



How mechanisms of perceptual decision-making affect the psychometric function[☆]

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ABSTRACT

Psychometric functions are often interpreted in the context of Signal Detection Theory, which emphasizes a distinction between sensory processing and non-sensory decision rules in the brain. This framework has helped to relate perceptual sensitivity to the “neurometric” sensitivity of sensory-driven neural activity. However, perceptual sensitivity, as interpreted via Signal Detection Theory, is based on not just how the brain represents relevant sensory information, but also how that information is read out to form the decision variable to which the decision rule is applied. Here we discuss recent advances in our understanding of this readout process and describe its effects on the psychometric function. In particular, we show that particular aspects of the readout process can have specific, identifiable effects on the threshold, slope, upper asymptote, time dependence, and choice dependence of psychometric functions. To illustrate these points, we emphasize studies of perceptual learning that have identified changes in the readout process that can lead to changes in these aspects of the psychometric function. We also discuss methods that have been used to distinguish contributions of the sensory representation versus its readout to psychophysical performance.

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Abbreviations: FEF, frontal eye field; LIP, lateral intraparietal area; MT, middle temporal area; ROC, receiver–operator characteristic; RT, response time; 2AFC, two-alternative forced-choice.

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1. Introduction

Psychometric functions quantify the relationship between perceptual performance and physical properties of the stimulus (Klein, 2001). These functions are often not merely descriptive but also can be used to help infer the underlying computational processes implemented in the brain. For example, psychometric

functions based on principles of Signal Detection Theory helped to discredit the idea of a sensory threshold that must be exceeded for a stimulus to have any effect on the observer. These functions instead emphasize the usefulness of distinguishing continuously variable sensory processing and a non-sensory decision rule (Green & Swets, 1966; Macmillan & Creelman, 2004). This distinction, and the underlying assumptions about distributions of signal and noise in the brain, have been central to studies relating psychophysical performance to “neurometric” analysis of neural data from single-unit recordings in monkeys and electroencephalography (EEG) and functional magnetic imaging (fMRI) in humans (Britten et al., 1992; Cohen & Newsome, 2009; Cook & Maunsell, 2002; Gerdjikov et al., 2010; Lee et al., 1995; Luna et al., 2005; Mountcastle et al., 1990; Philiastides & Sajda, 2006; Stüttgen & Schwarz, 2008; Tolhurst et al., 1983; Uka & DeAngelis, 2003; Vogels & Orban, 1990; Wutte et al., 2011).

However, these kinds of psychometric and neurometric analyses can paint an incomplete picture of sensory processing in the brain (Shadlen et al., 1996; Stüttgen et al., 2011). Consider, for example, a well-known study that recorded from motion-sensitive neurons in the middle temporal area (MT) of extrastriate visual cortex of monkeys performing a visual motion direction-discrimination task and found closely matching values of psychometric and neurometric sensitivity (Britten et al., 1992). These neurometric functions were computed from spike counts measured from individual MT neurons during a fixed-duration motion-viewing period, using the area under the receiver–operator characteristic (“ROC”) curve to quantify how well stimulus motion could be distinguished based on the neural responses alone (Green & Swets, 1966). Critically, this analysis is based on not only the measured responses of the given neuron, but also the assumption that those responses are read out in a particular way to form the perceptual decision: as a difference between the responses of the given neuron and of its complementary “anti-neuron”. However, the real decision process in the brain involves many more neurons, different temporal dynamics, and possibly more complex readout schemes (Cohen & Newsome, 2009; Geisler & Albrecht, 1997; Pouget et al., 2003; Seung & Sompolinsky, 1993). Thus, any effective model of perceptual performance must account for both the relevant sensory representation and how that representation is read out and combined with goals, task rules, and other cognitive factors to form the perceptual decision that instructs the behavioral response.

The idea that readout plays a key role in perceptual performance has been underscored in recent years in the field of perceptual learning. Perceptual learning describes long-lasting, training-induced improvements in perceptual sensitivity (Gold & Watanabe, 2010). These improvements can reflect a diversity of underlying neural mechanisms (Ahissar et al., 2009; Ghose, 2004; Gilbert et al., 2001; Petrov et al., 2011). For some tasks, improvements in performance correspond to changes in the response properties of neurons in early sensory areas, such as primary visual, auditory, or somatosensory cortex (Maertens & Pollmann, 2005; Recanzone et al., 1992a, 1993; Schoups et al., 2001; Schwartz et al., 2002; Yotsumoto et al., 2009, 2008). However, for other tasks, perceptual learning is accompanied by little or no changes in these early sensory areas (Ghose et al., 2002; Law and Gold, 2008). Instead, the key neural changes are thought to occur at later stages of processing, particularly those involved in using information from the sensory representation to form the perceptual decision (Doshier and Lu, 1998, 1999; Jacobs, 2009; Law and Gold, 2008; Mollon and Danilova, 1996; Petrov et al., 2005). Thus, perceptual sensitivity can be shaped by mechanisms of readout, even when the sensory representation is stable.

The goal of this article is to review how recent advances in our understanding of decision mechanisms in the brain have helped to

clarify their specific roles in perceptual performance, as quantified via the psychometric function. We focus, in part, on studies of changes in decision processes related to perceptual learning, because those studies have helped to elucidate how those processes relate to perceptual performance. However, we emphasize that the relationship between decision processing and performance is not specific to perceptual learning but rather must always be considered when attempting to interpret psychophysical data in terms of the underlying brain mechanisms. To illustrate these points, we first describe the readout process that is central to forming perceptual decisions, then describe the psychometric function and show that many of its commonly measured features depend critically on the nature of this readout process, and finally discuss methods for distinguishing contributions of representation and readout on psychophysical performance.

2. Background

2.1. Representation versus readout

Perceptual decisions involve the detection, discrimination, or identification of sensory stimuli. These decisions require several stages of complex processing in the brain between the extraction of relevant sensory information by receptors in the periphery to generation of the appropriate motor response to indicate the decision. Here we consider two important stages that can be distinguished based on their computational roles and neural implementations (Fig. 1) (Gold & Shadlen, 2007; Schneidman et al., 2003). The first is the representation, or “encoding,” of the extracted sensory information in the brain. The second is the readout, or “decoding,” of the encoded representation to form a decision variable that, when applied to a decision rule, determines the final choice (Graham, 1989).

The sensory representation consists of neurons whose activity is modulated by relevant features of the sensory stimulus. This activity is driven by the sensory input and is typically not strongly modulated by the task design and other cognitive variables, although top-down processes can have effects even on sensory representations in thalamus and primary sensory cortex (Bender and Youakim, 2001; Lima et al., 2011; Mehta et al., 2000; Saalman and Kastner, 2011). These neurons have been identified based on tuning properties that are appropriate for distinguishing between the alternatives under consideration, weak correlations between their activity and choice behavior (indicating a possible contribution to the decision variable but not the decision variable itself), and manipulations including microstimulation and inactivation that have a causal influence on perceptual performance (Parker and Newsome, 1998).

In contrast, readout reflects how information in the sensory representation is interpreted to form the decision variable that guides behavior. This process was first considered in detail in the context of peripheral nerves but soon was applied to stimulus-tuned neurons in the central nervous system (Britten et al., 1992; Hawken and Parker, 1990; Johnson, 1980; Johnson et al., 1973, 1979). In general, readout involves selecting relevant sensory signals, weighing their relative contributions to the decision process, and combining the weighed signals to form the decision variable. This goal-directed process, which is probably under the guidance of top-down control mechanisms, can take into account stimulus selectivity, response variability and other properties of the sensory representation to form a decision variable that maximizes the discriminability of the alternatives under consideration for the particular perceptual task (Chen et al., 2006, 2008; Geisler and Albrecht, 1997; Pouget et al., 2003; Scolari and Serences, 2010; Seung and Sompolinsky, 1993; Shadlen et al., 1996; Tanji and Hoshi, 2008).

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