Chapter 1

Introduction

1.1   Sensory predictions and temporal integration

The brain is often framed as a general purpose "prediction machine" (Hawkins & Blakeslee, 2004; Clark, 2013). In this framework, the sole evolved function of the neocortex is to minimize error in its representation of predictions about the physical world. This distillation of function is central to a number of models of neocortical function (e.g., Dayan, Hinton, Neal, & Zemel, 1995; Rao & Ballard, 1999; Lee & Mumford, 2003; Friston, 2005; George & Hawkins, 2009), but is surprisingly often overlooked in psychology and neuroscience investigations of sensory processing. For example, most experiments are designed to measure evoked responses to a randomly chosen, isolated stimulus under the tacit assumption that response variability is irrelevant noise that should be averaged out across many presentations. Computational models of perceptual processing often operate under similar assumptions in which stimuli are presented as random "snapshots" from which some common set of features should be learned to minimize representational variability across presentations (e.g., Riesenhuber & Poggio, 1999; Serre, Oliva, & Poggio, 2007; O'Reilly, Wyatte, Herd, Mingus, & Jilk, 2013; although see Foldiak, 1991, for a notable exception). These

experimental and modeling assumptions stand in contrast to the event structure of the physical world, which is highly structured from one moment to the next. It could be the case that response variability is not simply due to noise, but is related to meaningful predictive processing that captures this temporal structure (Arieli, Sterkin, Grinvald, & Aertsen, 1996; Wilder, Jones, Ahmed, Curran, & Mozer, 2013; Fischer & Whitney, 2014).

There are a number of important questions that need answered to fully characterize prediction and its role in sensory processing. What are the mechanisms responsible for making predictions? Computationally, there is a fundamental tradeoff in making decisions about and generating actions from the constant stream sensory information versus actively generating predictions about what will happen next. Do standard mechanisms balance these tradeoffs or is there special purpose, dissociable machinery specifically for predictive processing. Another line of questioning is concerned with how the brain knows *when* to make predictions. Prediction requires integrating information over some time frame and using the result to drive the actual prediction, but when should integration start? And for how long?

The goal of this thesis is to develop a line of research designed to provide answers to some of these questions and of course, to raise others. The work is largely predicated on a modeling framework referred to as LeabraTI (Temporal Integration), an extension of the standard Leabra cortical learning algorithm (O'Reilly & Munakata, 2000; O'Reilly, Munakata, Frank, Hazy, & Contributors, 2012) that describes how prediction is accomplished in biological neural circuits. The framework brings together a large number of independent findings from the systems neuroscience literature to describe exactly how multiple interacting mechanisms trade off prediction with sensory processing and learn associations across temporally extended sequences of input.

TODO: Figure out if there is anything left to say here – probably alpha since it will come up in next section.

1.2   Modulations of sensory processing related to prediction

Somewhat surprisingly, the extant literature makes little mention of predictability during sensory processing. Part of the reason for this is that stimulus predictability and attentional cues are often treated as equivalent in experiments (Summerfield & Egner, 2009; Kok, Rahnev, Jehee, Lau, & de Lange, 2012) with the latter being the construct that has gained greater traction in the literature. These issues will be discussed in detail in Chapter **??**, but for the purposes of establishing context for the overall current work, the literature on the attentional effects during sensory processing is briefly reviewed here with parallels drawn to sensory prediction where appropriate.

Attention can be characterized as spatial as well as temporal in nature. Spatial attention is characterized by enhanced processing of particular regions of visual space (e.g., the left side of space) or for specific features (e.g., horizontal edges). The computations provided by spatial attention and its implementation in the brain in terms of gain control circuits are relatively well-characterized and have gained widespread acceptance throughout the literature (see Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004, for comprehensive reviews). The temporal properties of attention, in contrast, are less well-understood. Attention has been shown known to fluctuate endogenously at a rate of approximately 10 times per second such that a weak stimulus presented at one moment in time might have a high enough signal-to-noise ratio to be perceived but not when presented 50 ms earlier or later (VanRullen, Busch, Drewes, & Dubois, 2011).

Experiments by Nobre and colleagues have attempted to tease apart the ability to orient attention spatially and temporally. Their experiments employ a stimulus that can be tracked independently in space and time, such as a ball that blinks across a display in a fixed or random trajectory with either a constant or irregular appearance interval (Doherty, Rao, Mesulam, & Nobre, 2005; Rohenkohl & Nobre, 2011). If the ball moves in a fixed trajectory, the next spatial location can be anticipated at any point in the sequence given the previous locations and attention can be allocated there to enhance processing relative to when the next spatial location is unknown. Importantly, attention can be allocated to the ball's next spatial location even when the temporal onset of the next

appearance is unknown. Similarly, if the ball appears and disappears with a constant interval, the onset of the next appearance can be anticipated, despite the next spatial location being unknown. Doherty et al. (2005) found that amplitude of the P1 EEG response was enhanced when spatial attention could be successfully allocated at the ball's next location, consistent with previous descriptions of the effects of attention on EEG responses (Luck, Heinze, Mangun, & Hillyard, 1990). Being able to anticipate the temporal onset of the ball did not modulate the amplitude of the P1 response by itself, but further potentiated the enhancement of spatial attention on the P1 when both the spatial location and temporal onset of the ball could be anticipated.

1.3   Organization of the thesis

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