving around ten billion nerve cells, called neurons.

The brain can be divided into three main parts, the forebrain, the midbrain and the hindbrain. The cerebral cortex, a part of the forebrain, controls higher functions.<sup>2</sup> Those are our focus. The cerebral cortex is composed of various systems with specific missions. The motor cortices (primary and secondary) are responsible for the planning and execution of voluntary motor functions. The sensory cortices are involved in the treatment of sensory information.<sup>3</sup> The prefrontal cortex is in charge of complex cognitive tasks, expressing personality, and moderating behavior.<sup>4</sup> The primary activity of the prefrontal cortex is thought to be cognitive control, that is the orchestration of thoughts and decisions in accordance with internally generated goals.<sup>5</sup> The forebrain also hosts the limbic system, a set of structures that support a variety of functions including the regulation and manifestation of emotions and the formation of memory.<sup>6</sup>

The brain is composed of many different types of cells but the main functional unit is the neuron. Neurons within the brain process and transmit signals. Some neurons convey information to the nervous system (afferent, sensory neurons) while others transmit signals from the nervous system (efferent, motor neurons). Neurons that connect neurons within the central nervous system are called interneurons. Even though neurons are highly specialized and there is a wide variety of them, a typical neuron can be described as follows. The central part of a neuron is called the soma. It has cellular extensions, called dendrites, that form a tree. Dendritic trees are the place where the neuron receives information. The

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<sup>1</sup>See for instance Thompson (2000), Shepherd (2003) and Nicholls et al. (2001).

<sup>2</sup>The midbrain and the hindbrain are involved in unconscious and autonomic functions. For instance, the cerebellum is responsible for the coordination of movements and the pons regulates respiration.

<sup>3</sup>These include the visual cortex (in the occipital lobe), the somatosensory cortex (in the parietal lobe), the auditory cortex (in the temporal lobe), the olfactory cortex (in the temporal lobe) and the gustatory cortex (in the parietal lobe).

<sup>4</sup>It is composed of the orbitofrontal (OFC), the ventromedial (vm-PFC), the dorsolateral (dl-PFC), the ventrolateral (vl-PFC), the medial (m-PFC), the anterior (a-PFC) as well as the cingulate cortex.

<sup>5</sup>See the theories of cognitive control and, in particular Miller and Cohen (2001).

<sup>6</sup>These are the hippocampus, responsible for the formation of long term memory; the amygdala, performing an important role in the processing and memory of emotional reactions; the hypothalamus, responsible for controlling body temperature, hunger, thirst, fatigue, anger, circadian cycles and maintaining overall homeostatic balance; and the thalamus, involved in the regulation of sleep and a primary relay station to translate sensory information in a form readable for the cerebral cortex.

signal then passes through the soma and travels away from it down the axon, which carries nerve signals to another cell. The axon may divide into a large number of branches enabling communication with many target neurons. The terminal of the axon contains synapses. There are two types of synapses. Electrical synapses are direct and electrically conductive junctions between cells. They are fast and very reliable and are found throughout the nervous system. They are used when a prompt response is required as for escape reflexes (in response to pain or danger). Yet, they are less common than chemical synapses. These structures release neurotransmitter chemicals to communicate with target neurons.<sup>7</sup>

If a neuron responds to a nerve impulse, then it responds completely (all-or-none principle). A series of events must occur for a neuron to respond and pass the signal to other cells. When a stimulus is received (e.g. after neurotransmitter release by a presynaptic neuron), the membrane is depolarized or said differently, its voltage is increased. This triggers the opening of sodium and potassium ion channels located in the axon. For small voltage increases, the potassium current dominates and the voltage returns to its normal resting value.<sup>8</sup> However, if the voltage increases past a critical threshold higher than the resting value, the sodium current dominates.<sup>9</sup> The positive feedback from the sodium current activates even more sodium channels.<sup>10</sup> Thus, the cell “fires”, producing an electrical impulse, called action potential or spike, that travels down the axon.<sup>11</sup> The action potential arrives at the synapse and produces an influx of calcium ions that trigger a biochemical cascade which results in neurotransmitter release.

Increasing the intensity of the stimulation does not produce a stronger signal but can produce more impulses per second. Neurons can be classified according to their discharge patterns. Some neurons are constantly active (e.g. some interneurons). They produce a

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<sup>7</sup>There exist many different neurotransmitters. Acetylcholine is associated with excitatory functions and governs muscle contractions and causes glands to secrete hormones. Gamma-aminobutyric acid (GABA) is correlated with inhibitory functions in the motor and visual systems. Dopamine is an inhibitory neurotransmitter involved in mood and the control of complex movements. Dopamine-sensitive neurons are located in the PFC. Other important neurotransmitters are serotonin, glutamate, adenosine, adenosine triphosphate (ATP).

<sup>8</sup>See Hodgkin and Huxley (1952) for a seminal model of voltages and currents of the action potential.

<sup>9</sup>The critical threshold voltage is usually around -45 mV, but it depends on the recent activity of the axon. A membrane that has just fired an action potential cannot fire another one immediately, since the ion channels have not returned to their usual state. The period during which no new action potential can be fired is called the absolute refractory period. After some but not all of the ion channels have recovered, the axon can be stimulated to produce another action potential, but only with a much stronger depolarization, e.g., -30 mV. Thresholds can be modified by secondary messengers (like hormones or neurotransmitters) that also communicate with the neuron.

<sup>10</sup>This “summation” of incoming information is made at the axon hillock, a region at the end of the soma and start of the axon.

<sup>11</sup>Some neurons do not generate action potential, but instead they generate a graded electrical signal. They are called non spiking neurons. They are generally sensory neurons or interneurons.

steady rate of firing and respond to increase intensity of a stimulus by increasing their firing frequency. Other neurons are phasic and firing decreases or stops when the stimulus becomes steady. Some neurons have fast firing rates (fast spiking neurons) while others have narrow action potentials (e.g. thin-spike interneurons in the prefrontal cortex).

Synapses can be excitatory, inhibitory or modulatory, depending on which effect they have on their target neurons.<sup>12</sup> The post-synaptic receptor is responsible for the action of the neurotransmitter released at the synapse. In other words, synapses will increase or decrease the activity in the target neuron. When excitatory synapses are activated, the target neuron is induced to produce nerve impulse. By contrast, when inhibitory synapses are activated, the action of excitatory synapses is counterbalanced to prevent nerve impulse. The total activation of synapses determines when nerve impulses are sent out to other neurons. The strengths of synapses (i.e. the effectiveness with which synapses produce or negate nerve impulse) vary largely. Information sent via strong (resp. weak) synapses is emphasized (resp. de-emphasized). Many neuronal mechanisms are in place to modify strength. Some cause persistent alterations that can last months or years, others cause short-term modifications lasting from fractions of seconds to a few minutes. The latter mechanisms are referred to as short-term plasticity.<sup>13</sup> Overall, synapses act as a filter of information for the brain.

The purpose of neurobiologists and physiologists is to answer a wide array of questions. They provide studies at the level of neurons to determine the properties of neuronal functioning and the way communication is enabled between them. They also provide evidence on brain processes and in particular on how a given stimulus is mapped into decisions. We will concentrate on an extremely reduced set of these studies.

### 3 Conceptual framework of decision-making

Simple decision-making has been studied in a myriad of neurophysiological studies in monkeys. The studies measure the animal's valuation of competing alternatives using single cell recording methods. Researchers sometimes manipulate the activity of small

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<sup>12</sup>For a thorough description of synaptic functioning, see Cowan et al. (2003). Note that much remains to be known on synaptic connections and their strength. It is widely believed that synaptic strength provides the basic mechanism for learning and memory. See Hebb (1949) for a seminal model of learning and memory.

<sup>13</sup>Short-term plasticity is correlated with the history of the activity of a synapse. It provides a way for a neuron to emphasize or de-emphasize particular types of information according to the pattern of activation in the past. It is a history dependent filter that decides which information is the most important in determining the output of a neuron. See for instance Klyachko and Stevens (2006) for a study of hippocampal synapses.

groups of neurons to identify causal links between neural activity and cognitive functions. This is done via a method called electrical microstimulation (see Cohen and Newsome (2004) for a review).

It is important to note that the fundamental unit of information in the brain is the action potential. However, given the all-or-none principle, an action potential per se does not carry much information. Rather, the timing of action potentials does. The response of a single neuron can be summarized as a list of dates  $t_1, t_2, \dots, t_N$  at which the neuron fired action potentials and simplified into a time-dependent variable  $r(t)$  (spike decoding method). This time series is called a spike train. The firing rate of a neuron is the average number of action potentials per unit of time. It is a measure often used but it is important to note that it implicitly assumes that the exact timing of spikes should play no role. Both measures (spike trains and firing rates) can be found in the literature.<sup>14</sup>

A typical experiment is the well-known random dot stimuli experiment (see for example Newsome et al. (1989) and Salzman et al. (1990)). A monkey is facing a black computer background showing moving white dots. The percentage of dots that move in the same direction, or *coherence*, can be manipulated by the experimenter. A 100 % coherence corresponds to the case they all move at the same speed and direction. A 0% coherence corresponds to the case they all move randomly. The monkey must identify the direction followed by the majority of dots by making a saccade. Correct answers are rewarded.

To clarify matters, we will denote by  $S$  the (unknown) true state of nature (e.g. the true direction). Each element  $S$  is an hypothesis. DM receives a signal, or stimulus,  $s$  (the more or less coherent dots display) containing information about  $S$  which is encoded by neurons in the sensory system. The experimental conditions are given by  $s$  and  $S$ . The neural responses of the encoding neurons is data available to the brain. We will call it  $D$ . The distinction between  $s$  and  $S$  is not always explicit in the literature, as results are explained as a function of experimental conditions (that is the pair  $(s, S)$ ). For the sake of clarity, we will reflect the difference in this paper. In the remainder of this review (and unless otherwise noted), we also assume there are only two possible states  $S = \{A, B\}$ .<sup>15</sup>

Neurophysiological studies reveal that the sensory and motor systems of the cerebral cortex are crucial structures (see Sugrue et al. (2005) for a review). In a typical two-alternative discrimination task, visual and oculomotor stems perform three distinct transformations. First, a visual representation from primary visual input is created. This

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<sup>14</sup>For a discussion of the similarities as well as list of pros and cons, see Abbot (1994) and Gerstner and Kistler (2002).

<sup>15</sup>Most of the literature concentrates on two-action discrimination tasks in which there are two possible hypotheses.

corresponds to the transformation of  $s$  into  $D$ . The sensory representation is made in areas of the parietal and frontal cortices where sensory neurons encode visual stimuli. Second, the sensory evidence is mapped out onto the probability of possible responses. Decision-making is also made in areas of the parietal and frontal cortices and the decision-related neurons make the animal's ultimate choice. Decisions are based on the sensory stimuli strength. Third, a process of action implementation renders the binary decision.

## 4 Perception and encoding

According to the Efficient Coding Hypothesis (Barlow (1961), (2001)), the purpose of early visual processing is to produce an efficient representation of the incoming visual signal. Information received from the outside world is encoded as compactly as possible in order to utilize the available computing resources most efficiently. In his seminal work, Barlow hypothesized that the spikes in the sensory system formed a neural code capable of representing sensory information in an efficient way.<sup>16</sup> His model treats the sensory system as a communication channel where neuronal spiking is an efficient code to represent  $s$ . To be efficient, the code must maximize the channel capacity and minimize the redundancy in the representation.<sup>17</sup> Overall, according to the Efficient Coding Hypothesis, neurons are capable of screening the relevant information and eliminating redundancies:<sup>18</sup>  $D$  is an efficient representation of  $s$ . In particular, if  $s$  is correlated with  $S$ , then  $D$  is correlated with  $S$  as well.

Given a stimulus  $s$  reflecting  $S$ , the response of neurons is given in terms of a probability distribution  $p(D|S)$ . For instance, in the random dot stimuli experiment,  $S$  would be the true direction of dots and  $s$  the more or less coherent display (the coherence is a measure of the correlation between the signal/stimulus  $s$  and the true state  $S$ ). In that setting,  $D$  represents neural activity in the area of neurons that encode  $s$ . This activity can be summarized by a probability distribution reflecting the confidence of neurons in

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<sup>16</sup>The Efficient Coding Hypothesis presupposes that the number of spikes required to transmit the signal is minimum.

<sup>17</sup>As such, the model offers a natural application for information theory (Shannon (1948)) which provides the mathematical framework for analyzing communication systems. It formally defines concepts such as information, channel capacity, and redundancy.

<sup>18</sup>Several theories related to information theory explain the goal of early stages of visual processing. All take into account neural limitations, such as the amount of information that can be handled at the later stages or the noisiness in the phototransduction process, or the small number of neurons carrying information to next stages. These include the predictive coding theory (Srinivasan et al. (1982)), the maximal decorrelation theory (Atick and Redlich (1992)), the maximal signal-to-noise ratio theory (McCarthy and Owen (1996)), and the maximal kurtosis theory (Field (1994)). These studies focus on information maximization and the conditions under which redundancy should be reduced. Under some conditions, in particular in presence of noise, it is efficient to add redundancy.

hypotheses  $S$ . More precisely, the probabilities of each possible responses are estimated by taking repeated measurements of the response of the neuron, which generates a curve describing the responses (Figure 1). This curve simply represent the likelihood of obtaining each possible response  $P(D|S)$ . We can derive such a curve for each hypotheses, which provides us with two probability measures  $p(D|A)$  and  $p(D|B)$ .<sup>19</sup>

[INSERT FIGURE 1]

Moreover, each neuron has a preferred direction (e.g. some are best at detecting movements to the left, others are best at detecting movements to the right). These preferred directions correspond to the possible hypotheses  $S$ . In Figure 2, the  $x$ -axis represents the preferred direction of neurons ( $A$  and  $B$ ) and the  $y$ -axis represents the number of spikes. Each dot corresponds to the response of a neuron: the  $x$  coordinate is its preferred direction and the  $y$  coordinate the number of times it spiked after receiving  $s$ .

[INSERT FIGURE 2]

□ *Variability.* Many analyses have shown that the neural response  $D$  is variable. Variability reflects the fact that the data used by the brain is not fully accurate and in particular that neurons do not fire in a fully consistent way. This can be seen in Figures 1 and 2. For a given stimulus, the response of a neuron is variable and neurons with the same preferred directions do not all show the same activity. A few hypotheses have been formulated leading to a myriad of experiments and theories. First, the transfer of information through the nervous system depends on neurotransmitter release. Studies have shown that neurotransmitter release is stochastic (see Stevens (2003) for a review). Neurotransmitter quanta are released at synaptic connections in a stochastic manner. Synaptic release probabilities are heterogeneous across synapses, sometimes dependent on the history of the activity. Second, there exist physical constraints in the brain. In particular there are metabolic costs associated with neural activity. The brain constitutes about 2% of total body weight, but it consumes approximately 20% of total oxygen. Oxygen drives the pumps that exchange ions across cell membranes, an essential asset to power electrical signaling between neurons. It is used to produce adenosine triphosphate (ATP), which is consumed to generate electrical activity (see Laughlin et al. (1998) for measurements made on the retina of the blowfly and Attwell and Laughlin (2001) for a study of energy expenditure in the grey matter). We can conjecture that the energy required for a task might not be always available (or it might be directed to an other task). Third, the reliability of the data depends on experimental conditions. For instance, firing distributions may differ in naturalistic conditions compared to other conditions (see

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<sup>19</sup>Of course, these curves make sense only if all the measurements are obtained under the same  $s$ .

Simoncelli (2003)). Natural and artificial scenes are shown to produce different results as well. For instance Lewen et al. (2001) show that the brain utilizes the increase of photon flux to extract more information from photoreceptors. This indicates that part of the noise in neural signals is due to the imprecision around the stimulus  $s$ . The studies show that the context in which  $s$  is displayed affects the perception about the true state of the world  $S$ . Overall, the probability distribution  $p(D|S)$  is ‘shaped’ by internal and external noises. It reflects the imperfect correlation between  $s$  and  $S$  as well as the imperfect correlation between  $D$  and  $s$ .<sup>20</sup>

□ *Aggregation of individual neuronal responses.* Another important aspect concerns the way individual neuronal responses to a given stimuli are aggregated into a visual representation. The term  $p(D|S)$  represents how neural responses are produced conditional on the possible hypotheses. It is important to determine how information is aggregated and how neurons read-out the information produced by other neurons. It has been shown that the prevalent reaction might result from either competition or cooperation between neurons with different perspectives. For instance Nichols and Newsome (2002) use a random dot stimuli task to study neurons in the visual area with different preferred directions (e.g. detect accurately their preferred direction and less well other directions). The authors show that neurons that have a wide range of preferred directions can cooperate to shape estimates for directions (consistent with a vector averaging model), while those with opposite preferred directions compete (consistent with a winner-take-all model).

Stimuli will be processed in different areas as well. For instance direction stimuli are processed in area V1 (striate cortex) and area MT (middle temporal visual area). It has been shown that MT neurons are specialized in motion processing and the neuronal responses to direction are generally stronger on MT neurons than V1 neurons (see Albright (1984)).<sup>21</sup> This suggests that some features may be emphasized in some areas and at the same time de-emphasized in others. It may also be the case that some areas receive information from others and a transformation of the incoming information is made in-between.<sup>22</sup>

From a more general perspective, sensory activity is encoded by the activity of a large population of neurons. Models are therefore needed to represent overall neuronal activity. Suppose neurons performing early detection produce an activity consistent with the graph in Figure 2b, it is important to determine how this will be interpreted by neurons that receive that information. A classical model is the population vector estimator. It

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<sup>20</sup>This latter noise is often assumed to be Poisson, because the variance increases with the mean activity, a feature consistent with the activity of cortical neurons.

<sup>21</sup>MT Neurons are not sensitive to a broad range of stimuli like color or form.

<sup>22</sup>In that typical example, area MT receives projections from V1 and V2 areas.

assigns to each neuron a vector. Its length is proportional to the neuron’s activity and its direction corresponds to its preferred orientation. Then, it sums all the individual vectors to form a population vector, and estimates the orientation from the angle of this vector (see Georgopoulos et al. (1986) for an application to neuronal activity in the motor cortex and Gielen et al. (1988) for the case of the auditory nerve). In the example of Figure 2b, this would result in fitting the neuronal activity with a cosine function. The peak of the function is the estimate of the true state  $\tilde{S}$  (Figure 3a). Other approaches have been proposed to represent neuronal activity of large populations of neurons. One common method is the maximum likelihood (ML) estimator (see Abbott (1994) for a review). Neural firing rates for a stimulus  $s$  are treated as random variables, and an overall estimate (the likelihood) of the probability of the set of observations (i.e.  $p(D|S)$ ) is taken. This method results in producing the solid curve in Figure 3b. The peak is the ML estimator  $\hat{S}$ .<sup>23</sup>

[INSERT FIGURE 3]

The question is then whether neuronal network are able to implement any of these estimators. Deneve et al. (1999) show that biologically plausible networks can implement ML.<sup>24</sup>

□ *Bayesian Inferences.* The central idea in the previous discussion is that neurons are able to make Bayesian inferences (an idea also in Barlow (2001)). According to Ma et al. (2006), the response of neurons is given in terms of the probability distribution  $p(D|S)$  that encodes the posterior distribution  $p(S|D)$  over the true state  $S$ . The theoretical Bayesian posterior belief following the observation of  $D$  is

$$p(S|D) \propto p(D|S)P(S).$$

Overall, probability distributions can be recovered from neuronal responses.<sup>25</sup> Ma et al. (2006) also show that Bayesian inferences are simple to implement by population codes with Poisson-like variability. Indeed, if variability is Poisson, simple linear combinations of populations of neural activity (say a population encoding visual cues and a population encoding auditory cues) achieve Bayesian inferences.<sup>26</sup>

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<sup>23</sup>The ML estimator is found to perform better as it has a minimum variance over trials under some conditions.

<sup>24</sup>In other words, if the network receives noisy pooled input from a population of neurons, the output activity of the network is an optimal ML estimator.

<sup>25</sup>The prior belief could be encoded by a population of neurons that spike before the beginning of the trial.

<sup>26</sup>Suppose there are two cues 1 and 2 encoded by two different populations representing likelihood functions  $p(D_1|S)$  and  $p(D_2|S)$ , Bayesian inferences can be achieved by constructing a third population

□ *Sequential Stimulation.* The notion of adaptation is recurrent. More precisely, evidence suggests that neuronal activity declines over trials when a stimulus is presented several times. Moreover Romo et al. (2002) show that when sequential stimuli are presented, the response of the neurons are a function of the first stimuli in the first period, but a combination of both the first and the second in the second period. These findings are presumably related to the functioning of synaptic connections and plasticity. They suggest that the brain is capable of learning and integrate subsequent pieces of information. Suppose  $D_1$  is the information extracted from the first stimulus and  $D_2$  the information extracted from the second, the response of the neurons in the first trial encodes  $p(D_1|S)$ . In the second trial, the theoretical Bayesian posterior belief is  $p(S|D_2) \propto p(D_2|S)P(S|D_1)$  and the response of the neurons in the second trial encodes  $p(D_2|S) \propto 1/p(D_1|S)$ .

The main message of the literature reviewed above is that neural networks are capable of deciphering the information received from the outside world in an efficient way. Neuronal responses are still variable. Importantly, neurons are capable of making Bayesian inferences, that is, the activity is given as a probability distribution that encodes posterior beliefs about the hypotheses.

## 5 Decision-making

So far, we have focused on perception, that is on (i) the translation of  $s$  into  $D$  and (ii) the resulting representation of the likelihood of  $S$ . The decision process consists in mapping the information about the world (contained in  $D$  and its probabilistic representation) into an adequate action, or alternative. For a given true state  $S$ , DM might have a preferred action. However,  $D$  is a noisy estimate of  $S$  and DM faces uncertainty. In this section, we review the evidence suggesting mechanisms to choose between alternatives.<sup>27</sup>

□ *Neural and behavioral responses.* A series of studies using a random dot stimuli experiment have suggested that perceptual judgements in that particular task are based on a relatively small number of neural signals present in the responses of MT neurons (see Britten et al. (1992)). In those experiments, a few neurons favoring a direction (state  $A$ ) are selected and the monkey must report whether the motion follows that direction or the null direction (state  $B$ ). It is shown that the sensitivity of MT neurons is very similar to the sensitivity of the animal's response. To show this correlation, researchers compare two sets

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with  $D_3 = D_1 + D_2$  as long as the prior is flat and variability is Poisson. This results extends under weaker conditions.

<sup>27</sup>See Schall (2001) for a review of recent findings showing the distinction between decision-making in simple or complex choices and describing how the brain makes and implements decisions (deciding vs. acting).

of data: behavioral data and neural activity. On the one hand, the proportion of correct answers can be plotted for each coherence level. This data can be fitted using standard statistical techniques to obtain a “psychometric function” (Figure 4). This function is a representation of behavior. On the other hand, it is possible to observe the number of spikes for each possible coherence level and each trial. Assuming that a decision is made in favor of the decision preferred by the neuron yielding the larger response, it is possible to estimate the probability that the decision rule give a correct response for each coherence level. This allows to compute a “neurometric function” comparable to the psychometric function. Those functions are usually not significantly different in this type of experiment. In these experiments, the decision favoring the preferred direction of the neuron (resp. null direction) predominates when the neuron fires strongly (resp. weakly).

[INSERT FIGURE 4]

Inspired by these results, Shadlen and al. (1996) propose a simple flexible pooling model that links (pooled) neuronal responses to decisions. Formally, suppose there are  $2N$  neurons each represented by a random variable,  $N$  of which favoring direction  $A$  and the remaining  $N$  favoring direction  $B$ . The response of each group of neurons (spike counts) is then averaged into a signal measure and the larger measure dictates the decision.<sup>28</sup> In other words, when the activity in favor of one alternative is higher, then this alternative is chosen. In the same lines, Ditterich et al. (2003) show that decision-making based on sensory evidence for competing propositions boils down to setting a decision-making threshold. To decide between two alternatives, the response of neurons with opposing preferences are compared to obtain net evidence for one alternative. The sign of the difference represents which alternative is more likely, and the magnitude represents the persuasiveness of the evidence.

□ *Reaction times.* In most of the previous studies, subjects were exposed during a fixed period of time to the stimulus. Gold and Shadlen (2000) noted however that decisions tend to be more accurate when subjects are given longer exposure to the stimulus. This suggests in particular that they accumulate evidence over time and improve decision-making. Roitman and Shadlen (2002) use a random dot stimuli experiment to study reaction times (hereafter RT). They measure activity of the neurons in the lateral intraparietal cortex (area LIP) of the monkey. These neurons respond to visual stimuli that are the target of a voluntary eye movement and their activity is known to predict eye movement response (see Shadlen and Newsome (1996), (2001)). They compare two treatments, one in which subjects were exposed to the stimulus for a fixed period of time, and a second in which they

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<sup>28</sup>The model also assumes the brain cannot compute the average with precision and considers a pooling noise. Pooling has the effect to depreciate sensitivity.

were exposed to it until they reached a decision. The spike rate was found to be correlated with coherence, response and response time. More precisely, a steeper rise in the spike rate was correlated with a stronger stimulus and a shorter RT. The authors found evidence in favor of a RT model (as in Hanes and Schall (1996) or Ratcliff and Rouder (1998) which will be reviewed below) and hypothesized that LIP neurons accumulate evidence (from extrastriate visual cortex, e.g. MT neurons) over time for or against a specific response.<sup>29</sup> Accumulation can be understood as a random walk toward a threshold representing the level of evidence necessary to make a decision. There exist a series of models to account for this evidence. Still, RT are not fully understood at this stage and they are the main focus of many current studies. We review below a few directions being explored.

Even though the analysis of RT on neurophysiological data is recent, RT distributions obtained from behavioral data have received a lot of attention in other areas. The related studies can help modeling neurophysiological data as well. In particular, the diffusion model (see Ratcliff (1978)) offers an appropriate framework to study simple two-choice decisions. It presupposes that decisions are made via a noisy process that accumulates information over time to one of two boundaries. The process terminates when a boundary is reached, which triggers a decision. Suppose there are two possible decisions  $a$  and  $b$  where  $a$  is the best response if the true state is  $A$  and  $b$  the best response if the state is  $B$ . The two possible boundaries are  $x$  and  $y$  and the following figure illustrates the model.

[INSERT FIGURE 5]

The rate of accumulation of information is the drift rate and it reflects the quality of the information contained in the stimulus. Accumulation is noisy and in particular processes with the same drift do not always reach a boundary at the same time—which produces RT distributions—and do not always reach the same boundaries—which generates errors. The decision model presupposes that RT is driven by three separate processes: an encoding process, a decision process, and a response output process. The sum of the times required by each is the total response time (see Ratcliff and McKoon (2008) for an illustration of the diffusion model using a random dot stimuli experiment on human subjects).<sup>30</sup>

This model is similar in spirit to a class of models proposed in neurophysiology to fit neural activity. In a pioneering work, Hanes and Schall (1996) designed an experiment

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<sup>29</sup>Ditterich et al. (2003), also show that quicker evidence are supported by stronger evidence. Besides, stimulated neurons cause the monkey to choose their preferred direction more often and more quickly. They also induce the monkey to choose the null direction more slowly.

<sup>30</sup>Ratcliff and McKoon (2008) showed that the model fits the behavioral data well and in particular error responses were slower than correct responses. The main difference compared to behavioral data obtained with monkeys is that RT distributions are right skewed with humans and symmetric with monkeys.

where eight targets were displayed visually to monkeys. Seven had the same color and monkeys had to detect the target with the different color by initiating a saccadic eye movement. The authors noted that the speed with which saccades were produced was variable. At the same time, neurons in the frontal eye field (an area responsible for voluntary eye movement) were found to be most active before a movement in their preferred direction. The authors showed that neurons rose to a peak firing rate very quickly and a decision process was initiated later on: neuronal firing rates continued to grow or dropped back to baseline. The authors proposed a model similar to the diffusion model to account for the behavioral and neurophysiological data.<sup>31</sup> This and further studies show that the diffusion process in the diffusion model accounts for neural activity (see Ratcliff and McKoon (2008) for details).

Other analyses examine to what extent the behavior of populations of neurons approximates diffusion processes (see Mazurek and Shadlen (2002)). Note last that a competing model, the ‘race’ model, is summarized by two neural integrators that correspond to the two alternatives and a choice is made when one of the integrators exceeds a threshold (see Luce (1986), Carpenter and Williams (1995), Shadlen and Newsome (2001)). For suitably chosen parameters, the race and diffusion models predict the same behavioral data (see Van Zandt et al. (2000) and Bogacz (2006) for details).

Gold and Shadlen (2001) propose a related model of neural computations in which information over time is accumulated into a single quantity: the logarithm of the likelihood ratio (LR) favouring one alternative over the other. As noted earlier (see Figure 1), the response of a sensory neuron (spike rate per second) is a random variable and the neural response varies as a function of the experimental conditions. Suppose the true state is  $A$  (resp.  $B$ ), the activity  $D$  can be summarized in the probability density function  $p(D|A)$  (resp.  $p(D|B)$ ) similar to the one obtained in Figure 1. In this experiment, the theoretical posterior belief that state  $S$  is the true state is

$$P(S|D) = \frac{P(D|S)P(S)}{P(D|A)P(A) + P(D|B)P(B)}$$

where  $P(A)$  and  $P(B)$  are prior beliefs. Interpreting the evidence in favor of  $A$  should result when  $P(A|D) > P(B|D)$ , that is when the likelihood ratio  $\frac{P(D|A)}{P(D|B)}$  is high enough,

$$\frac{P(D|A)}{P(D|B)} > \frac{P(B)}{P(A)} \tag{1}$$

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<sup>31</sup>The authors studied two specifications: a variable rate model and a variable threshold model. They also showed that regardless of the rate of increase in neuronal activity, the movement occurred roughly at the same time, providing support for a variable rate model. See also Schall and Thompson (1999) and Schall (2003) for further studies of the various stages (perception and response preparation) that contribute to reaction times.

Suppose now there are two neurons (or populations of neurons): the first detects signals in favor of  $A$  (and is more likely to fire if  $A$  is the true state), while the other detects signals in favor of  $B$  (and is more likely to fire if  $B$  is the true state). The response of the first is denoted by  $D_A$  and the response of the second is denoted by  $D_B$ . In that case the likelihood ratio is:

$$\frac{P(D_A, D_B|A)}{P(D_A, D_B|B)} = \frac{P(D_A|A)}{P(D_A|B)} \cdot \frac{P(D_B|A)}{P(D_B|B)}$$

taking the logarithm of the likelihood ratio linearizes the problem that can now be solved by taking simple additions. Gold and Shadlen (2001) conjectured that LIP neurons accumulate sensory responses from pools of neurons to form a decision variable that approximates log LR. It is sufficient to compare log LR to a threshold that triggers the action consistent with hypothesis  $A$  if log LR is above that threshold.

□ *Expected gains and values.* The studies reviewed before, and in particular those based on the random dot stimuli experiment, place the subject in a situation of uncertainty about the true state, and basically manipulate the correlation between the signal and the true state. Decision making is affected by other important parameters as well which are neglected here. In particular, decision theory conjectures that subjects make decisions by assessing the gain and the magnitude of the expected gains and losses. To test this hypothesis, Platt and Glimcher (1999) design an experiment in which information about the magnitude of a reward as well as the probability of the reward are displayed visually to rhesus monkeys. Subjects were then asked to choose an alternative and are rewarded accordingly. Single intraparietal neurons were recorded, as they are sensitive to the probability that a particular response will result in a gain. The authors show that rewards as well as the probability that a particular choice result in a reward modulate the activity of the neurons in the lateral intraparietal area. Moreover, when the subjects are free to choose between two responses, the expected gain influences both the choice and the activation of parietal neurons. In other words, probabilities and rewards are represented. Moreover, both activation and choice are compatible with expected payoff theory. According to this theory, the decision process can be represented by a standard maximization of expected payoff.<sup>32</sup> In a different but related vein, Padoa-Schioppa and Assad (2006,2008) studied the representation of economic value by analyzing the activity of neurons in the orbitofrontal cortex of the monkey. The authors found that those neurons encode the value of goods that are offered and chosen. Shortly after the offer, neurons encoding the value of one alternative or the other are active. Then, neurons encoding the value of the chosen alternative are active, independently of the characteristics of this alternative. Last and

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<sup>32</sup>See also Glimcher and Rustichini (2004) for a review of studies offering insights on how (and where) the desirability of options is represented.

after the choice is revealed, neurons encode the value of the chosen alternative.<sup>33</sup> Taken together, these studies show that the brain is able to represent both ‘objective’ rewards offered by the experimenters and ‘subjective’ values such as tastes. Overall payoffs and preferences are encoded.

□ *Decision criteria and efficient decision-making* . In the diffusion model for instance, there exists an evident trade-off between speed and accuracy. This trade-off is controlled by the distance between the boundaries  $x$  and  $y$ . Let  $y = 0$  (a convention), the higher  $x$ , the slower but more accurate the decisions. There is still uncertainty as to how subjects set decision criteria. It is believed that an important feature of criterion setting is related to the subject’s history of decision-making. Interestingly, there exist a correlation with aging. It is known that older adults are relatively slower than young adults in two-action discrimination tasks. Recent diffusion analysis models show that this is due to older adults’ conservativeness: they shift the criterion in order to avoid mistakes. Also, the quality of information on which older adults base their decisions (captured by the drift rate) is not significantly worse (see Ratcliff and McKoon (2008) for a review of these results). In particular, these findings show that the higher response times observed with older subjects are not due to a general slowdown of cognitive processes, a common earlier view.

A few studies investigated how decision criteria relate to efficient decision-making. Gold and Shadlen (2001) make an interesting proposal. As explained before, they hypothesize that LIP neurons form a decision variable that approximates log LR, and the best decision under hypothesis  $A$  (resp.  $B$ ) is triggered when log LR is above (resp. below) a decision threshold. They also explain that the threshold affect how the evidence is interpreted and as such can be responsible for poor or efficient decision-making. Suppose for instance that possible responses are rewarded in different ways, the threshold must make sure that the best rewards are obtained as often as possible. In other words, the threshold must be an indicator of the expected values of the possible responses.<sup>34</sup> Gold and Shadlen (2002) propose a diffusion model in which subjects choose  $x$  so as to maximize the reward obtained in the experiment. This gives rise to an optimal threshold mechanism (see Bogacz (2007) for a review) that accounts for behavioral data. Again, this optimization strategy affects endogenously the amount of information accumulated.

In the same spirit but with a different perspective, Brocas and Carrillo (2009) build an economic model of decision making that incorporates both uncertainty and rewards.

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<sup>33</sup>Moreover, the activity of a neuron in response to an alternative seems to be independent of the menu of alternatives that is offered.

<sup>34</sup>More formally, they propose that the left hand side of equation 1 should reflect not only prior probabilities but also accommodate reward values.

The model presupposes that evidence is produced (a stimulus  $s$ ) before a decision is made. Evidence is represented in a single variable  $D$  and the action consistent with hypothesis  $A$  is triggered if  $D$  exceeds a threshold. The authors explore the properties of the threshold that optimizes decision-making. The model is therefore close to the proposal made in Gold and Shadlen (2001). The authors derive a series of results in a non parametric framework (the model requires only the monotone likelihood ratio property to hold) and extend them to complex scenarios with many hypotheses  $S$  and many possible decisions. The results obtained are consistent with typical ‘biases’ observed in Social Psychology. In particular, if decisions are rendered according to a decision-threshold mechanism as described in the neurobiology literature, decision makers should exhibit some forms of confirmatory biases and hold ex-post beliefs correlated with the rewards associated with their decisions. Interestingly, the analysis suggests that in a ‘sequential stimulation setting’, the order in which evidence is produced affect decisions. It also points to the relationship between age and conservativeness (the confirmatory bias reinforces over time).

## 6 Conclusion

While the overlap between the paradigms in Economics and Neuroscience in general and Neurophysiology in particular have already been noted<sup>35</sup>, an open debate is still to determine how exactly can each field contribute to the understanding of the other. This article aims at providing a few reasons why Economists should pay attention to findings obtained in the Brain Sciences. We know from a large body of research that humans (e.g. from the Social Psychology and Experimental Economic literatures) and animals (e.g. from the Behavioral Ecology literature) often make decisions in ways that are efficient.<sup>36</sup> However, and rather systematically, decision-makers behave in a way that is not consistent with the previous view. The causes of departures are still unknown. We believe that a better understanding of brain functions and processes should help shedding light on systematic anomalies.

From the perspective of Economics, we can derive two strong messages from the evidence reviewed here. The first one is that economic decision making paradigms are roughly consistent with brain functioning. Neuronal processes both interpret and aggregate interpreted information to obtain a simple representation of the evidence. Moreover, neurons are able to make Bayesian inferences and represent the likelihood that a given hypothesis

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<sup>35</sup>See for instance Glimcher et al. (2005).

<sup>36</sup>Behavioral ecologists favor the hypothesis that evolution pushes animals toward efficient decision-making. They build models based on economic theory to account for the computations that animals perform. See Glimcher (2002).

(and related behavioral response) is correct. And besides, neurons are also capable of representing prior beliefs as well as expected payoffs. All these features are consistent with the standard paradigm in Economics: both ‘expected utility-like’ theory and ‘Bayesian-like’ information acquisition theory are relevant hypotheses.

Nevertheless, the standard paradigm in Economics takes for granted a large number of features that may distort our understanding of decision-making. Indeed, some important ‘details’ may cause differences between the predictions of these theories and observed choices.

Importantly, the brain accumulates information until there is enough information supporting a behavioral response. This means it uses an economical process in which the information just necessary to make a decision is taken into account. In other words, some information contained in the signal  $s$  but also in  $D$  is filtered out. The decision system operates as if it collects recommendations from various entities (neurons in the sensory systems) and aggregates this information before mapping it into a decision. We know from the Social Choice literature that any aggregation rule has a preferred direction and ultimately favors some features. Therefore, the aggregation of information throughout layers of populations of neurons will yield distortions of the signal, as some features will be emphasized and others de-emphasized or filtered out. The direction of the distortion will depend on the specific rule which simply reflects the objective of the decision-system. The combination of these features is the source of several biases in Brocas and Carrillo (2009). In particular, the paper shows that posterior beliefs do not capture all the information that is sent to the decision-maker, who may appear biased or non-Bayesian to an outside observer. The paper explains why this occurs and classifies bias directions as a function of the environment.

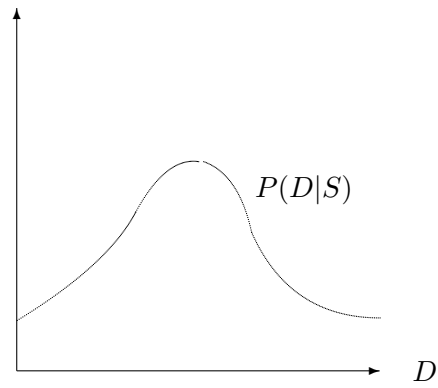
Brocas and Carrillo (2009) also shows that posterior beliefs are correlated with payoffs. Typically, an individual most afraid of the outcome in a particular state will tend to interpret any information as an instance of this state. He will therefore avoid making decisions that can possibly lead to that outcome. This simply suggests that at the time of deciding, the decision-maker applies probabilities that are functions of the outcomes. Therefore, the underlying utility representation resembles a rank-dependent utility or a security-potential/aspiration utility. This suggests that studying brain processes may help determining which alternative to expected utility fits best human behavior. Besides, if probabilities are shaped by payoffs, and eventual decisions hinge on the safe side, an individual might seem to have different degrees of risk aversion in different situations. For instance, if an individual is most afraid of the damages of an earthquake, he might decide to buy a very expensive insurance. If at the same time, he does not care as much about his

health, he might contract only a minimal health insurance. These decisions are internally consistent but might appear in contradiction to an outside observer.

Other features reviewed here may be the source of other anomalies. For instance, given neuronal variability, the notions of ‘complete information’, ‘perfect signal’ or even ‘objective probabilities’ might not be pertinent in the brain. Basically, the brain is typically ignorant or uninformed before a signal is sent and it decodes the signal through variable processes. This may account for framing effects in situations where information is presumably disclosed or verifiable.

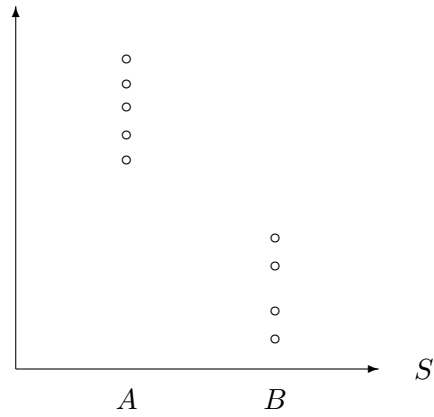
Last, from a normative perspective, it is useful to decompose the ingredients of a decision problem into utilities and probabilities. However, it is important to keep in mind that both concepts are represented in a similar way in the brain. Being offered a lottery, announced a weather forecast or showed a cookie triggers an informational process: neurons detect the characteristics of the item offered, fire in a probabilistic manner, pass the information along, part of the information is de-emphasized, this information is aggregated and processed to obtain a response, last the response is implemented. Actual decision making results from this underlying informational process. Understanding this mapping should shed light in a meaningful way on decision theoretic paradigms. Concretely, we may want to think about new theories in which brain processes are the primitives (or axioms) to derive utility representations. The constant effort to collect evidence should allow to build such new theories in the future.

Probability



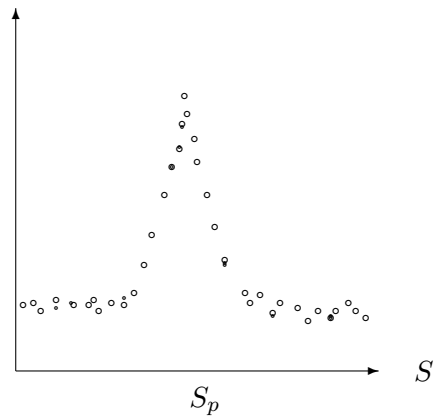
**Figure 1:**  $D$  represents the spike rate when the stimulus  $s$  signals the true state  $S$  (true direction) and the curve plots the likelihood of obtaining response  $D$ .

spike counts



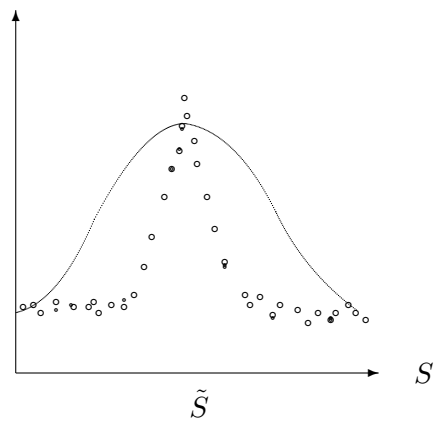
**Figure 2a:** Each dot represents the number of spikes obtained for a neuron with preferred direction  $A$  in a trial where the true direction is  $S$ . Values are recorded for all trials.

spike counts



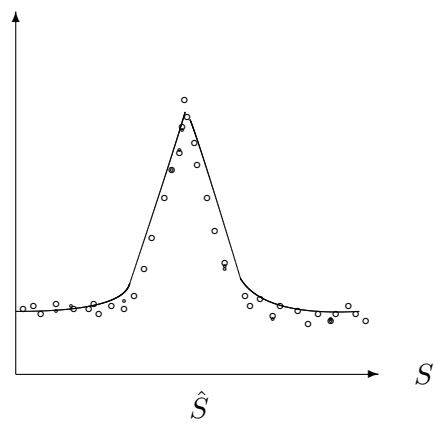
**Figure 2b:** Similar illustration with more than two states. The preferred direction of the neuron is  $S_p$

spike counts

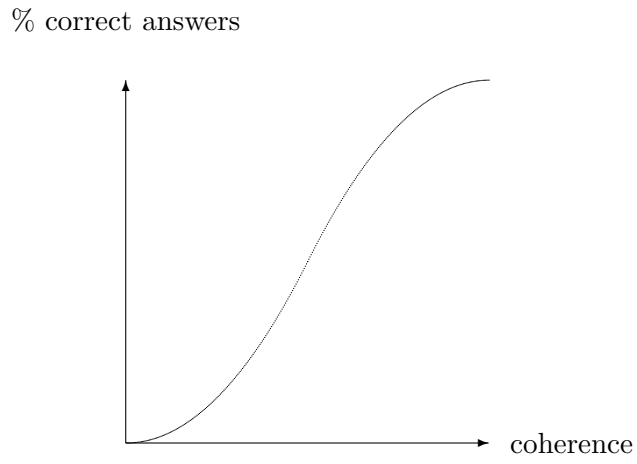


**Figure 3a:** Population vector estimator

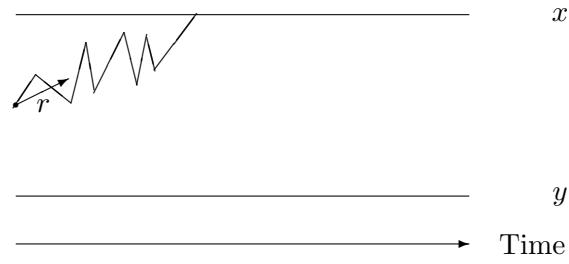
spike counts



**Figure 3b:** Maximum likelihood estimator ( $\hat{S}$  and  $\tilde{S}$  may not coincide)



**Figure 4:** Psychometric function.



**Figure 5:** Evidence is accumulated through time ( $r$  is the drift) until hitting the boundary  $x$  triggering  $a$  or the boundary  $y$  triggering  $b$ .

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