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Perceptual learning: Top to bottom

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ABSTRACT

Perceptual learning has traditionally been portrayed as a bottom-up phenomenon that improves encoding or decoding of the trained stimulus. Cognitive skills such as attention and memory are thought to drive, guide and modulate learning but are, with notable exceptions, not generally considered to undergo changes themselves as a result of training with simple perceptual tasks. Moreover, shifts in threshold are interpreted as shifts in perceptual sensitivity, with no consideration for non-sensory factors (such as response bias) that may contribute to these changes. Accumulating evidence from our own research and others shows that perceptual learning is a conglomeration of effects, with training-induced changes ranging from the lowest (noise reduction in the phase locking of auditory signals) to the highest (working memory capacity) level of processing, and includes contributions from non-sensory factors that affect decision making even on a "simple" auditory task such as frequency discrimination. We discuss our emerging view of learning as a process that increases the signal-to-noise ratio associated with perceptual tasks by tackling noise sources and inefficiencies that cause performance bottlenecks, and present some implications for training populations other than young, smart, attentive and highly-motivated college students.

1. Introduction

The brain is a noisy machine. Single-neuron, as well as neural-network dynamics are subject to both deterministic and random noise originating from processes that span the range from the molecular to the systemic (review in Faisal, Selen, & Wolpert, 2008). The concept of internal noise is fundamental to our understanding of how the brain encodes sensory stimuli, processes them and makes behaviorally relevant decisions about them. Signal detection theory (Green & Swets, 1966; Macmillan & Creelman, 2005) describes perceptual decision making in terms of the relationship between noisy decision variables (derived from noisy internal representations of the stimulus) and a subjective decision criterion. Internal noise therefore limits the accuracy of perceptual decisions and consequently of any behavioral task performance.

Dosher and Lu (2005) first suggested that perceptual learning is "learning the limiting process": inducing changes in those processes that act as bottlenecks to performance. These changes can manifest as an increase in the signal-to-noise ratio (SNR) due to signal enhancement (Gold, Bennett, & Sekuler, 1999; Gold, Sekuler, & Bennett, 2004; Hurlbert, 2000; Wright, 1996) and/or internal noise reduction (Dosher & Lu, 1998, 2005; Jones et al., 2013; Lu & Dosher, 2008), but they can also reflect changes in non-random inefficiencies such as response bias.

In this paper we expand the idea of perceptual learning as reducing the internal noise and inefficiencies responsible for processing bottlenecks. Models based on signal detection theory do not conceive of internal noise as being of specifically sensory origin or limited to the ascending neuronal pathways or networks associated with early sensory encoding. Physiological maskers such as breathing, heartbeats and blood flow (Shaw & Piercy, 1962; Soderquist & Lindsey, 1971), as well as fluctuations in attention, motivation, memory, or other factors related to the decision process may all limit decision accuracy. Even fluctuations of unknown origin in resting state activity may modulate variations at various stages of perceptual processing (Fox et al., 2007, 2006).

The source of the performance-limiting noise depends on what is being trained and what differs between tasks. Learning can thus be a high- or a low-level phenomenon, depending on the level at which the noise originates. What is learned in a given task may depend on the specific training conditions, as performance bottlenecks may be defined by task- as well as stimulus-related

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variables, among others. Moreover, we suggest that learning transfers to untrained tasks if and when both training and transfer task are subject to the same performance-limiting noise sources (see also McGovern, Webb, & Peirce, 2012). Conversely, different limiting processes affecting the trained and transfer tasks will result in specificity (i.e. non-transfer).

This paper presents evidence from our own work in the auditory domain as well as from previous work in the visual domain in support of this hypothesis. Using simple acoustic stimuli and varying task and stimulus parameters, we show that perceptual learning involves changes in internal noise sources and inefficiencies at multiple processing levels along the decision-making pathway.

2. Perceptual learning: bottom-to-top

We use a perceptual decision model (Fig. 1) adapted from Pelli (1991) and Dosher and Lu (1998, 1999) to illustrate the levels at which internal noise may limit processing. For simplicity, we separate internal noise into processes that directly impact on sensory processing and affect the internal representations of input stimuli (hence 'sensory' internal noise, Fig. 1A), later processes that affect the formation of the decision variable (Fig. 1B) and most likely originate in higher-level, cognitive processes (e.g., comparison mechanisms relying on working memory), and other sources of inefficiency affecting the decision-making process such as response bias or inattention (Fig. 1C). We are only concerned with noise intrinsic to the observer (or listener); learning in the presence of external noise has been discussed extensively elsewhere (e.g., Dosher & Lu, 2005; Vaina, Sundareswaran, & Harris, 1995), and is outside the scope of this paper.

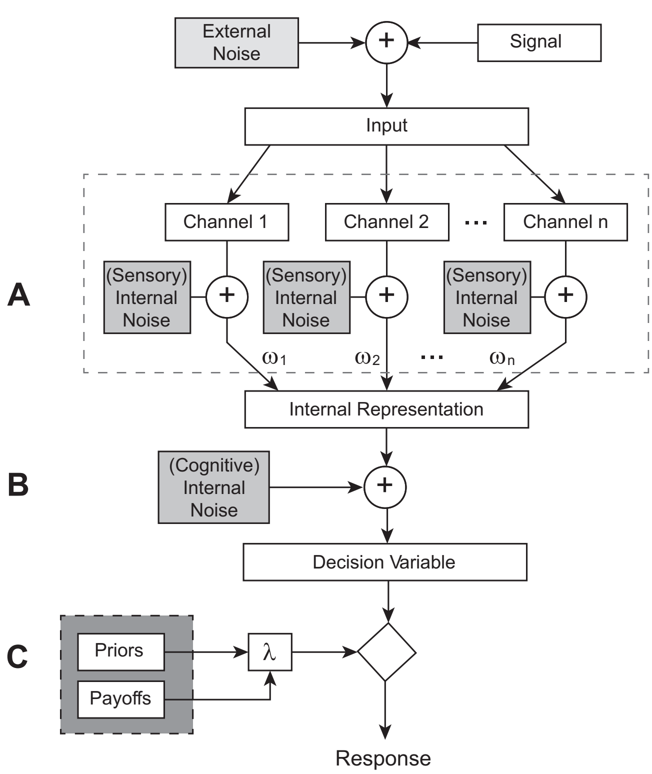

Fig. 1. A schematic perceptual decision model. The input to the system is a combination of the signal and external noise. This input is transformed into an internal representation by summing over the weighted outputs of n independent information channels, which are subject to internal noise (multiplicative, additive, or both; (A). Note that the label 'sensory' here does not refer to the source of the noise but rather to the type of processing affected by it. In forming the decision variable the internal representation may be further affected by late internal noise (B), which is generally of cognitive origin. To make a decision the observer compares the decision variable to a criterion, λ, which may or may not be ideally placed, e.g. due to bias (C). Other sources of internal noise, such as physiological noise (e.g. heartbeat, breathing) or inattention are not explicitly included in this model.

Computational models have been used to gain insight into the underlying mechanisms of learning and transfer. Although internal noise is integral to these models (Sperling, 1989), they are rarely concerned with the source of that noise, only its effect on decision making (c.f. Lu & Dosher, 2009). In this paper we focus on how noise of various origins can place limitations on sensory and cognitive processes and how it is affected by training, rather than its computational implementation. In separating noise sources into 'sensory' and 'cognitive', we follow in the footsteps of other authors (e.g., Durlach & Braida, 1969; Oxenham & Buus, 2000; Shinn-Cunningham, 2000), though we use these labels to refer to the processes affected rather than the specific sources or origins of noise. Thus, early 'sensory' noise can result from modulation by higher-level, cognitive processes. We provide evidence here that training can affect internal noise and sources of inefficiency throughout the processing hierarchy.

2.1. Noise affecting sensory representations or their readout

We define sensory noise as variability associated with the early sensory processing leading to the formation of the internal representation of the stimulus (Fig. 1A). Sensory internal noise can be intrinsic to the physiological processes along the ascending processing pathways. In the auditory domain its sources include (but are not exclusive to) non-deterministic transduction (e.g., due to Brownian motion of cochlear hair cells; Denk, Webb, & Hudspeth, 1989), and stochastic neural encoding and transmission both in the auditory periphery (Javel & Viemeister, 2000) and more centrally (e.g., Vogels, Spileers, & Orban, 1989). Moreover, top-down processes modulate auditory sensory processes as far down the neural hierarchy as the sensory epithelium and even affect middle-ear muscle activity (e.g., Maslin et al., 2013; Munro, Walker, & Purdy, 2007), and these too may contribute noise to sensory processes (see Amitay, 2009 for a discussion of the interaction between top-down and bottom-up processing in auditory learning).

How the channels described in the model (Fig. 1A) are conceived depends on the task and the level of analysis. For example, in a yes/no detection task each channel may be a frequency-tuned filter, in which case the internal representation corresponds to activity summed across spectral regions. The internal noise associated with individual channels is of sensory origin. Alternatively, each channel may represent temporal bins, such as observation intervals in a multi-interval forced-choice task. However the channels are defined, each weight, ω, indicates the relative degree to which the corresponding channel informs the decision process. As such, $|\omega|$ may be a metric of the amount of relevant information in the individual channels (bottom up) present in each presentation interval (or spectral region) or how much attention the listener pays to that interval or aspect of the physical input. Attentional fluctuations (Faisal, Selen, & Wolpert, 2008) or variations in resting state activity (e.g., Fox et al., 2007), may differentially affect sensory processing in individual information channels.

Internal noise affects sensory processing at very early stages. We have recently demonstrated (Amitay et al., 2013) that variations in the internal representation of identical input stimuli (1-kHz tones) can drive the decision process in an odd-one-out task (Fig. 2A). We showed that electrophysiological activity variations, observed as early as 100 ms after stimulus onset and associated with sensory encoding (N1–P2 complex), can predict the perceptual decision (Fig. 2B). These variations may have reflected noise of sensory origin or random fluctuations in attention during the