

**BEHAVIORAL AND COMPUTATIONAL  
INVESTIGATION OF THE EFFECT OF PRIOR  
KNOWLEDGE ON VISUAL PERCEPTION**

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BEHAVIORAL AND COMPUTATIONAL INVESTIGATION OF  
THE EFFECT OF PRIOR KNOWLEDGE ON VISUAL PERCEPTION

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January 2021

We certify that we have read this dissertation and that in our opinion it is fully adequate, in scope and in quality, as a dissertation for the degree of Doctor of Philosophy.

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# ABSTRACT

## BEHAVIORAL AND COMPUTATIONAL INVESTIGATION OF THE EFFECT OF PRIOR KNOWLEDGE ON VISUAL PERCEPTION

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Visual perception results from the dynamic interaction of bottom-up and top-down processes. Top-down prior knowledge and expectations can guide us to predict upcoming events and even determine what we see in an ambiguous or noisy sensory stimulus. Despite the well-established facilitating effects of expectations on recognition or decision-making, whether and how early sensory processes are affected by expectations remain unclear. This dissertation attempts to investigate the effect of expectations on early visual processes. To this end, we used behavioral experiments to examine the effects of expectation on visual perception at the threshold level and implemented a recursive Bayesian model and a recurrent cortical model to unravel the computational mechanisms underlying those effects. In the behavioral experiments, we systematically manipulated expectation's validity in separate sessions and measured duration thresholds, which is the shortest presentation time sufficient to achieve a certain success level. Our behavioral findings showed that valid expectations do not reduce the thresholds, rather unmet expectations lead them to increase. Next, using a recursive Bayesian updating scheme, we modeled the empirical data obtained in the behavioral experiments. Model fitting showed that higher thresholds observed in the unmet expectations are not due to a change in the internal parameters of the system. Instead, additional computations are required by the system to complete the sensory process. Finally, within the predictive processing framework, we implemented a recurrent cortical model to explain the behavioral findings and discuss possible neural mechanisms underlying the observed effects. The cortical model findings were in agreement with the Bayesian model results, revealing that longer processing is needed when expectations are not met. Overall, the computational models that are proposed in this study provide a parsimonious explanation for the observed behavioral effects. The proposed experimental paradigm and the computational models offer a novel framework that can be extended and used in

other stimuli, tasks, and sensory modalities.

*Keywords:* visual perception, perceptual inference, expectation, prior knowledge, predictive processing, computational modeling, Bayesian model, cortical model.

## ÖZET

# ÖN BİLGİNİN GÖRSEL ALGI ÜZERİNDEKİ ETKİSİNİN DAVRANIŞSAL VE HESAPLAMALI MODELLERLE İNCELENMESİ

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Görsel algı, aşağıdan yukarıya ve yukarıdan aşağıya işlenen bilginin dinamik bir etkileşimi ile gerçekleşir. Ön bilgi ve beklentiler, yaklaşan olayların tahmin edilmesi ve hatta belirsiz veya gürültülü bir duyuşsal uyaranda ne görüldüğünün belirlenmesi için rehberlik edebilir. Beklentilerin, tanıma veya karar verme süreçleri üzerindeki iyi bilinen kolaylaştırıcı etkilerine rağmen, erken duyuşsal süreçlerin beklentilerden etkilenip etkilenmediği ve nasıl etkilendiği belirsizliğini korumaktadır. Bu tez, beklentilerin erken görsel süreçler üzerindeki etkisini araştırmaktadır. Bu amaçla, beklentinin görsel algı üzerinde eşik seviyesindeki etkilerini incelemek için davranışsal deneyler yapılmış ve bu etkilerin altında yatan hesaplamalı mekanizmaları ortaya çıkarmak için yinelemeli bir Bayes modeli ve kortikal bir model kullanılmıştır. Davranışsal deneylerde, beklentinin geçerliliği ayrı oturmaumlarda sistematik olarak değiştirilmiş ve belirli bir başarı düzeyine ulaşmak için gereken en kısa sunum süresi olan süre eşikleri ölçülmüştür. Davranışsal bulgular, karşılanan beklentilerin süre eşiklerini azaltmadığını, karşılanmayan beklentilerin süre eşiklerini artırdığını göstermiştir. Daha sonra, yinelemeli bir Bayes modeli kullanılarak, davranışsal deneylerde elde edilen deneysel veriler modellenmiştir. Modelleme sonuçları, karşılanmayan beklentilerde gözlemlenen eşik süresindeki artışın, sistemin iç parametrelerindeki bir değişiklikten kaynaklanmadığını göstermiştir. Bunun yerine, duyuşsal sürecin tamamlanması için sistem tarafından ek hesaplamalar gerekmektedir. Son olarak, tahmine dayalı işleme çerçevesinde, davranışsal bulguların açıklanması ve gözlenen etkilerin altında yatan olası nöral mekanizmalarının tartışılması amacıyla kortikal bir model kullanılmıştır. Kortikal model bulguları, Bayes modeli sonuçlarıyla uyumlu olarak, beklentiler karşılanmadığında daha uzun bir işlemenin gerekli olduğunu ortaya koymuştur. Genel olarak, bu çalışmada önerilen hesaplamalı modeller, gözlemlenen davranışsal etkileri açıklayabilmektedir. Önerilen deneysel tasarım ve hesaplamalı modeller

geliştirilmeye açıktır ve farklı uyarılar, görevler ve duyuşal modalitelerde de uygulanabilir.

*Anahtar sözcükler:* görsel algı, algısal çıkarım, beklenti, ön bilgi, tahmine dayalı süreçler, hesaplamalı modelleme, Bayes modeli, kortikal model.

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# Chapter 1

## Introduction

Our sensory experiences in the world are not only guided by our own actions. We are usually surrounded by a complex, rich and dynamic environment where our visual experiences also cannot stay intact. Imagine that you are walking around Taksim Square in Istanbul. It may not be easy to find the tube station you want to walk. As the street is too crowded, it is almost impossible to process all sensory information around us, e.g. lots of tourists walking on the street for shopping, sounds of street musicians and demonstrators for entertainment, signboards and their lights, and so on. As our visual system cannot process all sensory information at once in detail, it searches for possible places that the sign of the tube station can be placed. In other words, our visual system uses *prior knowledge* to predict the most probable place among several other alternatives so that the efficacy of the process culminates.

### **1.1 Expectation and attention: involvement of higher-level mechanisms in visual perception**

As already stated in a dynamic and contextually rich environment the visual system cannot process all sensory information at the same level. For this reason,

it is suggested that high-level mechanisms in the brain are involved in information processing to make the process faster and more efficient. Attention is one of the well-known high level mechanisms which is comprehensively studied in the literature. Several studies suggested that while physical properties of a sensory input is being processed, the attention mechanism is involved in the process, allowing the selection of the *relevant* properties in the environment to the stimulus to be perceived [4]. For instance, if we are searching for a red mug in a room, we specifically look for *red* objects in the environment, which is the relevant feature (i.e. color) of the object. Through this, we do not have to search for every single item in the room. Thus, this mechanism leads the process to become faster, and detection of the stimulus becomes easier.

In more recent literature, however, it has been suggested that in addition to the attention mechanism, top-down information about prior knowledge and expectations also help in the processing of the sensory input [4]. Prior knowledge and expectations are suggested to help the system to resolve ambiguous input coming from the environment. Figure 1.1 shows a great example of the effect of prior knowledge on visual perception. When one is shown the image in Figure 1.1, it is usually hard to find a meaning in it at first sight. However, when it is told that there is a Dalmatian dog sniffing the ground, it becomes very easy to detect the dog from pebbles. Because prior knowledge is provided about the image, the dog can be detected in a short time. Other examples can be given from the effect of context-based prior knowledge on perception [4, 6]. For instance, we are faster in detecting a lamp in a bedroom (a usual context) than detecting a lamp on a beach (an unusual context) [4, 6]. Or when we want to find a painting in a room, we usually do not check every single place inside the room. Instead, we look at the locations where the painting is more likely to be placed, i.e. the wall. Thus, context-based prior knowledge about the objects leads expectations, which in turn make individuals become faster in detecting the objects.

The two top-down effects, expectation and attention, were previously not examined separately in detail because they show similar behavioral effects. Specifically, both attended and expected stimuli have been shown to be detected faster and more accurately than unattended and unexpected stimuli [4]. Therefore, in



Figure 1.1: **The well-known hidden Dalmatian dog picture, showing the effect of prior knowledge on visual perception.** Reprinted, with permission, from ref. [1]. See Appendix.

many previous studies the experimental paradigms/tasks examining expectation also necessitate attentional mechanisms to be involved in the process. Specifically, task-relevant features of stimuli (e.g. color), which lead attention mechanisms to involve in the process, were also determined as the ones that induce expectations for participants (e.g. color feature has a probability). This application has been done intentionally in some studies as the nature of the study does not specifically require disentangling the effects of expectation and attention. More recently, however, in the experimental paradigms while attention is defined as the *task-relevant* stimulus feature (e.g. color), expectation is defined as the stimulus probability (or probability of a stimulus feature) [7]. In some previous studies even though the purpose of the study is to examine the effect of expectation, a distinction between expectation and attention has been overlooked. When task-relevant features of stimuli are also determined as the ones that induce expectations for participants, this would complicate the interpretation of findings in the literature [7]. To this respect, the observed effect could be the result of attention or expectation or an interaction. For example, in a traditional Posner cueing paradigm participants were shown a direction cue, which informs about the upcoming stimulus location with a certain probability (e.g. 80%), and the task is to report the spatial location of the stimulus. The aim of this paradigm is to examine attentional shift. However, it should also be considered that the location in this paradigm is both expected and attended for participants. Therefore, the outcome may represent an interaction of attention and expectation.

Consistent with this, in more recent findings attention and expectation are suggested to be two distinct mechanisms, which usually interact [8] but may have different neural effects [4]. Attention has been suggested to modulate the response properties of neurons [9, 10, 11, 12, 13, 14, 15], and it has been consistently shown that there is an increase in neural activity (e.g. BOLD signal during functional magnetic resonance imaging) for an attended stimulus compared to an unattended stimulus [4]. On the other hand, one of the most interesting findings related to the effect of expectation is that expected stimuli lead to decreased neural response compared to the response elicited by unexpected stimuli [4, 8, 16, 17, 18]. The

mechanisms underlying this effect have been a controversial issue and are discussed later in *Section 1.3 Mechanistic understanding of the effect of expectation on visual perception*. Overall, the findings of these studies have revealed that attention and expectation should be examined separately at both behavioral and neural levels. However, even though we have a fairly comprehensive knowledge about attention mechanism, expectation research is still a field of study in which further work is needed.

## 1.2 Effect of expectation on visual perception

Prior knowledge and expectations have been shown to play a substantial role in visual perceptual processes. Our perceptual decisions can be strongly biased by expectations that are formed based on the information we previously exposed to [4, 7, 8, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29]. For instance, it is well-established that expected stimulus can be detected, discriminated or recognized more accurately and faster than the unexpected stimulus. Based on these findings expectation and prior knowledge have been interpreted to facilitate perceptual processes [6, 7, 19], leading to a more efficient processing. On the other hand, it should also be noted that in most of the previous studies the index that is used to examine or measure the effect of expectation was response times of the participants. As it is very well-known, response time is a measure which can incorporate not only early sensory process, but also cognitive and motor processes. Therefore, these findings may reflect expectation's effect on perceptual decisions, however, it is still possible that any difference in the role of expectations on different levels of information processing had gone unnoticed. Specifically, whether and how expectations affect early sensory processes is still unclear.

Beyond these, even though several research focused on the behavioral effects of expectation on visual perceptual processes, how such effects eventuate has still been a matter of intense debate [30]. In other words, the computational mechanisms that underlie the effects of expectation on perceptual processes have remained elusive. In perceptual decision studies there are two commonly used

models, namely the Drift Diffusion model and Bayesian model, that may account for the observed behavioral effects, and they are discussed in the next sections.

### 1.2.1 Drift-diffusion model

In the decision-making literature it is very common to use Drift-Diffusion model [31] to unravel possible mechanisms underlying perceptual decision making processes. Specifically, Drift-diffusion model is mainly used in reaction time measurement in the literature (see Figure 1.2 for a simplified illustration of basic Drift-diffusion model). The main assumption of this model is that decisions are based on the accumulation of evidence from a sensory input. More specifically, the Drift Diffusion Model assumes that binary decisions (e.g. 2AFC task) are based on a continuous process that fluctuates between two possible outcomes (e.g. decision for Left or Right). As soon as the process reaches a critical upper or lower value (which is called boundary or limit) for a decision alternative (e.g. Left or Right decision), a decision can be made for that particular decision alternative. The two main parameters of this model are drift rate and boundary separation. Drift rate is defined as relative amount of information per time unit (processing efficacy) while boundary separation is the distance between the two limits (boundaries), which is an indicator of total amount of information (sensory evidence).

In a recent study researchers investigated the effect of expectation on perceptual decisions using DDM [32]. In that study the task of the participants was to report the spatial location of target stimulus while the predictive cue was indicating the upcoming target stimulus category. During the experiment contrast of the target images was changed adaptively, and response times of individuals were recorded. Results indicated that expectation can modulate boundary separation, which is also defined as the threshold that is required to reach a decision, but not processing efficacy (drift rate).

It should be noted that the DDM model is mostly used in perceptual decision-making studies, where response time (RT) of participants were recorded, and

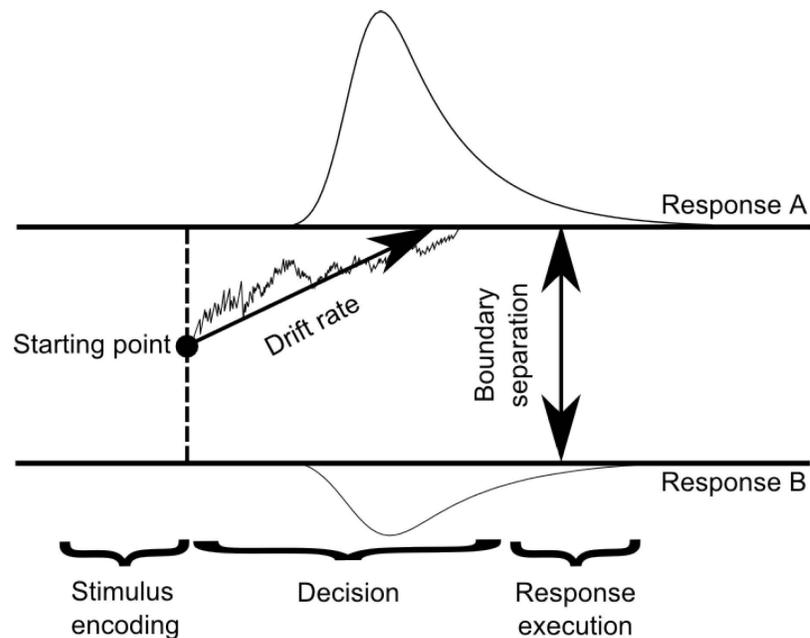


Figure 1.2: **A simplified illustration of Drift-diffusion model (DDM).** Decisions are suggested to be based on the accumulation of evidence from a sensory stimulus. This continues process fluctuates between possible outcomes until it reaches a critical limit or boundary for a decision alternative. When the process reaches the critical limit, a decision can be made for that particular decision alternative. See text for details. Reprinted, with permission, from ref. [2]. See Appendix.

used in the analysis. Therefore, as stated earlier, the effect found in perceptual decisions (using RTs) may reflect a combined effect of early sensory, cognitive, and motor processes. In addition, even though the DDM model is a highly useful model to understand the mechanisms underlying the observed effects it may not take accounts of some important aspects of experimental paradigms/tasks. For instance, in an experiment where the expectation is task-irrelevant (e.g. probability of the stimulus) it may not be possible to take the validity of expectation (e.g. 75%, 50%) into account. Also, the DDM model may not take the temporal dynamics throughout a trial into account [33]. Therefore, further work is needed to elucidate whether expectations affect even early sensory processes together with the mechanisms underlying those effects (if any).

### 1.2.2 Bayesian model

The challenges explained in the previous section may be resolved using Bayesian models. Over the last two decades Bayesian models of behavior have provided a mathematical explanation to understand, at least, how sensory information and prior knowledge can act together to give a plausible percept. This explanation gets its origin from Helmholtz's earlier work [34], where he suggested perception as an *unconscious inference processes*. The interpretation of an ambiguous or noisy sensory stimulus is suggested to be achieved with the involvement of prior knowledge. Bayesian models of behavior formalize this idea and suggest that during information processing sensory input is combined with prior knowledge to find the most probable causes of the sensory input. Among several other alternatives the visual system can usually achieve a single percept using prior knowledge. Figure 1.3 shows an example in this sense. The image shown in Figure 1.3 is a blurred image where the objects within the image can be found to be ambiguous at first sight. However, we usually see a street where a car is placed on the road and a pedestrian is placed near the road. In fact, the two objects, the car and the pedestrian, are exactly the same objects, and the differences between them are only their orientation and the location they are placed. Thus, even though we are shown exactly the same object, the system *interprets* one of them as the

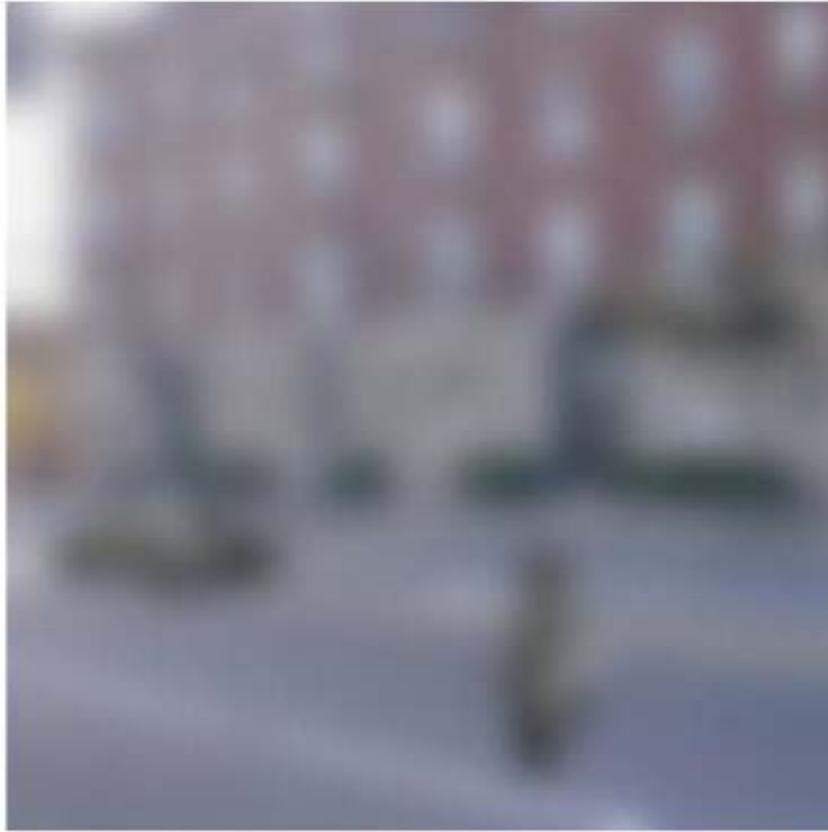


Figure 1.3: **The effect of context in visual perception.** Reprinted, with permission, from ref. [3]. See Appendix.

car and the other as the pedestrian. This reflects that our (context-based) prior knowledge has a modulatory effect on what we perceive. Indeed, a growing body of research revealed that empirical findings are largely consistent with the assumptions of Bayesian models of behavior [20, 23, 35, 36, 37, 38]. Findings of several studies support the idea that perception is a probabilistic inference process, where the system can make optimal interpretations in some circumstances, and consequently human behavior may approximate Bayesian ideal observer.

Consistent with the Bayesian models of behavior and behavioral findings, it has been consistently shown by numerous neuroimaging research that visual perception results from an interplay between bottom-up sensory input and top-down effects of prior-knowledge. While low-level properties of stimuli are processed via forward connections, there is also a top-down influence (e.g. context-based)

on perceptual processing conveyed from higher levels to lower levels of the cortical hierarchy [6, 22, 28, 39, 40, 41]. Specifically, top-down information coming from higher regions was shown to have a modulatory effect on the activity of early visual areas as well as further visual processing areas (e.g. FFA) [6, 19, 22, 26, 39, 40, 41, 42, 43, 44], which will be discussed in the next section.

### 1.3 Mechanistic understanding of the effect of expectation on visual perception

The neural evidence for the effect of expectations (or predictions or stimulus predictability) on perception and cognition comes from studies that used different types of stimuli (e.g., gratings [8, 19], faces [43], objects [45]), different experimental paradigms (e.g., explicit probabilistic cues for expectation [19], statistical learning paradigms [17, 45]), different measures/methodologies (e.g., spiking activity, local field potentials (LFPs) [17, 46, 47, 48], BOLD response in functional magnetic resonance imaging (fMRI) [8, 16, 19, 43], EEG and MEG [49, 50, 51, 52]) and different brain regions (e.g., primary sensory areas in humans [8, 19], lateral occipital complex (LOC), fusiform gyrus, inferior parietal cortex, posterior parahippocampal gyrus in humans [45], inferotemporal cortex in macaque [17, 46]). Due to this variability in methodology in the literature, it is not straightforward to draw a clear picture about the effect of expectations.

Some electrophysiological studies in non-human primates show that the inferior temporal cortex, an area known to play an important role in the visual processing of objects [53], has a higher response to unpredicted images following statistical learning [17]. On the other hand, some other work found no evidence for the expectation-related change in spiking activity and LFPs in macaque inferior temporal cortex [47, 48]. The discrepancy between these findings is suggested to be related to the length of exposure time (i.e., long-term or short-term exposure) to stimulus pairs [48, 54]. Following a long-term exposure to the stimulus pairs, expectations lead to reduced neural responses, but this effect is not consistently

revealed following short-term exposure [54].

Neuroimaging findings in humans suggest that expectations can influence early and late stages of visual processing [28]. In several studies it has been shown that expected stimuli lead to reduced neural response compared to the unexpected stimuli [4, 7, 16, 18, 19, 45], which is known as *expectation suppression*. Expectation suppression has been observed in several stages of information processing including the ventral visual stream: primary visual cortex [16, 19], LOC, fusiform gyrus, inferior parietal cortex, and posterior parahippocampal gyrus [45]. However, the mechanisms underlying the effect of expectations have been a controversial issue. Specifically, expectation suppression has been linked to two opposing hypotheses in the literature, which are called dampening and sharpening of sensory representations. Using fMRI and multivariate pattern analysis (MVPA), some research found evidence for the sharpening of the population response for the expected stimulus feature in the primary visual cortex despite reduced BOLD response [19]. Some other research suggested that expectation suppression is observed throughout the ventral visual stream, and expectations lead to dampening of the representations in object-selective regions for the expected stimuli (but not in early sensory areas) [45]. Alternatively, it is also suggested that both dampening and sharpening mechanisms may account for the findings in the literature because of the involvement of different subpopulations of neurons [55] during information processing [28].

Note that in the majority of studies investigating the effect of expectations, neural findings observed in expected and unexpected conditions were not compared with a baseline (neutral) condition. Therefore, the difference between the neural response observed in expected and unexpected conditions was interpreted in two ways: in some studies expectations are suggested to lead to decreased neural responses, while in some other studies unexpected conditions were suggested to elicit higher neural responses. Since the neural responses to the expected and unexpected conditions are not compared with a baseline condition, it is hard to interpret whether expectations lead to reduced neural responses or unmet expectations lead to higher neural responses (or both) [17, 28, 54]. Notably, when neural responses to expected and neutral conditions were compared in studies

that included the neutral condition, the finding that expectations lead to decreases in neural responses was not consistently shown (see [54] for an extensive review). Therefore, more careful investigations are needed to understand the effect of expectations in visual processing.

In light of these empirical findings, several mechanistic cortical models have been proposed, which are generic models for brain function (e.g., [5, 55, 56]). The models are called *predictive coding*, *predictive processing*, or *predictive computation* models in literature. Each model introduces its own structure and possible connections and has different theoretical constructs to unravel the flow of information processing between brain regions. For example, one of the well-known models, Predictive Coding Theory (PCT) [55], posits the brain as an active inference machine that computes internal predictions that are formed based on prior information. The idea is that during information processing, these predictions are compared with the sensory input, and they are continuously updated to minimize the prediction error. A simple illustration of the predictive coding model can be seen in Figure 1.4. The predictions are considered to be generated by specific subpopulations of neurons called *representation (or prediction) units* which are hypothesized to exist at each level of the cortical hierarchy, and these predictions are conveyed from higher levels to the lower levels via backward connections. Also, prediction errors are computed by *error units*, which are hypothesized to exist at each layer of the cortical hierarchy, and they are conveyed from the lower levels to the higher levels via forward connections.

Apart from the PCT, more recently, another biologically plausible cortical model [5] has been introduced and proposed a more simplified structure for information processing in the brain. In this model, different subpopulations of neurons for prediction or error computation are not defined. Instead, in this model, it is posited that the information processing can be executed only through feedforward and feedback connections. Specifically, in this model, the neural activity is considered to be determined by feedforward drive, feedback drive, and prior drive, and their contributions are governed by specific parameters of the model, which are suggested to correspond to the oscillatory activity and neuromodulators [5]. Despite differences in the structure of these models, both (and many)

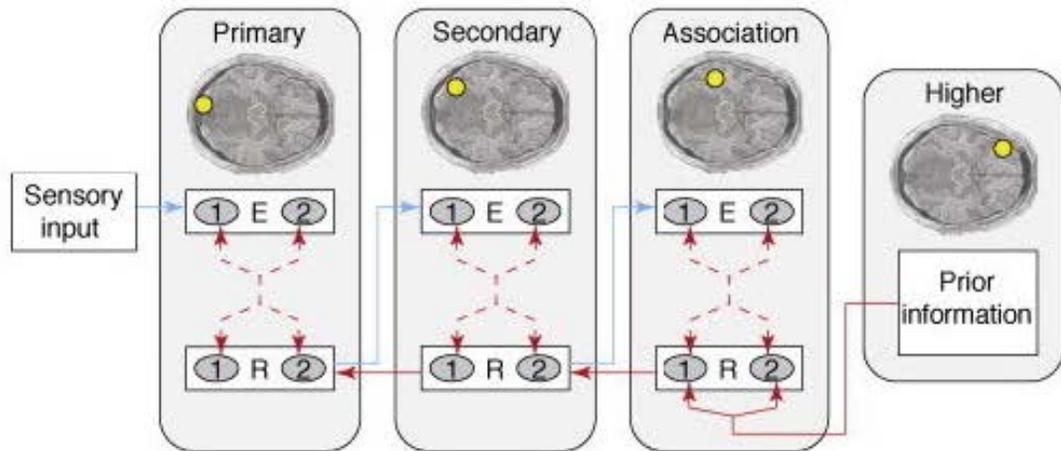


Figure 1.4: **A schematic illustration of the predictive coding model.**  $R$  represents representation (prediction) units, and  $E$  represents error units. In the predictive coding framework it has been suggested that based on prior knowledge brain computes internal predictions about the upcoming sensory stimulus. These predictions are compared with the actual sensory stimulus at each level of the cortical hierarchy. When there is a mismatch between the internal predictions and the sensory stimulus, a prediction error is computed. The predictions are conveyed from higher levels to lower levels via backward connections, and the predictions errors are conveyed from lower levels to higher levels via forward connections. This process has been suggested to be executed by representation (prediction) units, and error units. Reprinted, with permission, from ref. [4]. See Appendix.

of the predictive processing models make a basic assumption that the brain uses prior knowledge to predict the current state of the world, and this process is executed by a dynamic interaction of bottom-up sensory input and top-down prior knowledge and expectations.

Currently, we have considerable amount of empirical evidence that is consistent with the assumptions of the predictive processing models (see [57, 58], but also see [54]). Interpretation of empirical findings within the framework of these computational models is an important step to have a better understanding of the effects of expectation in visual processing. On the other hand, unlike rigorous efforts implemented in Bayesian models of behavior, the proposed mechanistic models have not usually been employed to test whether they can explain real data. Modeling on real human data would also allow us to examine whether the assumptions of the models comply with the empirical evidence in the literature. This would, in turn, help us to refine the models accordingly and develop new hypotheses to better understand the effect of expectations in visual processing.

## 1.4 Current Study

To advance our understanding of whether and how prior knowledge and expectations affect early sensory processing, this dissertation attempts to investigate the behavioral effects of prior knowledge and expectations on *early visual processing* and unravel the computational mechanisms that may underlie those effects. As stated earlier, despite the well-established effects of expectations on higher-order mechanisms, their effects on low-level sensory processing remain unclear. In this sense, Chapter 2 of this dissertation investigates the expectation's effect on early visual processing at the perceptual threshold level. Next, in Chapters 3, 4, and 5, we take a multi-modeling approach to unravel possible computational mechanisms underlying the observed behavioral effects. Specifically, in Chapter 3, we model the behavioral data with a recursive Bayesian model and examine the generalization of these modeling findings in Chapter 4. In Chapter 5, we

implement a recurrent cortical model to discuss possible neural mechanisms underlying the behavioral effects. Overall, our findings in this dissertation provide an insight into how early sensory processes can be influenced by expectations. From a broader perspective, this dissertation attempts to link human behavior, a behavioral model, and a mechanistic cortical model to better understand the effect of prior knowledge and expectations on sensory processing.

## Chapter 2

# Behavioral Effects of Expectation on Visual Perception

The studies and results presented in this chapter are based on a publication by B.M. Urgen and H. Boyaci, "Unmet expectations delay sensory processes", *Vision Research*, 181, 1-9, 2021.

Also, the studies and results presented in this chapter are presented in a preprint by B.M. Urgen and H. Boyaci, "When expectations are not met: unraveling the computational mechanisms underlying the effect of expectation on perceptual thresholds", *bioRxiv*, 545244, 2019.

### 2.1 Introduction

The effects of prior knowledge and expectations on recognition and decision-making processes are well-established. Expectations have been consistently shown to bias and facilitate perceptual decisions [4, 7, 8, 19, 20, 21, 22, 23, 24, 25, 26, 28]. Specifically, expected stimulus (or in a cued-paradigm *congruent* stimulus) is detected faster and more accurately than the unexpected (*incongruent*) one [25, 29].

However, it should be noted that majority of findings on this research are mostly obtained from perceptual decision studies. In these studies, researchers collected and analyzed reaction times of participants to investigate the expectation's effect on perception. However, reaction time is not the only measure to examine the perceptual processes. In fact, it represents expectations' effect on a combination of perceptual, cognitive and motor processes. Therefore, a more careful investigation is needed to find out whether there is an effect of expectation also on related low-level sensory processing. This would allow us to see whether expectations can bias even sensory processes or not.

For this aim, in this study we investigated the effect of expectations on visual perception at the threshold level using a 2-AFC task. Specifically we examined whether expectation has an effect on detecting the spatial location of a stimulus, which is also called *individuation*. We measured duration thresholds, which is the shortest presentation duration that the participants can successfully detect the location of the stimulus. This measure allowed us tap into sensory processes.

We also examined whether expectation's validity can modulate perceptual thresholds. Majority of previous studies that examined the effect of expectation used a fixed validity for expectation (e.g. only 75%), and compared the observed findings for expected and unexpected conditions. This application did not allow us to see whether/how expectation's validity modulates detection performance. More importantly, as the performances in the expected and unexpected conditions were not usually compared to a baseline condition (e.g. when there is no expectation), it is hard to differentiate whether the expected stimulus is detected faster or the unexpected is detected slower (compared to the baseline). For this aim, we systematically manipulated the expectation's validity in different experimental conditions. In this sense, validity of expectation was 100%, 75%, 50% and neutral (no expectation) in separate experimental sessions. We included the 100%-validity condition as a control condition where expectations were always valid, and the neutral condition as a baseline condition where there was no expectation. Thus, in our experiment there were congruent (expected), incongruent (unexpected) and neutral trials. We hypothesized that unexpected trials would show higher duration thresholds compared to expected trials, and this difference

might be modulated by the validity of expectation. In this respect, we conducted two experiments, and details of stimuli, experimental designs and procedures can be seen in the next sections.

## 2.2 Experiment 1

In Experiment 1 prior information was implicated in cues which were used to inform participants about which category of target stimuli will be presented. In other words, cues were indicators of upcoming target stimuli category. However, participants' task was to report the spatial location of that target stimuli. Therefore, prior information that is embedded in cues were task-irrelevant to minimize the effect of top-down attentional mechanisms on our results as much as possible.

We had two predictions in Experiment 1. Firstly, when cue validity is high (i.e. 75%), we expect to observe longer duration thresholds in the trials where the target category is not correctly predicted by the cue (incongruent trials) compared to the trials where the cue predicts the correct target category (congruent trials). Secondly, participants were expected to update their estimates of stimulus-cue associations for each experimental condition so that duration thresholds should not be different between congruent and incongruent trials when they are equally likely to occur (i.e. 50%)

### 2.2.1 Materials and methods

#### 2.2.1.1 Participants

Eight naive participants (4 female;  $24.5 \pm 2.33$  years) participated in Experiment 1. All participants had normal or corrected to normal vision and they did not report a history of neurological disorder. Participants gave their informed consent prior to the experimental sessions. The experiment was approved by the Research Ethics Committee of Bilkent University. Note that we performed a  $G^*$  power

analysis to estimate the sample size using the effect size of [25], and the estimated sample size was 4 (with 0.95 power,  $\alpha = .05$ ). Also note that similar number of participants are commonly used in studies that measure duration thresholds (e.g. [59, 60, 61, 62, 63, 64, 65]).

### 2.2.1.2 Stimuli

Stimuli consisted of ten face images (five female; age range was 19-69) taken from Face Database of the Park Aging Mind Laboratory [66] and ten house images from Scene Understanding Database from the Princeton Vision Group [67]. Pictures of cues (*informative*: face, house; *uninformative* (neutral): question mark) that were shown in the experiment were taken from The Noun Project’s website ([www.thenounproject.com](http://www.thenounproject.com); Person designed by Alex Fuller, House designed by OCHA Visual Information Unit, Question mark designed by Vicons Design) and were scaled to  $3.5 \times 3.5^\circ$  visual angle. As mask, scrambled version of the face and house images were generated. The images were divided into 49 cells by creating  $7 \times 7$  grids for each. After that each cell was randomly assigned to different locations. The stimuli including face images, house images, and mask images were scaled to  $10.5 \times 10.5^\circ$  visual angle, converted to grayscale, histogram-matched (scaled to the mean luminance of all stimuli) by using SHINE Toolbox [68], and adjusted and matched to a very low contrast value (2%). Stimuli were shown on a CRT monitor (HP P1230, 22", 1024 x 768 resolution), and the refresh rate was 120 Hz. Participants seated at 60 cm from the screen. Experiment was programmed in MATLAB 2016a using Psychtoolbox [69].

### 2.2.1.3 Experimental Design

Stimuli were presented on a gray background (RGB: 128, 128, 128). At the beginning of each trial a fixation dot and a cue were simultaneously shown at the center of the screen. Cues were presented for 2 seconds at the center of the screen and were either *informative* (face or house) or *neutral* (question mark) depending on the experimental condition (See each experimental condition for

details). Next, a target stimulus, which was an intact face or house image, and a scrambled version of the intact image were shown in left and right side of the screen at  $10^\circ$  eccentricity. Presentation duration of the images were determined by an adaptive staircase procedure. Therefore, the images stayed on the screen for different durations, which varied adaptively (See *Procedure* for details). Next, different scrambled versions of that target stimulus were shown as masks on the same locations for 64 ms. Then, an empty display with a gray background was shown and participants were asked to report their decisions. Participants' task was to detect spatial location of the target image as soon as possible by pressing left or right arrow key of keyboard. Participants were asked to maintain their fixation on the fixation dot during the trial. Finally, a feedback message was written on the screen, e.g. "correct" or "wrong" to the participants for 752 ms. Trials that include same category of the cue and image are called *congruent* (expected) trials. Trials that include different category of the cue and image are called *incongruent* (unexpected) trials. In each experimental condition, equal number of each cue (face and house) appeared in random order, and equal number of each target stimulus (face and house) was presented. Also note that the target stimulus was randomly assigned to one of the two locations (left or right) in each trial in each experimental condition. See Figure 2.1 for experimental design.

#### **2.2.1.4 Procedure**

Experiment 1 consisted of a training session and an experimental session which includes four experimental conditions. In all sessions, adaptive staircase procedure with a two alternative forced-choice (2AFC) paradigm was applied to derive duration thresholds for spatial location detection in congruent and incongruent trials. Presentation duration of the target image and scrambled version of it were varied adaptively from trial to trial. Each trial's duration was determined by the accuracy of the participants' response in the previous trial. Specifically, each wrong answer or two consecutive correct answers resulted in a 8 ms (step size) increase or decrease of the following trial's target presentation duration respectively. Multiple pseudorandom 2-up 1-down staircases were interleaved in the experiment.

Each staircase was set to interleave at least once before any of the other staircases interleaves for the second time. At the beginning of each experimental condition, one staircase started from a relatively short duration (minimum 8 ms, varied for each participant, and the other staircase started from a long duration (varied for each participant). The reason of the variation in initial durations between participants was the individual differences between participants. There were 30 trials in each staircase in all experimental conditions, but number of staircases were varied for each experimental condition (See experimental conditions for details).

**2.2.1.4.1 Training Session.** Prior to the experimental session, each participant completed a training session in order to stabilize their thresholds. Participants seated at 60 cm from the screen and their head were stabilized with a chin-rest. The training session consisted of at least 2 (up to 5) short experiments where the cue was always informative (face and house cue) and 100% valid in indicating the target stimulus category. Each experiment in the training session had 120 trials and there were equal number of face and house cue trials. Number of experiments completed in the training session varied for each participant, and it is determined by whether the participant’s threshold stayed in the same interval (in terms of step size: 8 ms) for at least two sequential experiments.

**2.2.1.4.2 Experimental Session.** All participants completed four experimental conditions in randomized order in separate sessions. Participants were informed about the probability of cue-validity prior to the experiments.

**100%-validity condition.** This experimental condition was included as a control condition. Cue (face or house) informed participants about the upcoming target stimulus category (either face or house image) with a 100% validity so that there was no violation of expectations. There were 120 trials in total including 60 trials where face image was presented following face-cue, and 60 trials where house image was presented following house-cue. There were four staircases in this condition.

**75%-validity condition.** In this experimental condition the cue was always informative (face and house cue) and 75% valid in indicating correct target stimulus category (face or house image) during the experiment. Equal number of face cue and house cue trials were presented. There were 16 staircases and 480 trials in total. There were 360 congruent trials where the target type was predicted by the cue, and 120 incongruent trials where the cue misled the participants about the upcoming target category in this condition.

**50%-validity condition.** In this experimental condition cue was always informative (face or house) and alerted participants about the upcoming target stimulus category (face or house image) with a 50% validity. Therefore, there were 240 trials in total including 120 congruent and 120 incongruent trials. Equal number of face-cue and house-cue trials were presented and number of staircases were eight.

**Neutral condition.** Similar to 100%-validity condition, this experimental condition was also included as a control condition. However, this condition was different from the other conditions in the way that there was no informative cue (face or house) that alerts participants about the upcoming target category. Rather, the cue was neutral, a question mark, during the experiment. Therefore, cue-based predictions regarding the category of the upcoming stimuli were not formed. Except the cue type, all experimental stimuli and design were the same with the other conditions. There were four staircases and 120 trials in total, and equal number of face and house images were presented.

#### 2.2.1.5 Statistical Analysis

Duration thresholds (70.7% accuracy) were estimated for each trial type, including congruent, incongruent and neutral trials, for each condition using Palamedes toolbox [70] with Logistic function using Matlab 2016a. A 2 (congruency: congruent, incongruent) x 2 (validity: 75%, 50%) repeated measures analysis of variance (ANOVA) was conducted to examine the effect of expectation on duration thresholds. Moreover, we conducted two-sample paired t-tests to investigate

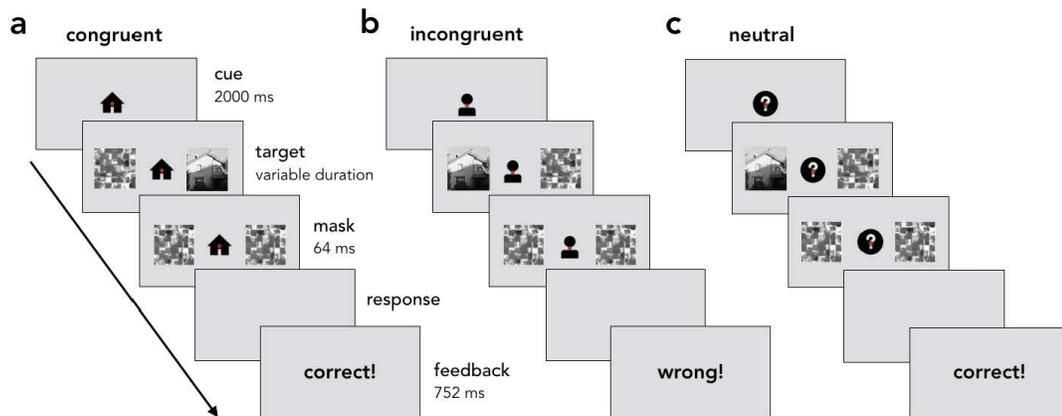


Figure 2.1: **Experimental design.** Sample trial sequences. a. Congruent (expected) trial. b. Incongruent (unexpected) trial. c: Neutral trial. Except the neutral trials, an informative cue predicted the category of upcoming target image with a certain validity. The validity of the cue was 100%, 75%, and 50% in different experimental sessions. In the neutral trials the cue was a question mark and was not informative about the upcoming target image category. Task of the participants was to detect the spatial location of the target image. See text for more details.

any difference between thresholds of 100%-validity condition and thresholds of neutral (no-expectation), 75%-validity and 50%-validity conditions respectively.

## 2.2.2 Results

Figure 2.2 shows duration thresholds of participants for each trial type in each validity condition (see Appendix for psychometric function fits of each participant). We performed 2 (congruency: congruent, incongruent) x 2 (validity: 75%, 50%) repeated measures ANOVA to examine the effect of expectation on duration thresholds. We found that the main effect of congruency is statistically significant ( $F(1,7) = 11.956$ ,  $p = 0.011$ ,  $\eta^2 = 0.104$ ). However, there was no main effect of validity or interaction ( $F(1,7) = 2.848$ ,  $p = 0.135$ ,  $\eta^2 = 0.024$ ;  $F(1,7) = 0.155$ ,  $p = 0.705$ ,  $\eta^2 = 0.001$ ). Next, we examined whether there is any difference between the thresholds of congruent and incongruent trials in each validity condition as the effect is present in nearly all participants at the individual level. We found that incongruent trials showed longer duration thresholds than the congruent trials in

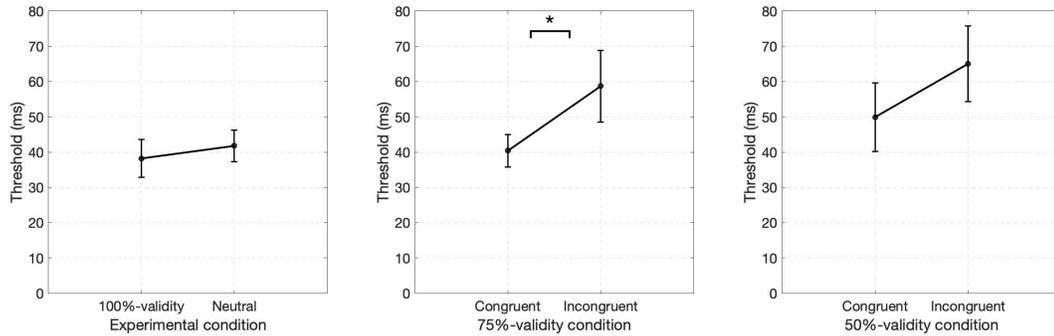


Figure 2.2: **Results of Experiment 1.** **a.** Duration thresholds of 100%-validity and neutral conditions. **b.** Duration thresholds of congruent and incongruent trials in 75%-validity condition. **c.** Duration thresholds of congruent and incongruent trials in 50%-validity condition.

75%-validity condition ( $t(7) = 3.079$ ,  $p = 0.018$ ,  $d = 1.089$ ). However, there was no difference between congruent and incongruent trials in 50%-validity condition ( $t(7) = 2.266$ ,  $p = 0.058$ ,  $d = 0.801$ ). Finally, we conducted two-sample paired t-tests between (1) 100%-validity and neutral conditions, and (2) congruent trials of 75%- and 100%-validity conditions, and (3) congruent trials of 50%- and 100%-validity conditions. All tests showed that the thresholds of the conditions were not different from each other ( $t(7) = 0.676$ ,  $p = 0.521$ ,  $d = 0.239$ ;  $t(7) = 0.457$ ,  $p = 0.661$ ,  $d = 0.162$ ;  $t(7) = 1.404$ ,  $p = 0.203$ ,  $d = 0.496$  respectively).

## 2.3 Experiment 2

All participants took part in Experiment 1 after they were gone under a training session. The training session was included in Experiment 1 in order to stabilize the thresholds of participants so that any effect of learning (between different experimental sessions) can be eliminated, and would not bias the results in different experimental conditions. However, it is also possible that the training itself affected the results as the validity of the expectation in the experiments were 100%. To eliminate any confounding effect of training on our behavioral findings, in Experiment 2 we conducted the same experiments on a separate group of participants who did not participate a training session.

## **2.3.1 Materials and Methods**

### **2.3.1.1 Participants**

10 participants (Group 1: 6 participants,  $26 \pm 1.78$  years; Group 2: 4 participants,  $26.25 \pm 2.22$  years ) participated in Experiment 2. All participants had normal or corrected to normal vision and had no history of neurological disorder. Informed consent form was taken prior to the experiment. The experiment was approved by the Research Ethics Committee of Bilkent University.

### **2.3.1.2 Stimuli, Experimental Design and Procedure**

All stimuli and experimental design were exactly the same as in Experiment 1. In Experiment 2 participants were randomly assigned to one of the two experimental groups: Group 1 completed two experimental conditions that include 75%-validity and neutral conditions, and Group 2 completed 50%-validity and neutral conditions. All participants completed each experimental condition in random order in different sessions.

### **2.3.1.3 Statistical Analysis**

We conducted two-sample paired t-tests separately for Group 1 and Group 2 to see whether duration thresholds of congruent and incongruent trials differ in 75%-validity condition and 50%-validity condition.

## **2.3.2 Results**

Results of Experiment 2 can be seen in Figure 2.3 (see Appendix for psychometric function fits of each participant). Results of Group 1 showed that in 75%-validity condition there was a statistically significant difference between congruent and

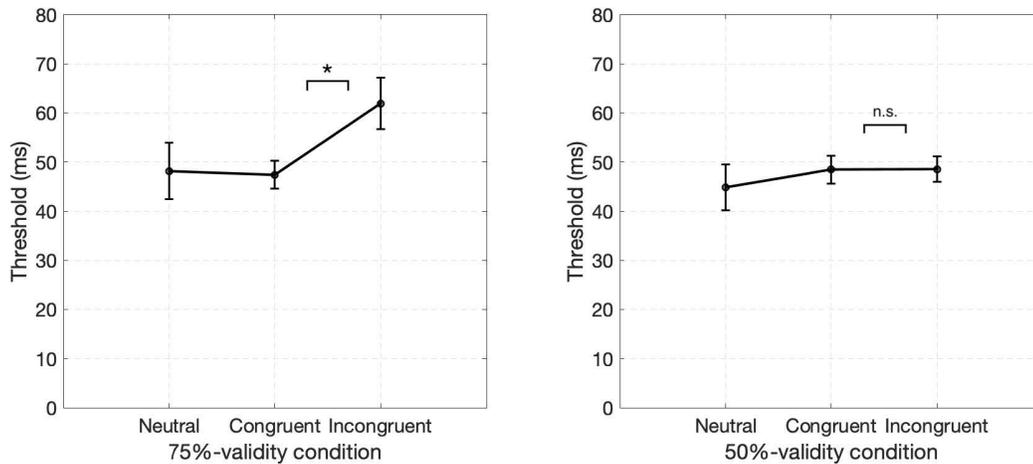


Figure 2.3: **Results of Experiment 2.** a. Results of Group 1 who completed 75%-validity and neutral conditions. b. Results of Group 2 who completed 50%-validity and neutral conditions.

incongruent trials in duration thresholds ( $t(5) = 2.782$ ,  $p = 0.039$ ,  $d = 1.136$ ). On the other hand, results of Group 2 showed that in 50%-validity condition there was not a significant difference between congruent and incongruent trials in duration thresholds ( $t(5) = 0.071$ ,  $p = 0.948$ ,  $d = 0.036$ ). Also, thresholds of neutral condition were not different from congruent trials of 75%- (Group 1) and 50%- validity (Group 2) conditions ( $t(5) = 0.148$ ,  $p = 0.888$ ,  $d = 0.061$ ;  $t(5) = -0.724$ ,  $p = 0.521$ ,  $d = 0.362$  respectively). Taken together, results of Experiment 2 confirmed that the findings of Experiment 1 are not due to an effect of training.

## 2.4 Summary and Conclusions

In this study we investigated the effect of expectations on early visual processes. Even though there is a growing body of literature indicating that expectations facilitate perceptual decisions, there is still a matter of intense debate about whether or not expectations affect even early sensory processes [30]. Therefore, in this study our aim was to gain insight into expectation's effect on early visual processes. For this aim, we conducted behavioral experiments where we measured

perception at the threshold level by using duration thresholds. We also systematically manipulated expectation's validity in different experimental conditions to reveal whether the validity of expectations also alters perceptual thresholds.

Our findings indicated that, indeed, expectations affect even early visual processes. However, this effect is different from what has been suggested for higher-order mechanisms. Previous studies suggested that valid expectations can facilitate the perceptual decisions. On the other hand, in our study we found that valid expectations do not reduce the perceptual thresholds, because we found no difference between the thresholds of neutral condition and 100%-validity condition. Rather, our findings showed that perceptual thresholds increase if expectations are not met.

Based on these findings, we suggest that there might be two possible mechanisms that can explain the observed effects. One possible mechanism might be that internal parameters, for example the decision thresholds or the speed with which the system reaches a decision may vary. For example, in a recent study, using DDM it has been suggested that expectations alter internal parameters [32]. Specifically, expectations have been shown to modulate boundary separation parameter, which is considered as the internal decision threshold in the system. Considering this finding, in the current study we might also observe a difference between congruent and incongruent trials in the thresholds specifically in 75%-validity condition. In other words, a change in the internal threshold due to expectations could be one possible reason that underlies higher perceptual thresholds in the unexpected trials in the current study. On the other hand, it is also possible that expectations do not alter the internal parameters, but rather they may entail the system to make more computations. Thus, another possible mechanism might be that expectations lead to longer processing so that we observe higher duration thresholds in unexpected trials than expected trials. In order to resolve which of the two alternative mechanisms underlie the behavioral results we modelled our behavioral data with a recursive Bayesian updating scheme in Chapter 3.

## Chapter 3

# A recursive Bayesian model: computational mechanisms underlying the effect of expectation on perceptual thresholds

The studies and results presented in this chapter are based on a publication by B.M. Urgen and H. Boyaci, "Unmet expectations delay sensory processes", *Vision Research*, 181, 1-9, 2021.

Also, the studies and results presented in this chapter are presented in a preprint by B.M. Urgen and H. Boyaci, "When expectations are not met: unraveling the computational mechanisms underlying the effect of expectation on perceptual thresholds", *bioRxiv*, 545244, 2019.

### 3.1 Introduction

One of the main ideas that has emerged in recent years is that information processing in the brain can be understood and explained within the Bayesian framework. This idea gets its origin from Helmholtz’s earlier work [34], where he proposed that perception is an unconscious inference process, and sensory input is combined with prior information. Bayesian framework gets its origin from this idea and suggests that the brain computes the statistics of the environmental stimuli, determines the possible probabilities for the sensory input, and tries to adapt these computations to the real observations. Indeed, several behavioral findings have been suggested to be consistent with the Bayesian models of behavior [20, 23, 35, 36, 37, 38]. For instance, ambiguity in the processing of objects can be eliminated with prior information [36]. Also, several motion illusions can be explained within the Bayesian framework [20]. Today, a large and growing number of empirical studies in the literature shows that human perceptual decision-making is quite consistent with the Bayesian framework.

The success of the Bayesian models in explaining the human behavior have led us to use a recursive Bayesian updating scheme to understand the processes underlying our behavioral findings in Chapter 2. Our behavioral findings revealed that there might be two possible mechanisms that underlie the observed effects. First, expectation might modulate the internal parameters of the system in a way that internal noise or decision criteria might be altered. This might be a possible mechanism that lie behind the higher thresholds in the unexpected trials. Alternatively, it is also possible that even though the internal parameters do not change, the process might take longer just because the system needs to process a stimulus which is not expected.

Presuming that perception is a dynamic inference process, we present a *recursive* Bayesian updating scheme in which the prior is not fixed, but updated even within a trial to model the behavioral data in Chapter 2. Our aim was to disentangle which of these possible mechanisms plays a role on the behavioral findings. We suggest that modeling our behavioral data within the Bayesian framework is

quite important for several reasons. First, this implementation would be helpful to understand the underlying computational mechanisms. Also, several mechanistic predictive processing models in the literature which are also of interest in this dissertation, get their origins from Bayesian framework. Therefore, this implementation would also make the connection between a behavioral model and a cortical model in explaining the behavioral findings.

## 3.2 Conceptual Understanding of Bayesian Model

In Bayesian models of perception, perceptual decisions can be made based on prior (beliefs) and sensory input [71]. Specifically, the main assumption is that through experience a (Bayesian) observer learns the statistics of the sensory environment. The beliefs about the statistical regularities in the environment are combined with the actual noisy sensory input. The beliefs, which are also called prior, are represented as a probability distribution, and the sensory processing for the observation of the noisy sensory input is represented as a likelihood function [72]. The aim of this process is to adapt the internal generative model to the observed sensory input in order to make a successful decision. The combination of the priors with the actual sensory input results in a posterior estimate (a posterior probability distribution). This process is called Bayesian inference. In this inference process, the observed sensory input is translated into posterior beliefs, and a decision can be made by the observer accordingly. See Figure 3.1 for a simple illustration of the process explained here.

The posterior belief computed in the inference process may sometimes be updated within a single observation because the noise in that sensory observation may change as a function of time. Thus, the inference mechanism may continue to process and compute new posteriors until a decision is made. In addition, it may sometimes result in the favor of the prior or actual sensory input. For instance, if there is too much noise in the sensory input, then the posterior estimates may be dominated by the prior. Consequently, the behavioral perceptual decisions will also be dominated by the prior.

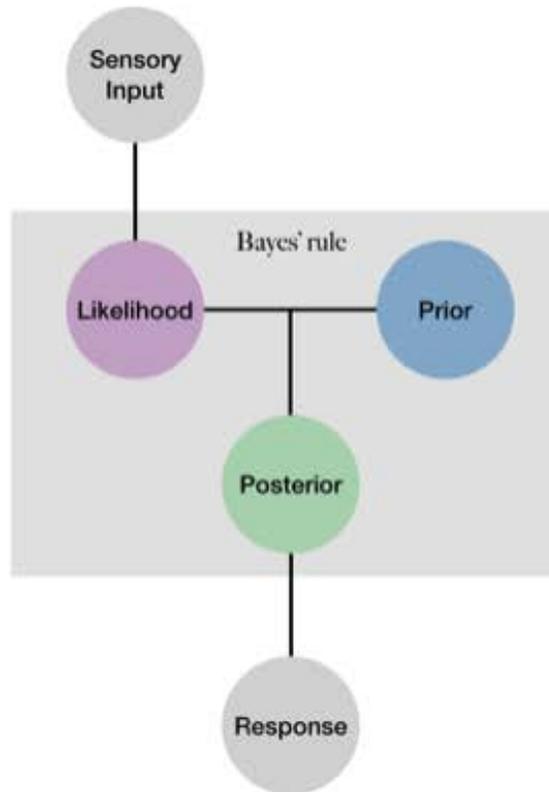


Figure 3.1: **A simple illustration of the components of a basic Bayesian model.** In this framework, an observer learns the statistical regularities in the environment, e.g. stimuli used in a task. The beliefs about the statistical regularities in the environment, also called prior, are represented as a probability distribution. The sensory processing for the observation of the actual sensory stimulus is represented as a likelihood function. While making decisions, the prior and the actual sensory input are combined, and this process results in posterior estimates. Consequently, a decision can be made based on the posterior beliefs, and a response can be executed by the observer.

## 3.3 Methods

### 3.3.1 Implementation of Bayesian Model

We implemented a generative model for which Bayesian inference equations were derived [73]. We adapted the model to our experimental paradigm, and implemented calculations separately for the observation on left and right side in each trial of the experiment. Figure 3.2 shows the calculations of a single trial from 75%-validity condition.

We defined feature values for the *input* (also shown in light gray boxes in Figure 3.2)

$$s = \begin{cases} s_1 = -1 & \text{for a house image} \\ s_2 = 0 & \text{for a scrambled image} \\ s_3 = 1 & \text{for a face image.} \end{cases} \quad (3.1)$$

These would be the abstracted values received by the system if there were no noise. Next, we postulated that the *abstracted observation* extracted by the system,  $x_t$ , is drawn from a normal distribution

$$x_t \sim N(s, \sigma^2). \quad (3.2)$$

During each trial we calculated  $x_t$  at iteration  $t$  based on the presented images on the corresponding sides. Next, we defined *generative models* for each decision alternative,  $A_i$ :  $A_1$  for house,  $A_2$  for scrambled, and  $A_3$  for face-image. We calculated the likelihood of  $x_t$  under each decision alternative as

$$p(x_t|A_i) = \frac{1}{\hat{\sigma}\sqrt{2\pi}} \exp\left(-\frac{(x_t - s_i)^2}{2\hat{\sigma}^2}\right). \quad (3.3)$$

We defined the *initial* values of the *priors* as

$$p(A_i) = c_i, \quad i = 1, 2, 3 \quad (3.4)$$

where  $c_i$  are defined based on the cue validity (i.e. 100%, 75% or 50%), *and* the cue presented at that trial (i.e. face or house). For example in a trial under the

75%-validity condition if the cue is a *house* then the priors are

$$c_1 = 3/8, c_2 = 4/8, c_3 = 1/8 \quad (3.5)$$

or in a trial under the 50%-validity condition if the cue is a *face* then the priors are

$$c_1 = 2/8, c_2 = 4/8, c_3 = 2/8. \quad (3.6)$$

Next, we combined the likelihoods with the priors to compute *posterior estimates* for each decision alternative as follows

$$p(A_i|x_1) = \frac{p(x_1|A_i)p(A_i)}{\sum_{j=1}^3 p(x_1|A_j)p(A_j)}. \quad (3.7)$$

Within a single trial posterior estimates are updated recursively over time ( $N$  times: number of iterations) until a decision is made by the model

$$p(A_i|x_{1:t}) = \frac{p(x_t|A_i)p(A_i|x_{1:t-1})}{\sum_{j=1}^3 p(x_t|A_j)p(A_j|x_{1:t-1})}. \quad (3.8)$$

Note that, this amounts to using priors that are not fixed but updated in each iteration: posterior of the previous iteration becomes the prior for the next iteration. Number of iterations,  $N$ , in a single trial is determined by

$$N = \tau/\Delta t \quad (3.9)$$

where  $\tau$  represents the duration of presentation of the target images in this particular trial, and  $\Delta t$  defines how long each iteration lasts in the system. Next, we calculated the *total probability of observing an intact image (face or house)* for left and right side,  $T_{LEFT}$  and  $T_{RIGHT}$ , as the sum of the final posterior of face-image and house-image (blue boxes in Figure 3.2). At the last step, a *final decision* is made by the model using the criteria shown in black box in Figure 3.2. Specifically, the ratio of  $T_{LEFT}$  to  $T_{RIGHT}$  is compared to the *decision criteria*,  $\lambda$ . This evaluation determines whether the model decides *left* or *right*. If this criteria cannot be met, then a decision is made randomly.

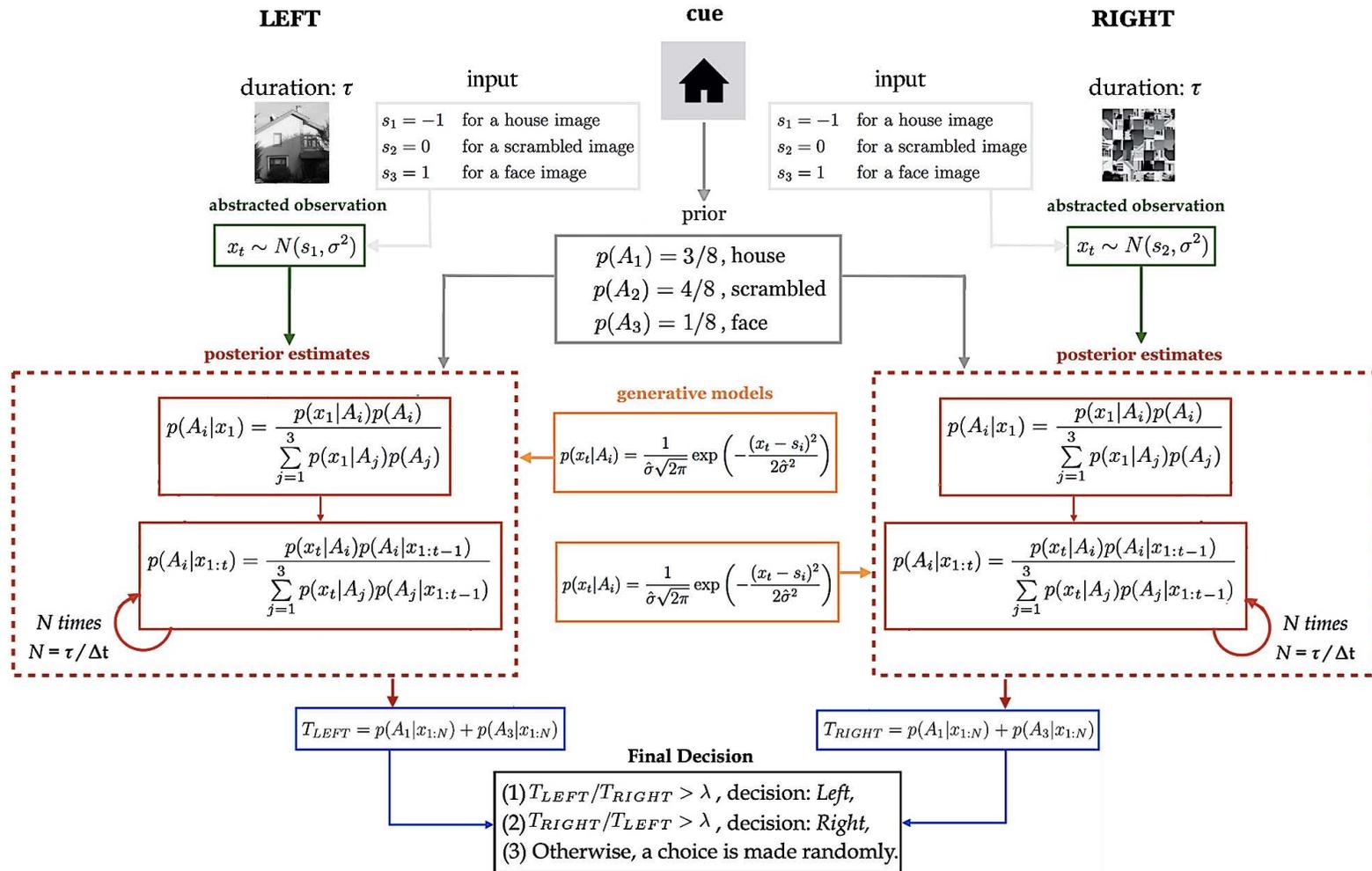


Figure 3.2: **Bayesian model adapted to the current experimental paradigm.** Figure shows the calculations done for a single trial from 75%-validity condition. See text for details.

Table 3.1: **Notations for Bayesian model.**

Symbol	Description
$s$	Feature (category) value that would be extracted by the system under a noise-free observation. 1: House; 0: Scrambled; -1: Face
$x_t$	Noisy sensory input at iteration $t$ , drawn from a normal distribution with mean $s$
$A_i$	Decision alternatives (house, face or scrambled)
$p(A_i)$	Prior probabilities of the alternatives
$p(x_t A_i)$	Likelihood of the observation, $x_t$ , under the alternative $A_i$
$p(A_i x_t)$	Posterior probability of alternative $A_i$ given the observation, $x_t$
$\tau$	Presentation duration of the stimulus in the trial
$\lambda$	Decision criteria (free parameter)
$\Delta t$	How long each iteration lasts in the system (inverse of speed, free parameter)
$\hat{\sigma}$	Internal uncertainty of the generative models (free parameter)
$N$	Number of iterations performed in the trial, $\tau/\Delta t$

### 3.3.2 Model fitting for individual data

Expectations have been previously shown to modulate the boundary separation parameter in the Drift Diffusion Model (DDM) whereas the drift rate did not change due to expectations [32]. The boundary separation parameter can be considered to be the internal threshold to reach a decision and the drift rate reflects the processing efficacy. In light of these findings, in our Bayesian model three free parameters were optimized for each participant’s data;  $\lambda$  (decision threshold),  $\Delta t$  (how long each iteration lasts in the system), and  $\hat{\sigma}$  (the internal uncertainty of the decision maker’s representation of its observations). Note that in our model  $\Delta t$  and  $\hat{\sigma}$  parameters can be linked to the drift rate parameter of the DDM and  $\lambda$  (decision threshold) may correspond to the boundary separation parameter of the DDM. After  $\lambda$ ,  $\Delta t$ , and  $\hat{\sigma}$  parameters were optimized for each participant’s data, we ran 1000 simulations of the model using the optimized parameters. We implemented a separate model for 100%-, 75%-, 50%-validity conditions, and the model fitting procedure was applied to the data of these validity conditions for each participant. There was only a single difference between the models of different validity conditions, and it was the initial values of the priors (See gray box in Figure 3.2). The priors were determined based on expectation’s validity

at each experimental condition. Note that we did not include neutral condition in modeling, because the expectation’s validity is the same in 50%-validity and neutral conditions, and the neutral condition is different from the other ones in terms of its experimental structure (no prior/expectation).

### 3.3.3 Model comparison

In order to examine whether underlying parameters of the system are different in different trial types, two models are defined: *restricted* and *unrestricted* models. In restricted model a single set of parameters (3 parameters:  $\lambda$ ,  $\Delta t$ , and  $\hat{\sigma}$ ) was optimized for all validity conditions and trial types (all trials in 100%-, 75%-, 50%-validity conditions) for each participant. In unrestricted (or free) model five different sets of parameters were optimized; one for each trial type and each validity condition for each participant (5 conditions (100%, 75%-congruent, 75%-incongruent, 50%-congruent, 50%-incongruent) x 3 parameters = 15 parameters).

Next, a chi-square nested hypothesis test was performed to test whether the unrestricted model predicts the data better than the restricted model for each participant’s data. Twice the difference between the log-likelihoods of the two models has an approximate chi-square distribution, with degrees of freedom equal to 12, which is the difference in the number of parameters between the two models under the null hypothesis. Accordingly, the null hypothesis is rejected if

$$2 \times (\log L_1 - \log L_0) \geq \chi_{12}^2, \quad (3.10)$$

where the likelihoods  $L_0$  and  $L_1$  are calculated for the restricted and unrestricted model respectively.

Note that  $L$  is defined as

$$L = \prod_{i=1}^n P(Y_i|B_{model}), \quad (3.11)$$

where  $n$  is equal to the total number of trials in each experimental condition,  $Y_i$  corresponds to the participant’s response in each trial, and  $B_{model}$  corresponds to the model’s prediction at each duration presentation level.

### 3.4 Results

Modeling findings showed that our Bayesian scheme can successfully capture the pattern observed in the real observers as seen in Figure 3.3, 3.4, 3.5, 3.6, 3.7, 3.8, 3.9, and 3.10. The figures show Bayesian model fits of all validity conditions and trial types for restricted and unrestricted model for each participant. Similar to the results of 75%-validity condition in psychophysical findings in Chapter 2, Bayesian fits of incongruent trials (in both models) are also shifted compared to the congruent trials. This indicates that participants require a longer time to detect the location of an image presentation if it is an incongruent trial.

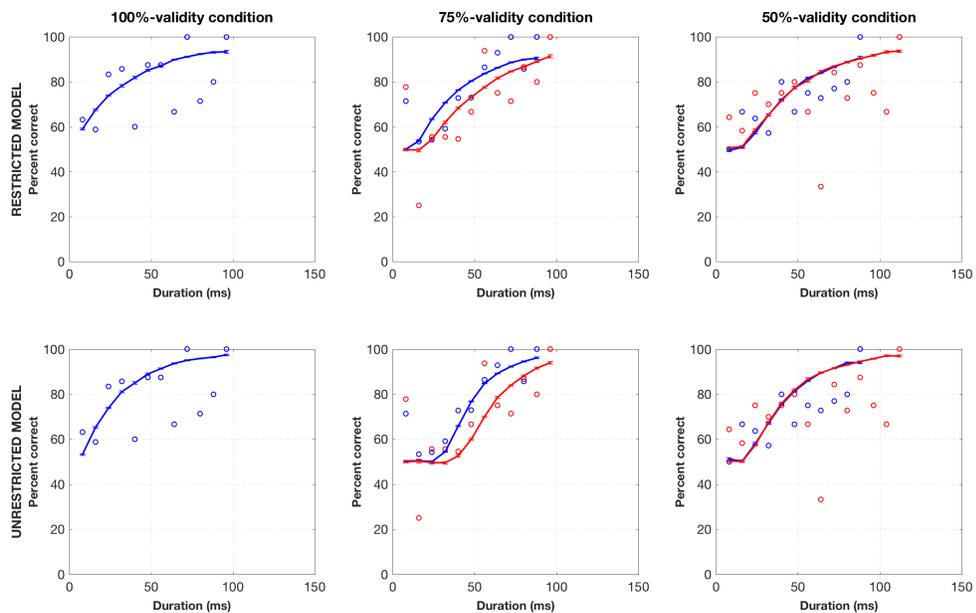


Figure 3.3: **Bayesian model fitting of restricted and unrestricted model for Subject 1.** Upper panel shows results of the restricted model and lower panel shows results of the unrestricted model for 100%, 75% and 50%-validity conditions. Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

In order to examine whether any change in the underlying parameters of the system leads to the longer durations in incongruent trials, we compared the restricted and unrestricted models. The results of the likelihood-ratio tests showed

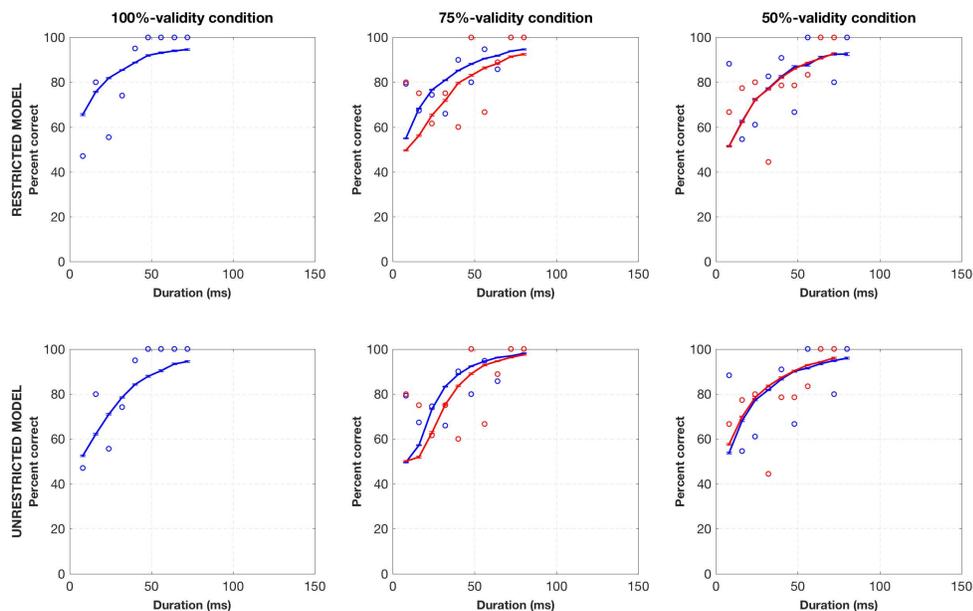


Figure 3.4: **Bayesian model fitting of restricted and unrestricted model for Subject 2.** Upper panel shows results of the restricted model and lower panel shows results of the unrestricted model for 100%, 75% and 50%-validity conditions. Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

that the two models are not different from each other in any participant. This suggests that the internal parameters ( $\lambda$ ,  $\Delta t$ ,  $\hat{\sigma}$ ) do not change with expectation (trial types: congruent, incongruent) and/or its validity.

Based on the findings on model comparison, we anticipated that the number of iterations that are needed to make a decision would change based on expectation. Specifically, the number of iterations calculated by the model would be greater for the incongruent trials. To test our second hypothesis, we calculated the number of iterations computed by the (restricted) model in congruent and incongruent trials in all validity conditions. Figure 3.11 shows results of number of iterations (posteriors) computed in each validity condition and trial type.

We performed 2 (congruency: congruent, incongruent) x 2 (validity: 75%, 50%) repeated measures ANOVA to investigate the effect of congruency and validity on

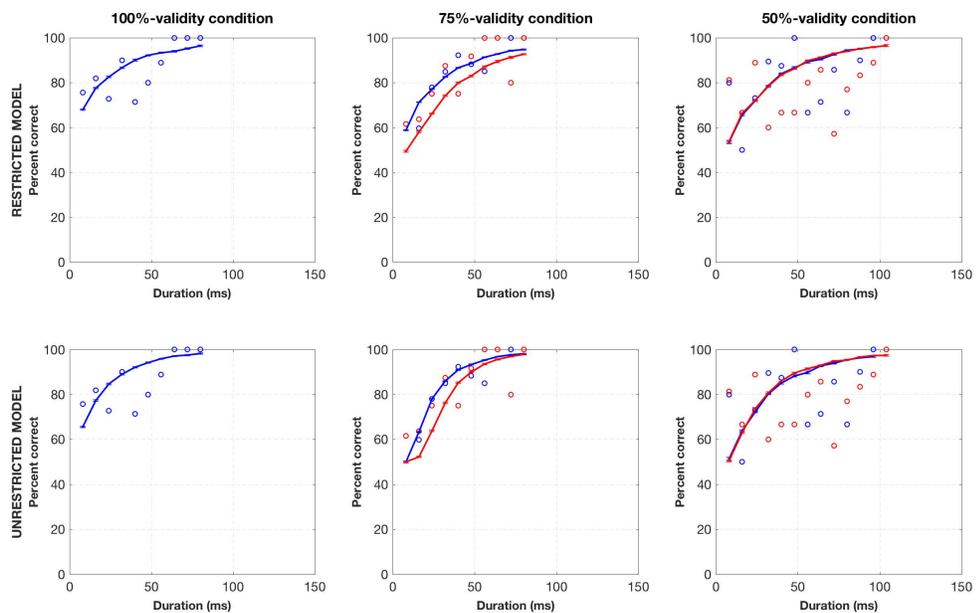


Figure 3.5: **Bayesian model fitting of restricted and unrestricted model for Subject 3.** Upper panel shows results of the restricted model and lower panel shows results of the unrestricted model for 100%, 75% and 50%-validity conditions. Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

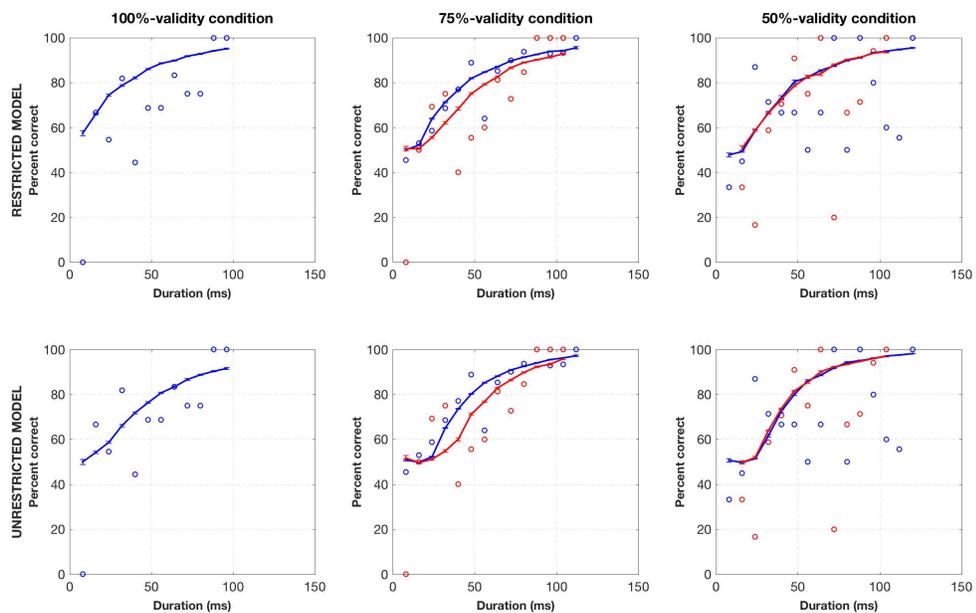


Figure 3.6: **Bayesian model fitting of restricted and unrestricted model for Subject 4.** Upper panel shows results of the restricted model and lower panel shows results of the unrestricted model for 100%, 75% and 50%-validity conditions. Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

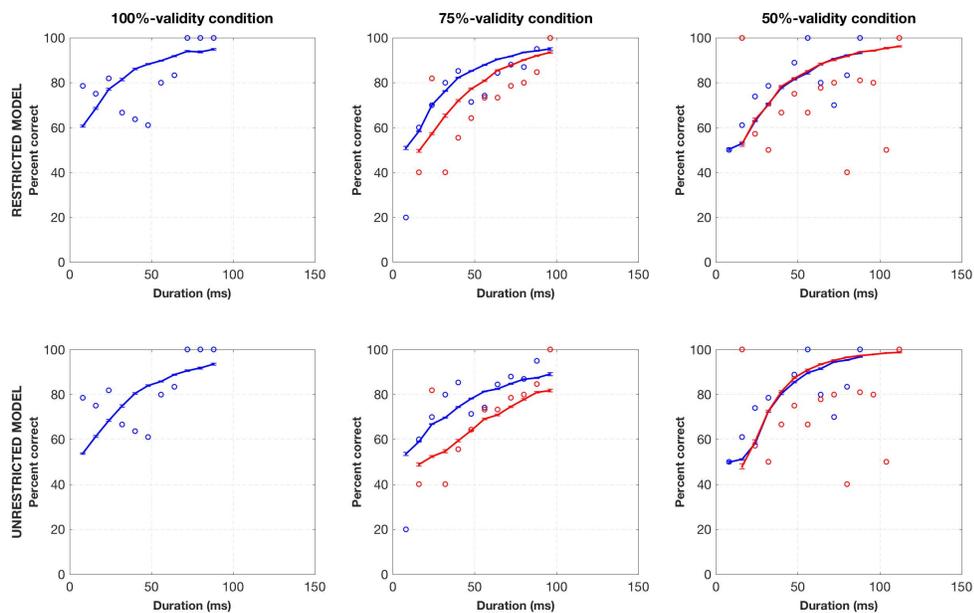


Figure 3.7: **Bayesian model fitting of restricted and unrestricted model for Subject 5.** Upper panel shows results of the restricted model and lower panel shows results of the unrestricted model for 100%, 75% and 50%-validity conditions. Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

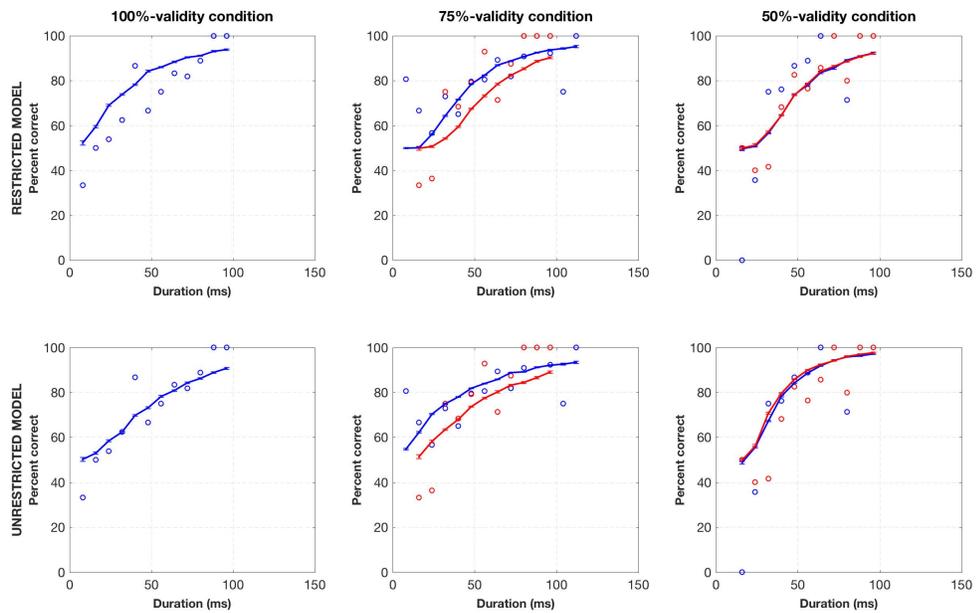


Figure 3.8: **Bayesian model fitting of restricted and unrestricted model for Subject 6.** Upper panel shows results of the restricted model and lower panel shows results of the unrestricted model for 100%, 75% and 50%-validity conditions. Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

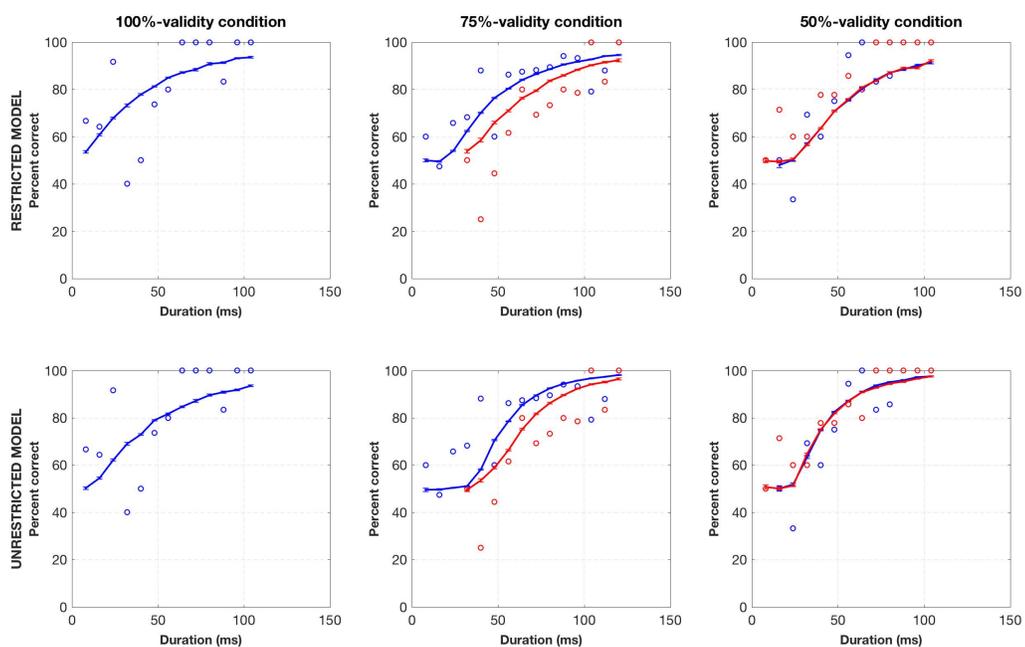


Figure 3.9: **Bayesian model fitting of restricted and unrestricted model for Subject 7.** Upper panel shows results of the restricted model and lower panel shows results of the unrestricted model for 100%, 75% and 50%-validity conditions. Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

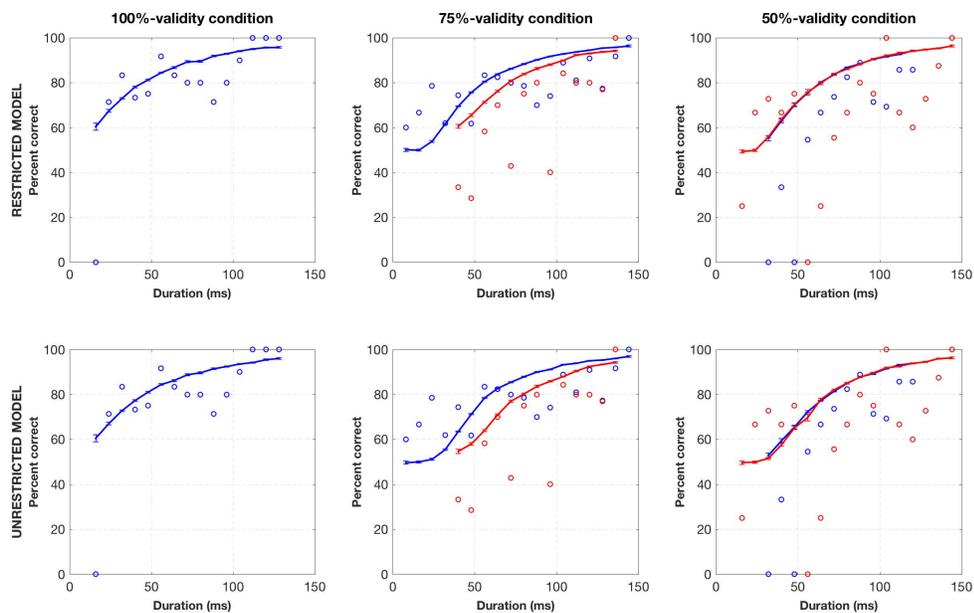


Figure 3.10: **Bayesian model fitting of restricted and unrestricted model for Subject 8.** Upper panel shows results of the restricted model and lower panel shows results of the unrestricted model for 100%, 75% and 50%-validity conditions. Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

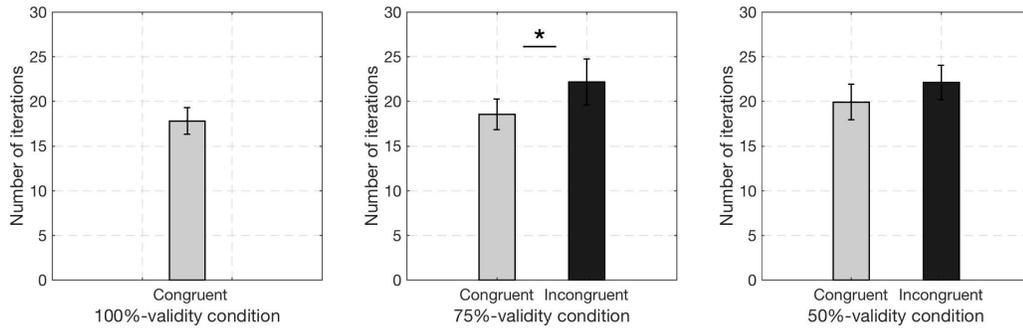


Figure 3.11: **Number of iterations, N (posterior computations) in congruent and incongruent trials in all validity conditions averaged across all observers' fits.** a. 100%-validity condition. b. 75%-validity condition. c. 50%-validity condition.

number of iterations (posteriors). As expected, the main effect of congruency was significant ( $F(1,7) = 13.987, p = 0.007$ ). However, there were no main effect of validity and interaction ( $F(1,7) = 0.348, p = 0.574$ ;  $F(1,7) = 0.669, p = 0.440$ ).

Next, we tested whether the number of iterations differ based on congruency specifically in each validity condition. In 75%-validity condition number of posteriors computed in incongruent trials are higher than the congruent trials ( $t(7) = 3.467, p = 0.010$ ). However, there was no difference between congruent and incongruent trials in 50%-validity condition ( $t(7) = 1.950, p = 0.092$ ). Also, there was no difference in number of iterations between (1) congruent trials of 75%- and 100%-validity conditions as well as between (2) congruent trials of 50%- and 100%-validity conditions ( $t(7) = 1.085, p = 0.314$ ;  $t(7) = 1.948, p = 0.092$ ). Overall these results agree well with the behavioral data.

### 3.5 Summary and Conclusions

In this chapter we investigated the possible mechanisms that underlie the effect of expectation on perceptual thresholds. In Chapter 2 our behavioral findings revealed that unmet expectations lead to higher perceptual thresholds. Here, we took a step further and examined why there is such a difference between

the thresholds of expected and unexpected trials. For this aim, we modeled our behavioral data with a Bayesian model.

Overall, our modeling results agree well with the behavioral findings. That is, similar to the human observers the Bayesian model predictions (for a certain success level) are shifted in unexpected trials only in 75%-validity condition. The model comparison analysis showed that the unrestricted (free) model does not explain the empirical data better than the restricted model. This indicates that expectations do not lead to a change in the internal parameters of the system. This finding may be interpreted as inconsistent with some previous findings in the literature. For instance, in a study by [32] the authors suggested that expectations can change internal parameters, specifically internal threshold. The empirical data in that study was modeled with a drift-diffusion model (DDM) [31], and it was found that unmet expectations lead to higher boundary separation parameter, which is considered to be the internal threshold to reach a decision in the system. Considering that the experimental paradigm used in that study is also similar to the present study, our results may seem to be inconsistent with their findings. However, it should be noticed that the dependent measures used in the two studies are different. In that study reaction time of individuals were recorded, which incorporates not only early sensory processes but also several information processing stages including non-decision processes. Therefore, we argue that their findings, i.e. a change in the internal parameters, may not *only* rely on early sensory processes. On the other hand, in the present study as the perceptual thresholds are measured we could directly tap into sensory processes. Further to that the DDM model may not be as efficient as the Bayesian model in some respects, and they are discussed in detail in General Discussion section.

As no change was found in the internal parameters, we specifically examined the number of iterations computed for expected and unexpected trials. Our results showed that the model needs to calculate more iterations in unexpected trials than expected trials. This reveals that longer processing is required by the system to make a successful decision when expectations are not met. We suggest that this longer processing might be the mechanism underlying higher perceptual

thresholds in the unexpected trials in the behavioral experiments.

Taken together, the modeling findings indicated that our Bayesian updating scheme can capture the effects found in the behavioral experiments in Chapter 2. As a next step, it is important to examine whether or not this can be generalized to other visual stimuli and perceptual tasks. We addressed this issue in Chapter 4. Also, modeling the behavioral data within the Bayesian framework allowed us to examine the possible mechanisms underlying the behavioral effects found in Chapter 2. We found that further, and consequently longer processing, may lead to higher perceptual thresholds in unmet expectations. In order to discuss possible neural mechanisms underlying this finding we implemented a mechanistic cortical model in Chapter 5, and modeled the same empirical data using this cortical model.

# Chapter 4

## Generalization of the Bayesian model predictions on empirical data

### 4.1 Introduction

In Chapter 3 we investigated the computational mechanisms underlying the effect of expectations on visual perception. For this aim, we implemented a recursive Bayesian updating scheme to model our behavioral data. Our findings indicated that the Bayesian model can successfully predict the effects observed in the empirical data. Specifically, in unexpected trials the predictions of the model shift to the right, indicating that the model can make a successful decision in higher threshold values in unexpected trials compared to the expected ones. Even though our modeling findings are quite promising to indicate that our model can successfully approximate the real observer data, it is also important to examine the generalization of these findings. This would allow us to extend our findings to other visual features and perceptual tasks. For this aim, in this Chapter we modeled the experimental data of another study where the effect of expectations on contrast thresholds is investigated [74]. This way we aimed to confirm that the Bayesian modeling findings in Chapter 3 can be generalized to other visual features and perceptual tasks as well.

## 4.2 Methods

### 4.2.1 Details about the Experiment

Stimuli, experimental design and procedure of this experiment can be found in ref. [74] in detail. Briefly, at the beginning of each trial participants were shown a predictive cue, either a vertical or horizontal grating, at the center of the screen. This cue were informative about the upcoming target stimulus orientation with a certain probability. Next, the target stimulus, a vertical or horizontal grating embedded in noise, was shown on the left or right periphery simultaneously with a random noise pattern at the opposite side. Participants' task was to report the spatial location of the grating. As in the experiment in Chapter 2 the validity of the cue was 100%, 75%, and 50% in different experimental sessions.

As stated above, the task in this experiment [74] was exactly the same as in the experiment in Chapter 2. However, there are two main differences between the two experiments. First, the stimuli used in this experiment were gratings, instead of face or house images. Also, the duration presentation of the gratings was kept constant, but at each trial the contrast of the gratings was changed adaptively. Therefore, the contrast detection thresholds were measured for each participant for each validity condition. Overall, the results of this experiment showed that incongruent (unexpected) trials can be detected in higher contrast values compared to congruent (expected) trials in 75%-validity condition, but not in 50%-validity condition [74].

### 4.2.2 Modeling

In order to model the empirical data of the experiment [74], we used the same recursive Bayesian updating scheme implemented in Chapter 3. However, we made some modifications in the model based on the current experimental design. Details can be found in the next section.

### 4.2.2.1 Implementation of the model

We implemented the following calculations for left and right observations separately.

First, feature values for the *input* were defined:

$$s = \begin{cases} s_1 = 0 & \text{for a horizontal grating} \\ s_2 = 90 & \text{for a vertical grating.} \end{cases} \quad (4.1)$$

It is postulated that the abstracted observation extracted by the system,  $x_t$ , is drawn from a normal distribution

$$x_t \sim N(s, \hat{\sigma}). \quad (4.2)$$

During each trial we calculated  $x_t$  at iteration  $t$  based on the presented grating on the corresponding location. Note that

$$\hat{\sigma} = \frac{\sigma}{C_i} \quad (4.3)$$

where  $C_i$  corresponds to the contrast of the grating at each trial.

We defined generative models for each decision alternative,  $A_i$ :  $A_1$  for horizontal grating,  $A_2$  for vertical grating, and  $A_3$  for noise. We calculated the likelihood of  $x_t$  under  $A_1$  and  $A_2$  as

$$p(x_t|A_i) = \frac{1}{\hat{\sigma}\sqrt{2\pi}} \exp\left(-\frac{(x_t - s_i)^2}{2\hat{\sigma}^2}\right). \quad (4.4)$$

Note that we separately defined  $A_3$ , noise, as

$$p(x_t|A_3) = 1/180. \quad (4.5)$$

Next, the initial values of the priors were defined as

$$p(A_i) = c_i, \quad i = 1, 2, 3 \quad (4.6)$$

where  $c_i$  are defined based on the cue validity (i.e. 100%, 75% or 50%), and the cue presented at that trial (i.e. vertical or horizontal grating). For example in a

trial under the 75%-validity condition if the cue is a *horizontal grating* then the priors are

$$c_1 = 3/8, c_2 = 1/8, c_3 = 4/8 \quad (4.7)$$

or in a trial under the 50%-validity condition if the cue is a *vertical grating* then the priors are

$$c_1 = 2/8, c_2 = 2/8, c_3 = 4/8. \quad (4.8)$$

Next, we combined the likelihoods with the priors to compute posterior estimates for each decision alternative as follows

$$p(A_i|x_1) = \frac{p(x_1|A_i)p(A_i)}{\sum_{j=1}^3 p(x_1|A_j)p(A_j)}. \quad (4.9)$$

In a single trial posterior estimates are updated recursively over time ( $N$  times: number of iterations) until a decision is made by the model

$$p(A_i|x_{1:t}) = \frac{p(x_t|A_i)p(A_i|x_{1:t-1})}{\sum_{j=1}^3 p(x_t|A_j)p(A_j|x_{1:t-1})}. \quad (4.10)$$

Number of iterations,  $N$ , in a single trial is determined by

$$N = \tau/\Delta t \quad (4.11)$$

where  $\tau$  represents the duration of presentation of the target grating in each trial (i.e. 33 ms), and  $\Delta t$  defines how long each iteration lasts in the system. Next, we calculated the *total probability of observing a target grating (vertical or horizontal)* for each location,  $T_{LEFT}$  and  $T_{RIGHT}$ , as the sum of the final posterior of vertical grating and horizontal grating. Finally, a final decision is made by the model using the same criteria shown in Figure 3.2.

### 4.3 Results

We optimized three free parameters in the model;  $\lambda$  (decision threshold),  $\Delta t$  (how long each iteration lasts in the system), and  $\sigma$  (the internal uncertainty

of the decision maker’s representation of its observations). Using the optimized parameters 1000 simulations were run for each participant’s data in each validity condition (100%-, 75%-, 50%-validity conditions).

Figure 4.1, 4.2, 4.3 and 4.4 show model simulations of all validity conditions and trial types for each participant. Similar to the findings in Chapter 3 the Bayesian model simulations of incongruent trials in this experiment are also shifted to the right only in 75%-validity condition. There is not a clear difference between congruent and incongruent trials in 50%-validity condition. This shows that the model requires higher contrast to detect the spatial location of the grating in incongruent trials when the expectation’s validity is relatively high (i.e. 75%).

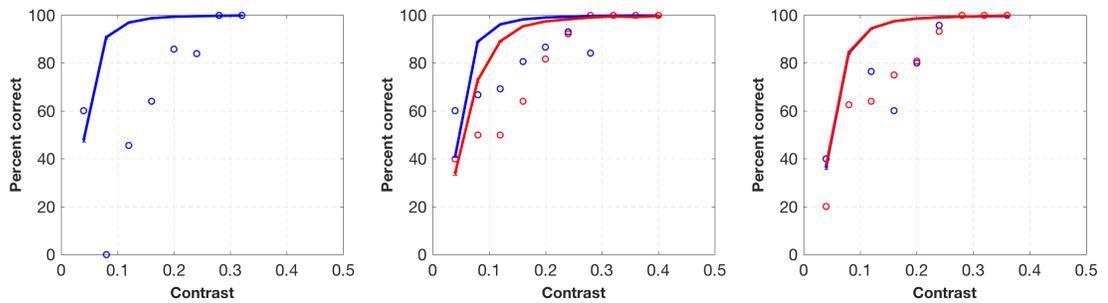


Figure 4.1: **Bayesian model fitting of a single participant (participant 1) in contrast detection experiment.** Panels show results of 100% (left), 75% (middle) and 50%-validity (right) conditions respectively. Blue circles indicate observer data in congruent trials, and red circles indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

## 4.4 Summary and Conclusions

In this study we aimed to extend our findings on Chapter 3, where we investigated the effect of expectation on duration thresholds using a recursive Bayesian model. In that study our findings showed that the Bayesian model predictions can approximate the effects observed in the real data. In this chapter we examined whether this can be extended to another perceptual task which uses a

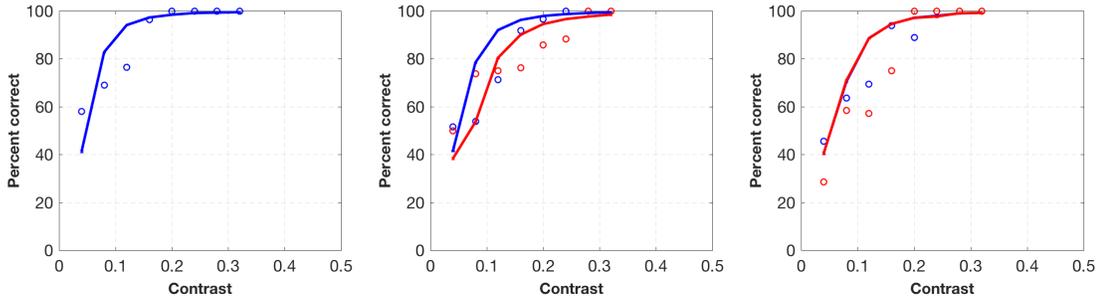


Figure 4.2: **Bayesian model fitting of a single participant (participant 2) in contrast detection experiment.** Panels show results of 100% (left), 75% (middle) and 50%-validity (right) conditions respectively. Blue circles indicate observer data in congruent trials, and red circles indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

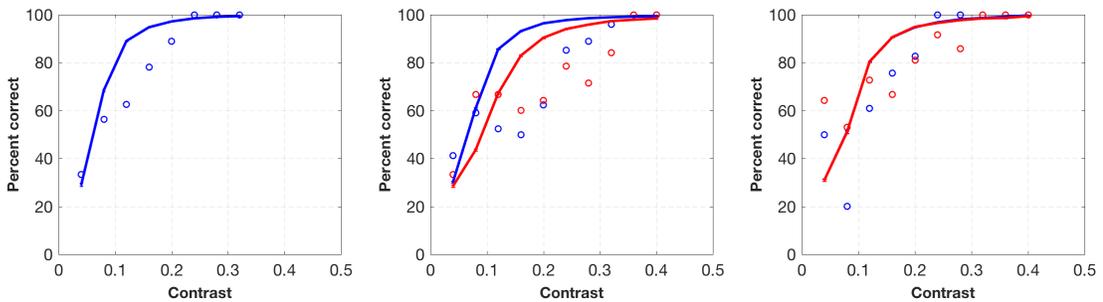


Figure 4.3: **Bayesian model fitting of a single participant (participant 3) in contrast detection experiment.** Panels show results of 100% (left), 75% (middle) and 50%-validity (right) conditions respectively. Blue circles indicate observer data in congruent trials, and red circles indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

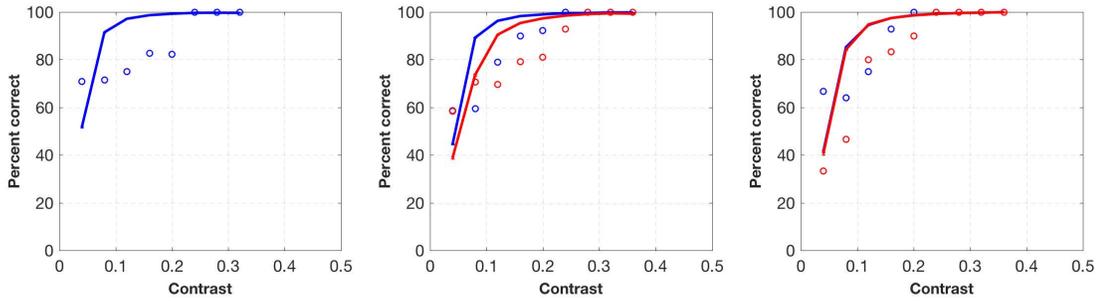


Figure 4.4: **Bayesian model fitting of a single participant (participant 4) in contrast detection experiment.** Panels show results of 100% (left), 75% (middle) and 50%-validity (right) conditions respectively. Blue circles indicate observer data in congruent trials, and red circles indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

different visual feature.

Here, we modeled another experimental data [74] using the same Bayesian model. In that experiment the aim was to investigate the effect of expectation on contrast detection thresholds. The behavioral findings indicated that the thresholds were higher in incongruent trials than congruent trials [74]. In this chapter, we modeled each participant’s data for each validity condition using the Bayesian model. Our modeling findings showed that the model can successfully capture the pattern observed in the real data. Specifically, the model was able to make a decision at higher contrast levels in incongruent trials compared to congruent trials. This finding indicates that the results in Chapter 3 can be extended to another visual feature (orientation) and perceptual task (contrast detection threshold). Future work can further investigate whether our findings can be generalized to other visual features and perceptual tasks.

Overall, the behavioral and the Bayesian modeling findings showed that when expectations are not met, additional processing may be required to complete the sensory process. In order to discuss possible neural mechanisms that may account for this finding we implemented a mechanistic cortical model in Chapter 5, and modeled the empirical data obtained in Chapter 2.

# Chapter 5

## A recurrent cortical model: a bridge that links the behavior to brain

### 5.1 Introduction

Bayesian approaches to understand the brain function, not only behavior, have gained considerable interest in literature [5, 56, 55]. Empirical findings have been interpreted within the framework of these mechanistic models, which are also called *predictive processing* models. Despite certain differences in the structure of these models, at a common and fundamental level these models suggest that information processing in the brain can be implemented via dynamic interplay between bottom-up sensory input and top-down effects of prior knowledge. Currently we have considerable amount of evidence that is in agreement with the main assumptions of these models, however, a very crucial step has been overlooked in many studies. Unlike Bayesian models of behavior, the proposed mechanistic models have not been usually employed to empirically test whether those models can explain real human data. Conceptual interpretation of empirical findings as consistent with a computational model would be a post-hoc evaluation of results. Even though this is an important step, without a rigorous effort to perform modeling on empirical data, it may not be possible to see whether the assumptions

of the models comply with the empirical evidence.

Recently a biologically plausible and empirically testable mechanistic cortical model has been proposed in which neural activity in each brain region is determined by feedforward drive, feedback drive, and prior drive [5]. Feedforward drive indicates the relevant activity driven by sensory input. Prior drive reflects the prior knowledge, and feedback drive indicates the context-based information from the next processing stage. It is proposed that the terms of the energy function in this model are analogous to the ones in Bayesian inference [5]. Thus, the theory can sometimes approximate Bayesian inference. In the model two main state parameters are proposed, which govern the contribution of the three drives. These state parameters are called  $\alpha$  and  $\lambda$ , which are suggested to correspond to neuromodulators and oscillatory activity. Figure 5.1 shows a simplified illustration of the model.

In Figure 5.1, panel A and B show a network architecture with only feedforward drive. Each box in A shows a channel, and several number of neurons are suggested to exist at each channel. As can be seen in B, a neuron's response ( $Y_i^{(j)}$ ) is calculated as follows: first it gets input from the previous layer ( $Y_{i-1}^{(j)}$ ) and computes a weighted sum of its input ( $V_i^{(j)}$ ). Since it is assumed that there is a non-linear computation here, this weighted sum is followed by an output nonlinearity ( $Z_i^{(j)}$ ). In other words, a neuron's response ( $Y_i^{(j)}$ ) is the nonlinear function of weighted sum of its input in a feedforward structure.

In Figure 5.1 panel C and D, a recurrent neural model is proposed [5]. Here, there is feedforward drive, feedback drive and prior drive. In this model, the same computations are implemented for feedforward processing as in B, but the neuron's activity is not only based on the feedforward drive. Feedback drive from the next layer ( $Y_{i+1}^{(k)}$ ) also contributes to the processing. In addition, the same neuron receives prior input, which can be either static or computed recursively. Thus, the response of each neuron is updated over time through the three inputs: feedforward drive, feedback drive, and prior drive. Note that each neuron provides two outputs in time: (1) feedforward drive to the next layer, and (2) feedback drive to the previous layer. The computations shown in Figure 5.1 panel D

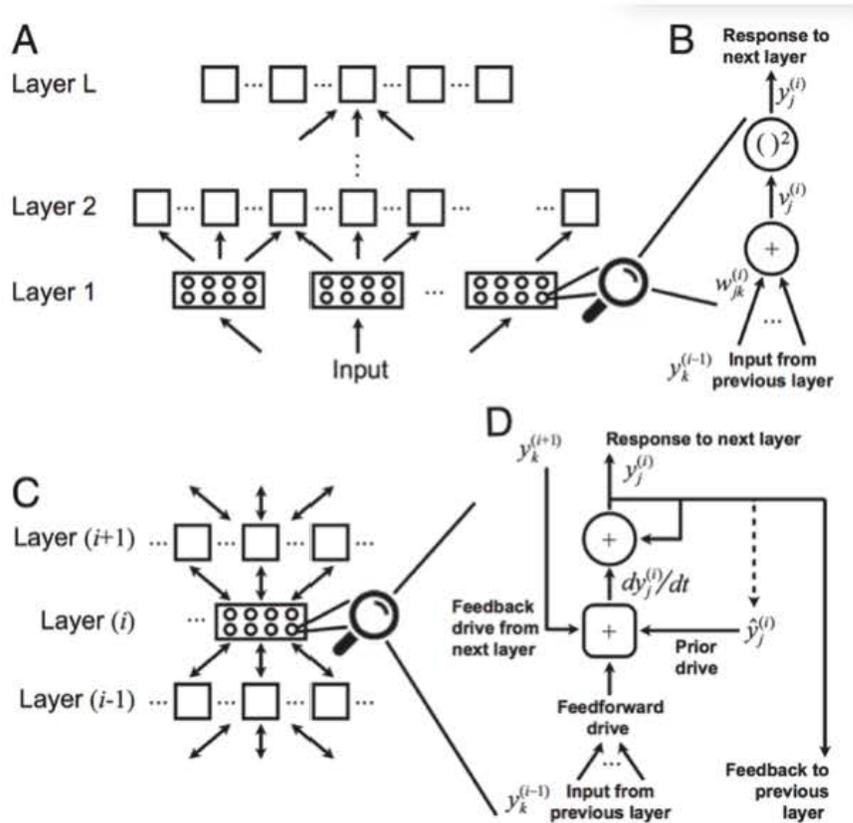


Figure 5.1: **Neural network architecture.** Each square at each layer in the figure indicates a neural unit that includes thousands of neurons. Panel A and B show a feedforward architecture, where response of each neural unit only depends on input from the previous layer, and each unit also gives response to the next layer. Panel C and D shows a neural net structure where each neural unit gets input from the previous layer, gives response to the next layer, and it also gives feedback to the previous layer. Reprinted, with permission, from ref. [5]. See Appendix.

demonstrate a single neuron’s activity, but it is proposed that the responses of all neurons from all layers converge to minimize an energy function [5].

Note that the feedforward drive and feedback drive in this model are also analogous to those in the predictive coding models [55]. However, there are some certain differences in the model structures and theoretical constructs between the two models. For instance, in this model different subpopulations of neurons for prediction or error computation are not specified. On the other hand, in the predictive coding models when there is a mismatch between the predictions and the actual sensory input, prediction errors are suggested to be computed by specific subpopulations of neurons (error units), which are propagated forward in time. In line with this, several empirical findings in the literature showed an increased neural activity (e.g. BOLD response) to an unexpected stimulus compared to an expected stimulus (e.g., [16, 75, 76]). In some studies this finding was interpreted to reflect the prediction error signal of the error units. On the other hand, when an expected stimulus is presented, even though there is a match between the predictions and the sensory input, a sustained neural activity exists and does not go to zero in time, which is suggested to be inconsistent with the findings in the literature [5].

In this study, we implemented the model proposed in ref. [5], and adapted this model to our experimental paradigm. Our aim was to examine whether a mechanistic cortical model can explain the empirical findings observed in the behavioral experiments. For this aim, we modelled our behavioral data with the cortical model. Further to that we believe that as we also modeled the same data with a Bayesian model in Chapter 3, this application would also allow us to see whether the behavioral model and the cortical model findings are consistent with each other. Following sections describe the implementation of the cortical model used in the current work.

## 5.2 Methods

### 5.2.1 Energy Function

In the current model, the response of each neuron is updated by the contributions from the three inputs: feedforward drive, feedback drive, and prior drive. Figure 5.2 shows a simplified outline of the model and the calculations, and Figure 5.3 shows a simple illustration of the cortical model.  $Y_{ij}$  indicates unit responses for house, scrambled and face images respectively in each layer:  $i$  indicates layer number and  $j$  indicates unit number. See Table 5.1 for notations in the cortical model.

Here's the energy function of the current model:

$$E = \sum_{j=1}^3 \alpha^{(j)} \left[ \gamma^{(j)} \sum_{i=1}^3 \left( f_i^{(j)} \right)^2 + (1 - \gamma^{(j)}) \sum_{i=1}^3 \left( P_i^{(j)} \right)^2 \right], \quad (5.1)$$

where indices  $i$  and  $j$  run over units and layers respectively, and

$$\begin{aligned} f_i^{(j)} &= (Y_i^{(j)} - Z_i^{(j)})^2 \quad (\text{feedforward drive}) \\ Z_i^{(j)} &= \left[ \sum_{k=1}^3 W_{i,k}^{(j-1)} Y_k^{(j-1)} \right]^2 \\ P_i^{(j)} &= (Y_i^{(j)} - \hat{Y}_i)^2 \quad (\text{prior drive}), \end{aligned} \quad (5.2)$$

$\hat{Y}_i$  are priors,  $Y_i^{(j)}$  are unit responses. The parameters  $\gamma^{(j)}$  can have values between 0 and 1, and determine the relative weights of the feedforward and prior drives, whereas  $\alpha^{(j)}$  determine relative contributions of layers.  $W_{i,k}^{(j-1)}$  are the weights of connections between units of different layers. Unit responses are updated by minimizing the energy function (Eq. 5.1) with respect to  $Y_i^{(j)}$  using gradient descent:

$$Y_i^{(j)}(t) = Y_i^{(j)}(t-1) - a \frac{\partial E}{\partial Y_i^{(j)}}, \quad i, j = 1, 2, 3; \quad 0 < t \leq N \quad (5.3)$$

where  $a$  is the inverse of a time constant and equal to 1/5. Note that the feedback and ‘‘horizontal’’ interactions between different units in the same layer emerge in the equations after taking the derivative of the energy function. Number of

iterations,  $N$ , is determined by

$$N = \tau / \Delta t \quad (5.4)$$

where  $\tau$  is the duration of presentation of the images in the trial, and  $\Delta t$  determines how long each iteration lasts in the system. At the beginning of a trial ( $t = 0$ ) intermediate layer unit responses are randomly drawn from a normal distribution with mean 0

$$Y_i^{(j)} \sim N(0, \sigma_u), \quad i, j = 1, 2, 3, \quad (5.5)$$

where  $\sigma_u$  defines the noise in unit responses [77].

The values of the priors,  $\hat{Y}_i$ , are initialized based on the *cue* and its *validity* at the beginning of a trial ( $t = 0$ ). Later ( $t > 0$ ) the priors are updated based on the responses of layer 3 units in previous iterations. This amounts to using priors that are updated over time.

## 5.2.2 Implementation of the cortical model

The following calculations are done separately for the observations on the left and right side of the screen. At the beginning of each trial ( $t = 0$ ) we computed the layer and unit responses as following:

### 5.2.2.1 Input layer

We first defined the input,  $\mathbf{s} = (s_1, s_2, s_3)$ , as a three element vector

$$\mathbf{s} = \begin{cases} (1, 0, 0) & \text{for a house image} \\ (0, 1, 0) & \text{for a scrambled image} \\ (0, 0, 1) & \text{for a face image,} \end{cases} \quad (5.6)$$

and at each iteration we computed a noisy abstracted observation

$$x_i \sim N(s_i, \sigma_s). \quad (5.7)$$

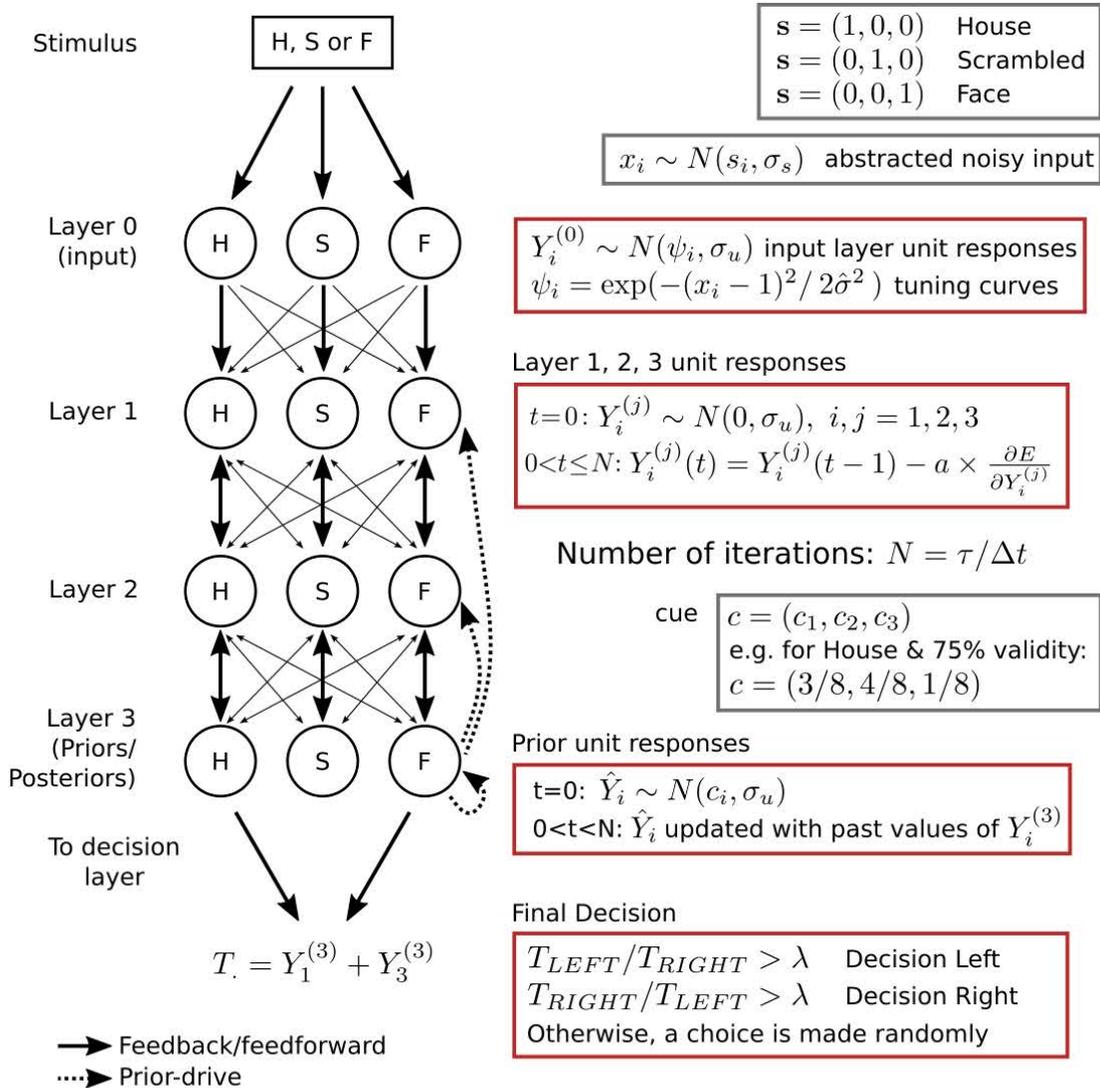


Figure 5.2: **Cortical model.** The model has one input, one decision and three intermediate layers, and three category-specific feature units for house (H), face (F) and scrambled (S) images. Weights of the connections are depicted by the thickness of the arrows. Priors,  $\hat{Y}_i$ , are initialized in the beginning of the trial based on the cue and its validity. Later they are updated with past values of layer 3 unit responses. All unit responses are updated until the end of the presentation. Number of iterations in a trial is determined by the stimulus presentation duration,  $\tau$ , divided by  $\Delta t$ , where  $\Delta t$  defines how long each iteration lasts in the system. A final decision is made by the model based on the sum of layer 3 house and face unit responses on the left and right side of the visual field.

Table 5.1: **Notations for cortical model.**  
**Description**

Symbol	Description
$E$	Energy function (minimized)
$\mathbf{s} = (s_1, s_2, s_3)$	Feature (category) value that would be extracted by the system under a noise-free observation. (1,0,0): House; (0,1,0): Scrambled; (0,0,1): Face
$x_i(t)$	Noisy sensory input to unit $i$ in layer 0 at iteration $t$ , drawn from a normal distribution with mean $s_i$ and variance $\sigma_s^2$
$\psi_i$	Tuning curves at the input layer
$Y_i^{(j)}$	Response of the $i$ th unit in layer $j$ , updated in each iteration to minimize $E$
$\hat{Y}_i$	Prior unit responses, updated in each iteration with past values of layer 3 unit responses
$f_i^{(j)}$	Feedforward drive for the $i$ th unit in layer $j$
$P_i^{(j)}$	Prior drive for $i$ th unit in layer $j$
$\gamma^{(j)}$	State parameter: trade-off between feedforward and prior drive
$\alpha^{(j)}$	State parameter: contribution of each layer to $E$
$W_{i,k}^{(j-1)}$	Weights of unit connections between $j$ -th layer and the layer below, $j - 1$
$\tau$	Presentation duration of the stimulus in a trial
$\lambda$	Decision criteria (free parameter)
$\Delta t$	How long each iteration lasts in the system (inverse of speed, free parameter)
$\hat{\sigma}^2$	Variance of input layer tuning curves (free parameter)
$N$	Number of iterations in a single trial, $\tau/\Delta t$

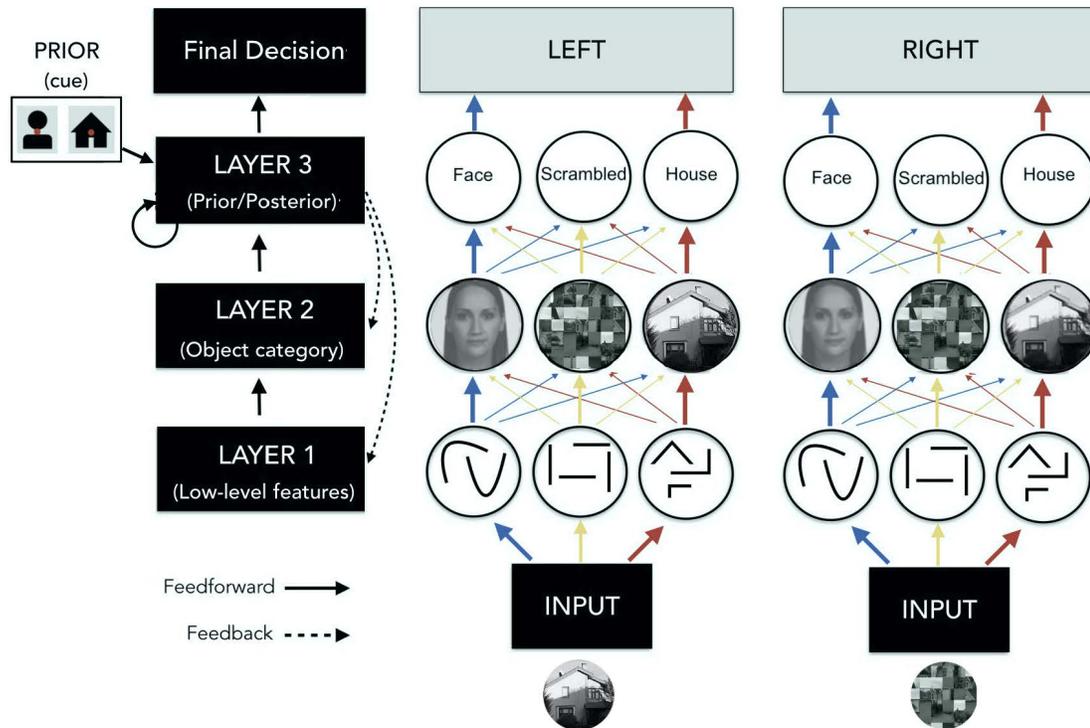


Figure 5.3: **A basic schematic illustration of the cortical model.** The model shows the same architecture as in Figure 5.2 except that here for simplicity only a feedback connection is shown in the left side of the figure, but all units (on the right side of the figure) have feedback connections with the previous layer. As input a house or face image and a scrambled version of it are given to the network. Layer 1 is assumed to process low-level features, which may correspond to early visual areas. Layer 2 is assumed to process higher-level visual information, e.g. object categories, which may correspond to fusiform face area (FFA) or parahippocampal place area (PPA). The cue, a face or a house sign, is assumed to drive Layer 3 unit responses at each trial, and the unit responses are updated recursively as shown in the figure. Finally, face and house unit responses are conveyed to the decision layer for the final decision.

where  $\sigma_s$  defines the noise level. Next, we calculated the input layer responses

$$Y_i^{(0)} \sim N(\psi_i, \sigma_u), \quad (5.8)$$

where  $\psi_i$  are tuning curves defined as

$$\psi_i = \exp(-(x_i - 1)^2 / (2\hat{\sigma}^2)). \quad (5.9)$$

Note that the input layer units did not receive any feedback or prior drive. They were also not involved in the energy minimization.

### 5.2.2.2 Prior

At the beginning of each trial ( $t = 0$ ) we defined initial prior probabilities,  $c = (c_1, c_2, c_3)$ , which depended on the cue and its validity. For example in a trial under the 75% validity condition, if the cue is a *face*,

$$c = (1/8, 4/8, 3/8). \quad (5.10)$$

or in a trial under the 50% validity condition, if the cue is a *house*,

$$c = (2/8, 4/8, 2/8). \quad (5.11)$$

Then we computed the activity of prior units at  $t = 0$  as follows:

$$\hat{Y}_i \sim N(c_i, \sigma_u). \quad (5.12)$$

For  $t > 0$ , the prior unit activities were updated recursively at each iteration (in a single trial) with the past values of  $Y_i^{(3)}$  unit responses. The values of  $Y_i^{(3)}$  in the previous iteration become the prior in the next iteration.

### 5.2.2.3 Decision

We calculated the sum of last layer's (Layer 3) face and house unit responses for left and right locations separately ( $T_{LEFT}$ ,  $T_{RIGHT}$ ). Then, a decision is made by

the model

$$(1) \quad T_{LEFT}/T_{RIGHT} > \lambda, \quad \text{decision: left} \quad (5.13)$$

$$(2) \quad T_{RIGHT}/T_{LEFT} > \lambda, \quad \text{decision: right}, \quad (5.14)$$

where  $\lambda$  is the decision threshold [78]. If these conditions are not satisfied, a decision is made randomly.

### 5.2.3 Cortical model fitting for individual data

We implemented a model for each validity condition: 100%, 75%, and 50%. Note that the only difference between the models is the initial values of the prior. Because the initial prior value is determined by the cue at each trial *and* its validity, these values are defined separately for the models of each validity condition for each trial.

Similar to the Bayesian model fitting, three parameters were optimized in our cortical model. These parameters were chosen based on the parameters used in the Bayesian modeling to keep the optimized parameters similar to each other in both models:

- (1)  $\lambda$ : decision threshold,
- (2)  $\Delta t$ : implies how long each iteration lasts in the system,
- (3)  $\hat{\sigma}^2$ : is thickness of input layer tuning curves.

Using the optimized parameter values we ran 1000 simulations of the model for each participant's data for congruent and incongruent trials for each validity condition.

## 5.3 Results

Figure 5.4, 5.5, 5.6, 5.7, 5.8, 5.9, 5.10, and 5.11 show cortical model simulations of all validity conditions and trial types for each participant. The cortical model

simulations of incongruent trials are shifted to the right only in 75%-validity condition just as the psychometric function fits and the Bayesian model predictions did, indicating that the cortical model requires a longer duration to detect the location of the target image in an incongruent trial.

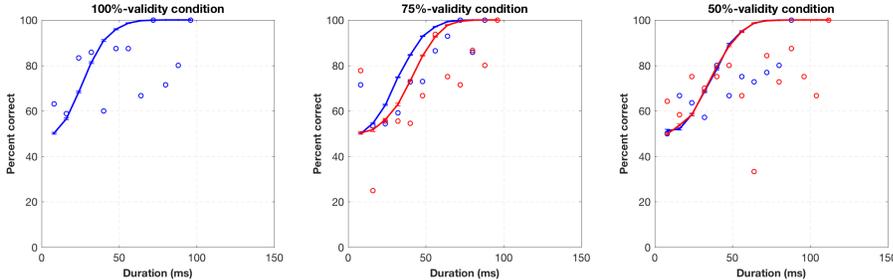


Figure 5.4: **Cortical model simulations for Subject 1.** Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

Next, we computed the number of iterations calculated at each validity condition as we did in Bayesian modeling. Figure 5.12 shows results of number of iterations performed in each validity condition and trial type. We performed 2 (trial type: congruent, incongruent trial) x 2 (validity: 75, 50) repeated measures ANOVA to investigate the effect of expectation and validity on number of iterations. We found that the main effect of trial type was statistically significant ( $F(1,7) = 18.511, p = 0.004$ ), but there were no main effect of validity

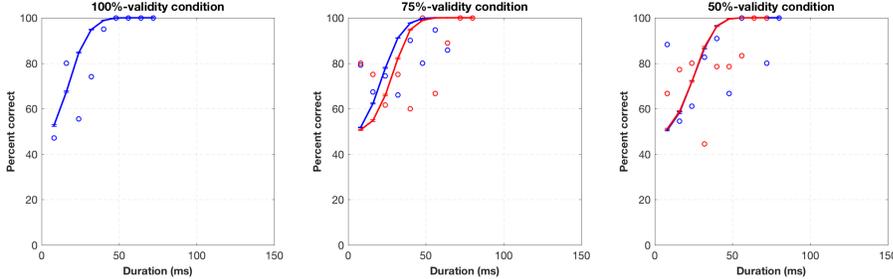


Figure 5.5: **Cortical model simulations for Subject 2.** Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

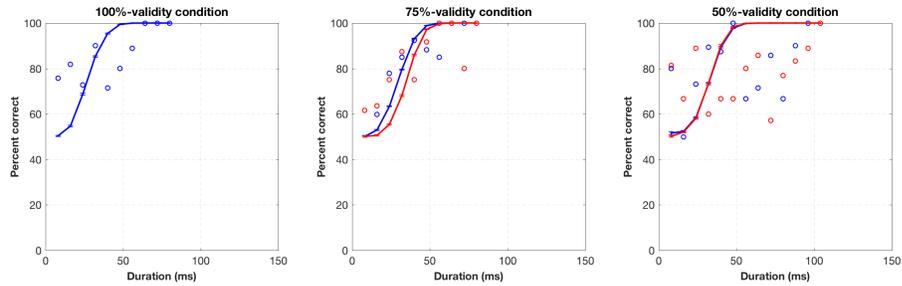


Figure 5.6: **Cortical model simulations for Subject 3.** Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

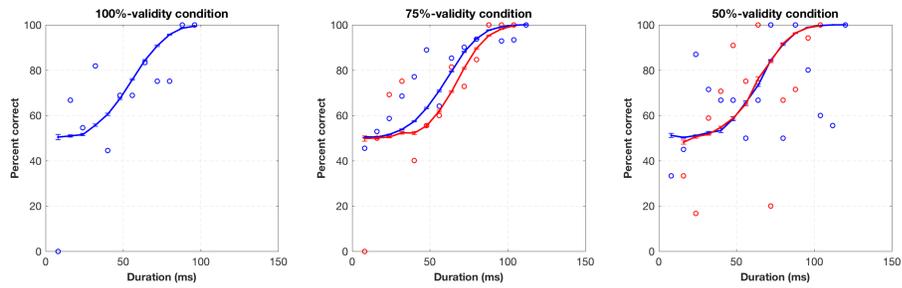


Figure 5.7: **Cortical model simulations for Subject 4.** Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

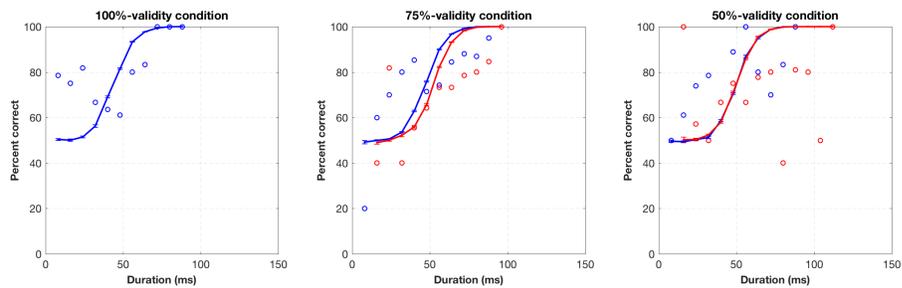


Figure 5.8: **Cortical model simulations for Subject 5.** Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

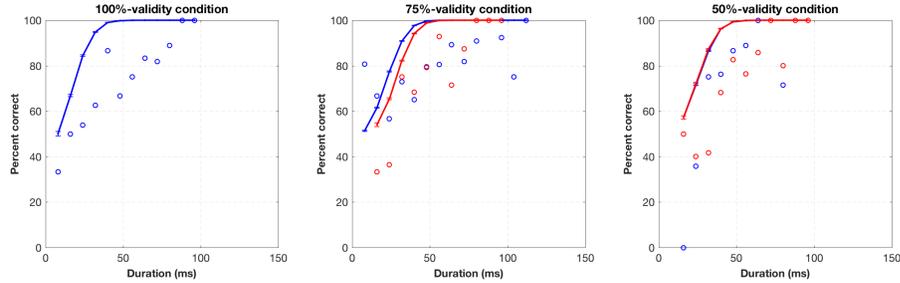


Figure 5.9: **Cortical model simulations for Subject 6.** Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

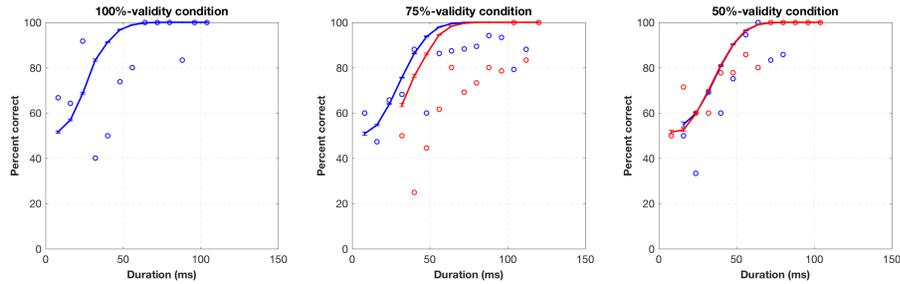


Figure 5.10: **Cortical model simulations for Subject 7.** Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

and interaction ( $F(1,7) = 0.299, p = 0.602$ ;  $F(1,7) = 0.738, p = 0.419$ ). Specifically, number of iterations were significantly higher in incongruent trials than congruent trials only in 75%-validity condition ( $t(7) = 3.220, p = 0.015$ ). There were no difference in number of iterations between (1) congruent and incongruent trials in 50%-validity condition ( $t(7) = 2.047, p = 0.08$ ), (2) congruent trials of 75%-validity and 100%-validity condition ( $t(7) = -1.247, p = 0.253$ ), and (3) congruent trials of 50%-validity and 100%-validity condition ( $t(7) = -1.829, p = 0.110$ ). These results are quite consistent with the behavioral findings as well as Bayesian modeling.

As the number of iterations in incongruent trials were found to be higher than congruent trials, we also examined how the model behaves in congruent and incongruent trials at the layer level. For this aim, we simulated unit responses of

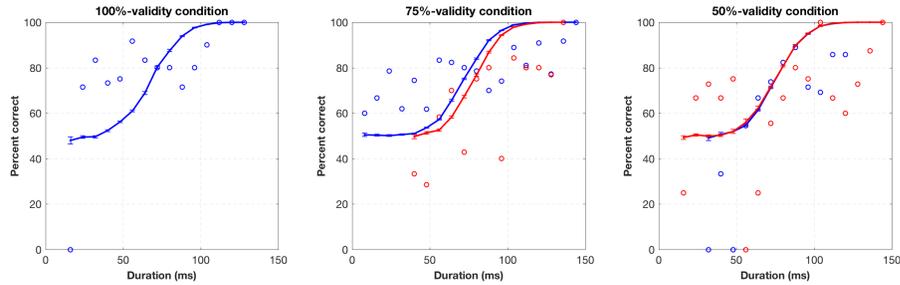


Figure 5.11: **Cortical model simulations for Subject 8.** Blue dots indicate observer data in congruent trials, and red dots indicate observer data in incongruent trials. Blue and red lines indicate model fits for congruent and incongruent trials respectively.

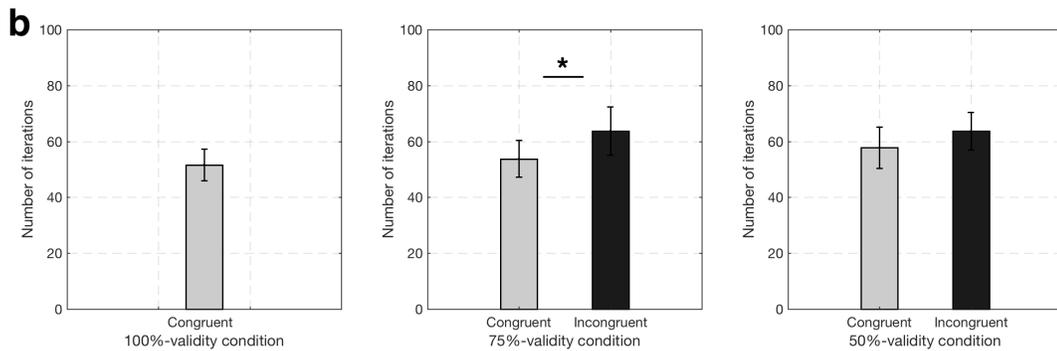


Figure 5.12: **Cortical model number of iterations,  $N$  (posterior computations) in congruent and incongruent trials in all validity conditions.** a. 100%-validity condition. b. 75%-validity condition. c. 50%-validity condition.

each layer for a congruent and incongruent trial in a 75%-validity condition.

Figure 5.13 shows cortical model unit responses at each layer throughout a trial specifically when a face-cue is presented in a 75%-validity condition. As can be seen in the figure both in a congruent and an incongruent trial face unit responses respond higher than other units at the beginning of the trial. However, this trend starts to change within the trial. Specifically, in the congruent trial the face units continue to be the most responsive unit until the end of the trial. However, in the incongruent trial the responses of face units are decreasing as a function of time while house unit responses are gradually increasing during that period.

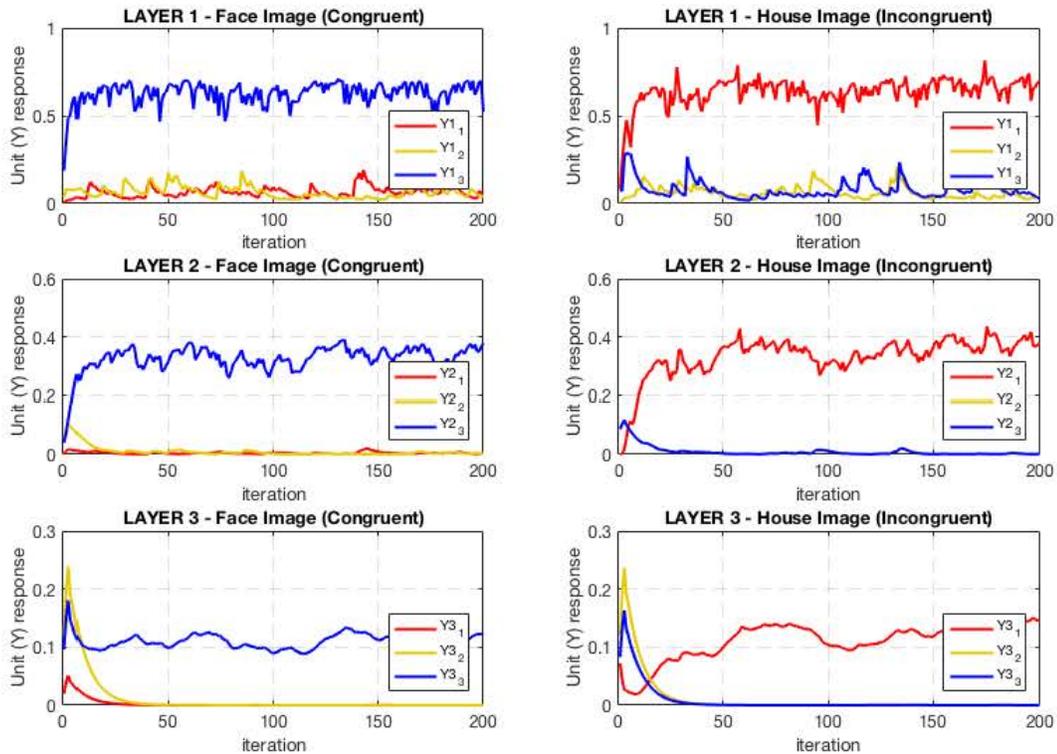


Figure 5.13: **Cortical model simulations for each unit response at each layer.** This simulation shows category-specific (face (blue), house (red) and scrambled (yellow)) unit responses in a congruent (left) and incongruent (right) trial when a *face cue* is presented in a 75%-validity condition.

## 5.4 Summary and Conclusions

In this chapter we implemented a mechanistic cortical model [5] to model the behavioral data in Chapter 2. Our purpose was to examine whether the cortical model can explain the real human data, and discuss possible neural mechanisms that may underlie the observed behavioral effects. In the literature a majority of findings has been interpreted to be consistent with the predictive processing models. However, most of these studies did not employ the models to examine whether their data can be explained with the proposed models. In this study, we adapted the cortical model [5] to our experimental paradigm, and implemented the model on a trial-by-trial basis. Within each trial of the behavioral experiment the prior is updated recursively over time to capture the temporal dynamics

throughout a trial. Model fitting revealed that the cortical model can successfully predict the effects observed in both behavioral experiments and Bayesian modeling. Specifically, a successful decision can be made through higher number of iterations by the cortical model in an incongruent trial compared to a congruent trial. This finding is in agreement with the results in Bayesian model, further supporting the idea that longer processing is needed when expectations are not met. Overall, modeling the behavioral data in this study allowed us to reveal whether the proposed cortical model can explain the behavioral effects of expectation. Also, this approach made it possible to examine whether the cortical model predictions approximate the Bayesian model implemented in Chapter 3.

# Chapter 6

## General Discussion

Prior knowledge and expectations have been proposed to play a fundamental role in information processing. Specifically, the facilitating effects of prior knowledge and expectation on decision-making processes are well-known. However, how even early sensory processes are affected by expectations has been a matter of intense debate [30]. This dissertation aimed to unravel the effect of expectation on early visual processing. To this aim, in Chapter 2 using a behavioral paradigm we systematically manipulated the expectation's validity in different experimental conditions, and measured duration thresholds to measure the shortest presentation duration sufficient to achieve a certain success level. The duration threshold measurement was important to investigate whether the perceptual thresholds to detect a stimulus vary depending on expectation and/or its validity. Next, we presented and used a recursive Bayesian updating scheme in Chapter 3 to elucidate the underlying mechanisms of the findings we observe in the behavioral experiment, and in Chapter 4 we validated how successful the model is in predicting the empirical findings. Finally, in Chapter 5 we also used a cortical model to model the behavioral data in order to examine how successful a cortical model is in explaining the empirical evidence. The cortical model we used was a parsimonious one where the information processing is assumed to be executed only by feedforward and feedback connections (without specifying specific populations

of neurons for prediction and error computation). The main purpose of this implementation was to investigate whether even such a parsimonious model can give an explanation for the empirical data. Previous behavioral findings already showed that under several circumstances human behavior is nearly Bayes-optimal, and perceptual decision-making processes are strongly influenced by expectations. Also, findings of several neuroimaging studies revealed that empirical evidence is consistent with the predictive processing accounts of brain function. However, our work in this dissertation goes beyond these findings because, to our knowledge, this is the first study that systematically investigates the behavioral effect of expectation on *early visual processes* at the threshold level *and* unravels possible computational mechanisms underlying the behavioral effects using both a *recursive* Bayesian updating scheme and a parsimonious mechanistic cortical model. Our experimental paradigm and the computational models can be used and extended to study other sensory stimuli, tasks and sensory modalities.

## 6.1 Expectation affects perceptual thresholds

In Chapter 2 our behavioral results showed that early visual processes are affected by expectations. Specifically, we found that perceptual thresholds change when expectations are *not* met specifically when those expectations are relatively strong (*i.e.* 75%). It should also be noted that we found no difference in perceptual thresholds of 100%-validity and neutral conditions as well as congruent trials of 75%- and 100%-validity conditions, and congruent trials of 50%- and 100%-validity conditions.

Several findings in the literature revealed that (valid) expectations facilitate perceptual *decisions*. Even though we also found that expectations affect the perceptual thresholds, the effect we observe in our study is different from those found in the literature. Our behavioral findings revealed that valid expectations do not reduce the perceptual thresholds. Instead, the thresholds change when expectations are not met. We suggest that the reason of the inconsistency between our results and the previous findings in the literature could be the result of distinct

mechanisms involved in perceptual decisions and sensory processes. For instance, a study [32] showed that valid expectations speed up perceptual *decisions* by measuring response times (RT), which is a measure that incorporates several information processing stages, including early visual, decision-making and non-decision (e.g. motor) processes. In our study, however, we examined the effect of expectations using duration thresholds, the shortest presentation time required to achieve a certain success level, which allowed us to leave out non-decision processes, and test the expectation’s effect on sensory processes. It should also be noted that we also systematically manipulated the validity of expectation (e.g. 100%, 75%, 50%) and used a control condition (i.e. neutral) in our behavioral experiments. Several previous studies examined the effect of expectation on perceptual decisions under a fixed probability (e.g. 75%), and compared the findings of expected and unexpected conditions. On the other hand, our manipulation allowed us to examine whether the perceptual thresholds change with expectation’s validity. More specifically, we addressed whether the thresholds decrease because of valid expectations or they increase when the expectations are not met. In this respect, our study furthers the findings in the literature and shows that not only perceptual decisions, but even early visual processes are affected by expectations. However, this effect is observed only when expectations are not met, specifically when those expectations were high. Further investigations may help us to examine whether these findings can be extended to other stimulus features and different validity conditions.

## **6.2 Unmet expectations delay early visual processes**

The behavioral findings in Chapter 2 led us to consider two non-mutually exclusive possible mechanisms that may explain the observed results. First, internal parameters of the system (*e.g.* the decision threshold) may differ with expectation and/or its validity. Another possible mechanism is that further processing

may be required to make a decision when there is a mismatch between the expectations and the sensory input. In Chapter 3 we tested these hypotheses using a recursive Bayesian model.

We implemented a recursive Bayesian model where the prior is not fixed but updated as a function of time within a trial. Next, we defined two models, restricted and unrestricted, to model the behavioral data of each participant for the 100%-, 75%-, and 50%-validity conditions. We performed Bayesian model simulations for both the restricted and unrestricted model for each participant's data. Finally, we took a model comparison approach, and compared the two model predictions to examine how successful they are in explaining the empirical data. In general, our findings on both models revealed that the Bayesian model can successfully predict the pattern observed in the empirical data. Specifically, the Bayesian model simulations took longer to converge on a decision in the incongruent trials compared to the congruent trials in 75%-validity condition. However, this pattern was not observed in 50%-validity condition as in psychophysical findings. This finding also supports the idea that in some circumstances perceptual decisions can be made by combining the sensory input with the prior in a probabilistic manner [35, 36]. Furthermore, the model comparison analysis revealed that the restricted and unrestricted models are not different from each other even at the individual participant level. This finding argues against the first alternative mechanism to explain the behavioral data, and reveals that expectations do not alter the underlying parameters of the system.

To test the other possible mechanism, we calculated the number of iterations computed in congruent (expected) and incongruent (unexpected) trials in all validity conditions and trial types. Our results showed that more number of iterations are calculated in incongruent trials compared to the congruent trials when the expectation's validity is relatively high (75%). This reveals that more posteriors should be computed in incongruent trials to make a decision, pointing further processing within a single trial. This finding is remarkably consistent with our behavioral findings in Chapter 2 and suggests that additional processing (rather than a change in the system's internal parameters) lies behind the observed increase in the perceptual thresholds of incongruent trials.

Previously, using a similar experimental paradigm and drift-diffusion model (DDM) [31], expectations were suggested to facilitate perceptual decisions [32]. Specifically, boundary separation parameter of the DDM, which is considered as the internal threshold to reach a decision, was shown to be higher in the unexpected stimuli compared to the expected stimuli. Our findings in modeling are not in agreement with this finding, because we found no evidence showing that the internal parameters change with expectation. On the other hand, it should be noted that even though the DDM model is a highly useful model to understand the mechanisms underlying perceptual decisions, it may not be able to capture certain characteristics of the current experimental paradigm. For instance, the validity of the expectation in our experiment or the temporal dynamics within a trial may not be modeled with DDM [33]. However, our Bayesian model provides us the opportunity to (1) define task-irrelevant prior, (2) set its validity, and (3) recursively update posterior estimates within a single trial considering that perception is a *dynamic* inference process. This outcome further shows that the recursive Bayesian model can capture some important details about the dynamics of the underlying processes that the DDM model cannot. Notably, the findings in Chapter 4, where another set of experimental data is modeled with the same Bayesian model, were in agreement with the results in Chapter 3. Specifically, even though the stimuli used and the dependent variable measured in the experiment in Chapter 4 are different than those in Chapter 3, our modeling findings indicated that the Bayesian model implemented in this study can successfully predict the effects observed in the real data. The proposed model can be used, extended and tested in new and novel studies that use other sensory stimuli, tasks, and experimental paradigms.

### **6.3 A recurrent cortical model can explain the behavioral effects of expectation**

There has been several mechanistic cortical models which have computational constructs that are analogous to the ones in Bayesian framework [5, 56, 55, 79].

Despite differences in the formulation and constructs of these models, referred as predictive processing models here, these models have provided a compelling framework to resolve how the information processing can be implemented with the involvement of top-down effects of prior knowledge. Recent neuroimaging findings provide neural evidence that top-down information coming from higher regions have a modulatory effect on the activity of early visual areas as well as higher visual processing areas (e.g. FFA) [6, 19, 22, 26, 39, 40, 41, 42, 43, 44]. Expectations have been shown to influence several information processing stages (e.g., [16, 19, 45]). Accordingly, recent neural evidence has been interpreted to be consistent with the predictive processing account of brain function. However, implementation of the proposed models and testing them with the empirical data are also needed to understand whether the models are useful for explaining the data. Without modeling efforts it may not be possible to resolve whether their assumptions comply with the empirical findings in the literature, and to refine the models accordingly. In this sense, our primary effort in this study was to computationally link the model to the empirical data.

For this aim, we implemented a recurrent cortical model [5], and adapted it to our experimental paradigm in Chapter 5. The cortical model used in this study is a very simple and parsimonious one that does not include subpopulations of neural units, e.g. error or prediction computation [5]. It is assumed that information processing in the brain can be accomplished simply by feedforward and feedback connections. In our cortical model there is an input layer, a decision layer, and three intermediate layers which are hypothesized to process low-level and high-level visual information. The third layer has been hypothesized to be driven by prior information, and that information is conveyed to the other layers via backward connections. Note that the prior is continuously updated, specifically at each iteration, within a trial in the model. This allowed us to update the information throughout a trial. As we did in Bayesian modeling in Chapter 3, we simulated the cortical model's responses for congruent and incongruent trials for each participant's behavioral data. This also allowed us to see whether the two models, a behavioral and a cortical model, are consistent with each other in explaining the empirical findings.

Modeling the behavioral data with the cortical model showed that in unmet expectations the cortical model also needs to compute more number of iterations, further supporting the idea that additional steps of computation is responsible for the higher perceptual thresholds in unmet expectations. We suggest that when we are exposed to an unexpected stimulus, there might be a change in feedforward-feedback interactions, e.g. additional neural units may become active and get involved in the process. This may in turn elicit further processing, and consequently result in longer computations. This idea can account for why unexpected stimulus leads to higher duration thresholds and delay in sensory processes. Taken together, the cortical model findings in Chapter 5 showed that even such a simple and parsimonious model can successfully elucidate the behavioral effects of expectation on perceptual processes.

It is also possible that the predictive coding models would account for the observed behavioral findings in the current study. The predictive coding theory (PCT) posits that the brain computes internal predictions about the upcoming sensory input, and these predictions are continuously compared with the actual sensory input. When the predictions and the actual sensory input disagree, a prediction error is computed, and this updating mechanism continues until an equilibrium is reached [80, 81]. This mechanism would also account for the behavioral findings in this study, because this updating process would result in longer neuronal processing, which might be the mechanism that lies behind the higher perceptual thresholds in unmet expectations.

Several neuroimaging studies showed that an unexpected stimulus leads to higher BOLD activity compared to an expected stimulus [19, 16, 75, 76]. This finding has been interpreted within the predictive coding framework. Specifically, it has been suggested that the increase of BOLD activity to the unexpected stimulus may be an indicator of the *prediction error* signal [4], which is consistent with the assumptions of the predictive coding theory (PCT) [55]. In the PCT the prediction and prediction error computations are suggested to be executed by distinct subpopulations of neurons, which are prediction (or representation) units and error units respectively. Accordingly, in the current literature it has been suggested that higher BOLD activity to the unexpected stimuli may reflect

the prediction error signal of the error units [4]. This interpretation can account for the neural effect observed in several studies.

Alternative to this prominent interpretation, the modeling findings in this study suggest that additional processing may be another possible mechanisms that underlie the observed effects in the literature. When an unexpected stimulus is presented, there is a mismatch between the initial predictions and the actual sensory input. Thus, the system may not achieve the sensory evidence that is required to detect an unexpected stimulus. However, as the sensory evidence is updated with additional feedforward and feedback interactions by the involvement of greater number of neural units, the required evidence can be acquired. This process might appear as an increase in BOLD response, which was previously interpreted as the prediction error signal of the error units. This would also offer a simple alternative explanation to the findings in literature. Future work is needed to investigate the possible neural mechanisms that can better explain the empirical findings.

## 6.4 Future Work

To examine the possible mechanisms that underlie the effect of expectations on visual processing rigorous modeling efforts, neuroimaging studies and other recording techniques are needed. In this study the behavioral and modeling results suggest that unexpected stimuli lead to additional processing. When expectations do not match with the sensory stimulus, further, and consequently longer, processing is required by the system. Time-resolved methods, e.g. EEG and MEG, may help us to further investigate the neural basis of additional processing.

In addition, even though functional magnetic resonance imaging (fMRI) has a relatively weak temporal resolution, there are still valuable indicators that may help us to understand the neural basis of additional processing. For instance, full width at half maximum (FWHM) has been suggested to be related to the duration

presentation of a stimulus, processing time spent for a task, and time taken to make a decision in a task [82, 83, 84, 85]. In this sense, the key objectives could be the FWHM, time-to-peak (TTP), and amplitude of the BOLD response. The full width at half maximum and time-to-peak could be examined together with the amplitude of BOLD response in expected, unexpected and neutral conditions in order to investigate whether any change in these parameters will be observed depending on the condition type. Also, effective connectivity may help us to evaluate how the connectivity in the processing of expected, unexpected, and neutral conditions would differ. These investigations could guide us to understand the mechanisms underlying the effect of expectations on visual processing.

Furthermore, it is still necessary to employ modeling to test whether the proposed mechanistic models can explain the findings observed in the literature. Testing the computational models with the empirical data can bring reciprocal benefits. First, a unified theory that can explain the empirical data is necessary to form a mechanistic understanding of how the information processing can be executed. At the same time, empirical evidence can help the models to be refined accordingly. To make this possible, the computational models should provide and specify the neuroanatomical or neurophysiological sources behind the computational constructs [86]. This would allow us to develop appropriate hypotheses, determine better experimental designs and conduct new experiments [86] to examine the effect of expectations in visual processing.

## 6.5 Conclusion

This dissertation examines whether and how prior knowledge and expectations affect early sensory processes. To this respect, we investigated the effects of expectations on perceptual processes using behavioral experiments, and examined the possible mechanisms underlying those effects using a Bayesian and a cortical model. It is well-established that higher level mechanisms can be strongly affected by expectations. Therefore, we specifically focused on the effect of expectations on early visual processes. Our findings showed that unmet expectations delay

early visual processes, which might be due to a need for additional processing in the system.

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# Appendix A

## Psychometric Function Fits in Behavioral Experiments

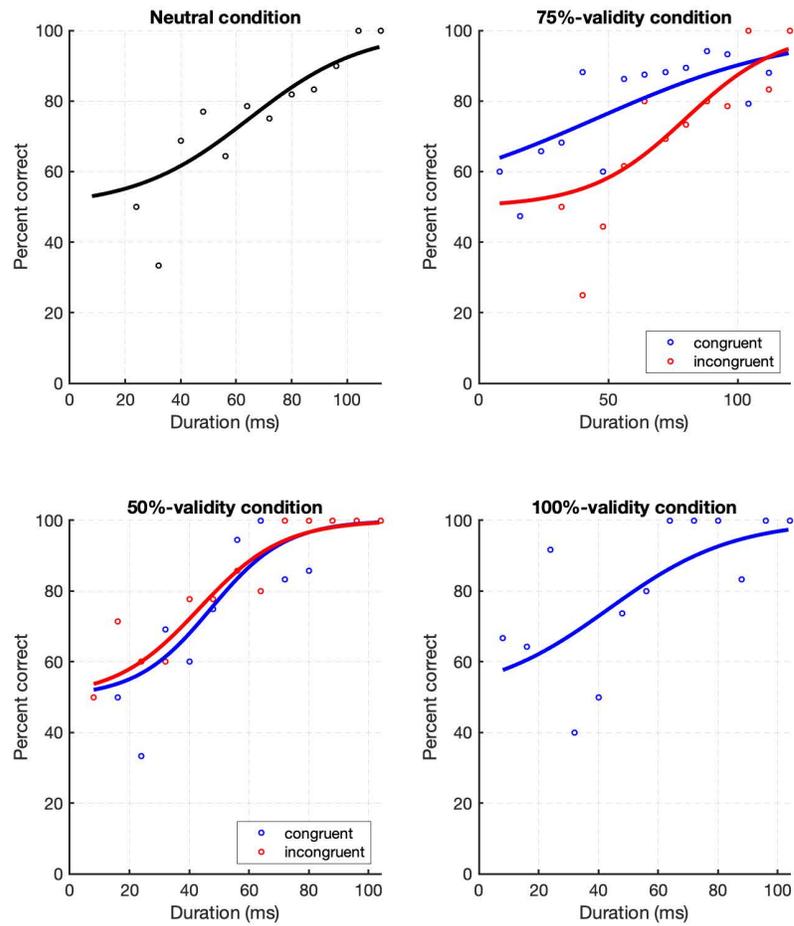


Figure A.1: Logistic function fits for a single participant (1) for each experimental condition in Experiment 1.

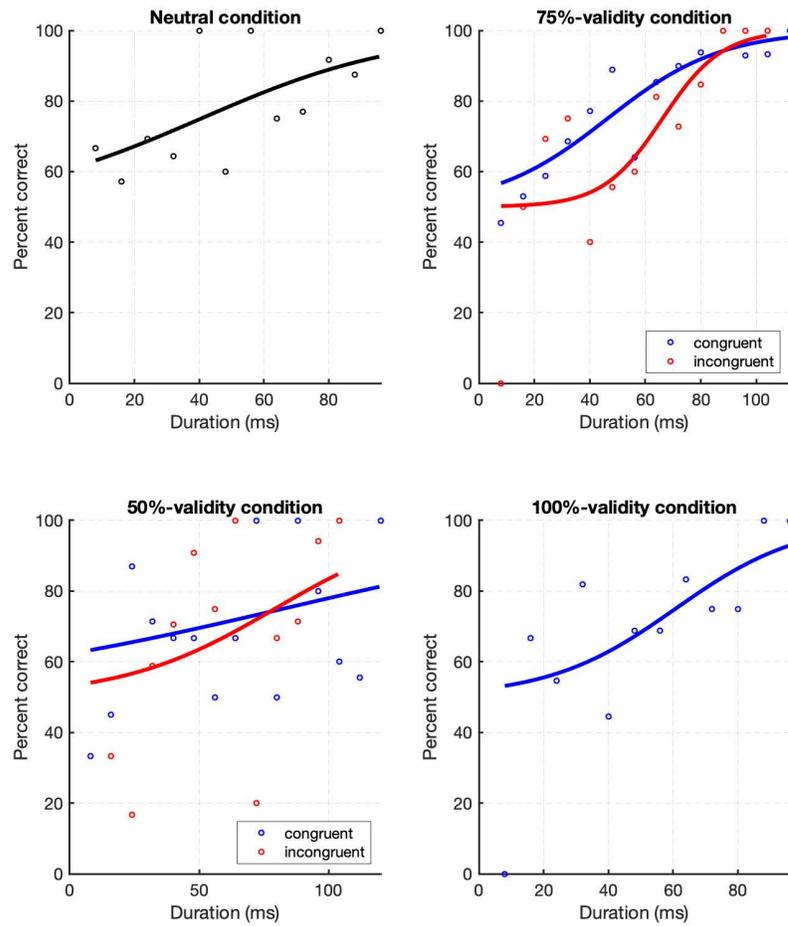


Figure A.2: Logistic function fits for a single participant (2) for each experimental condition in Experiment 1.

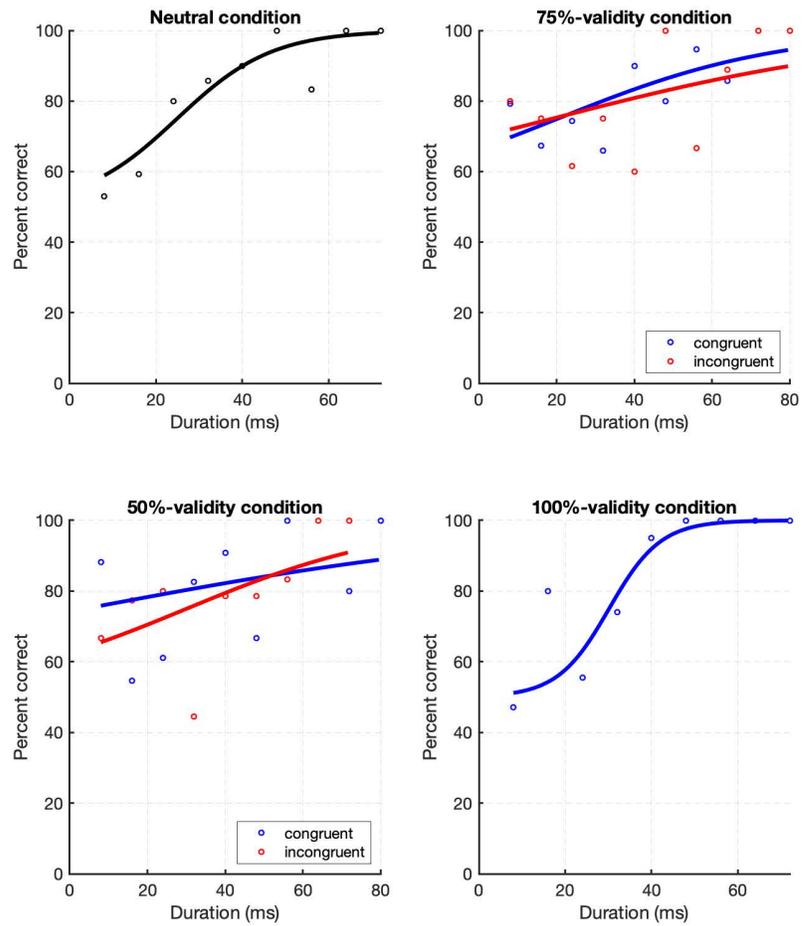


Figure A.3: Logistic function fits for a single participant (3) for each experimental condition in Experiment 1.

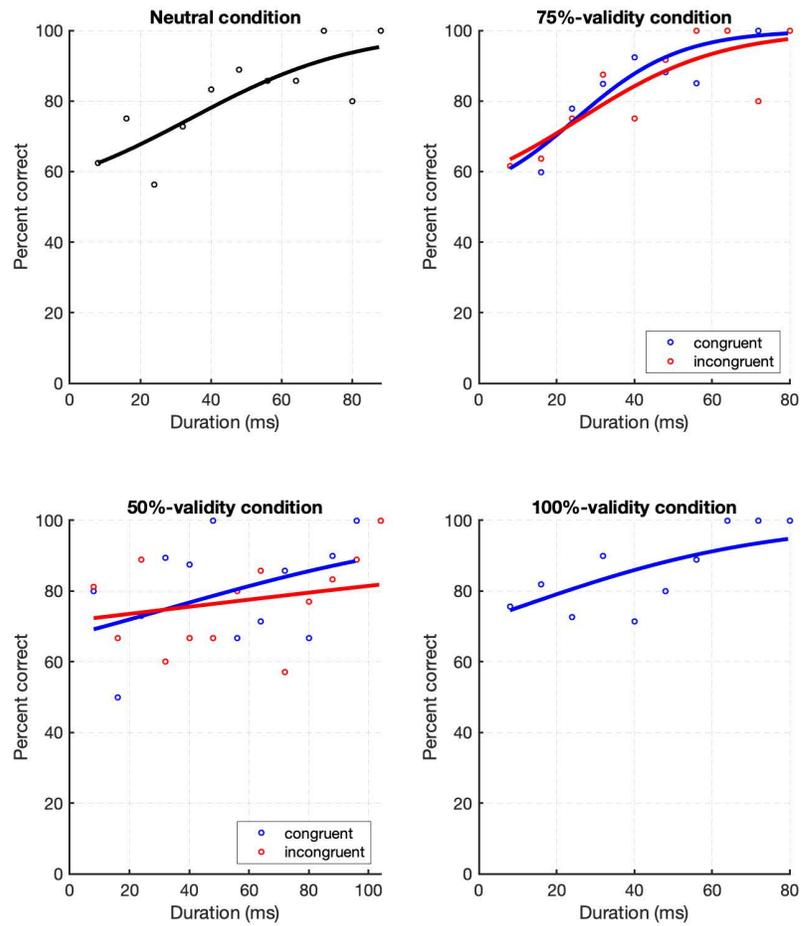


Figure A.4: Logistic function fits for a single participant (4) for each experimental condition in Experiment 1.

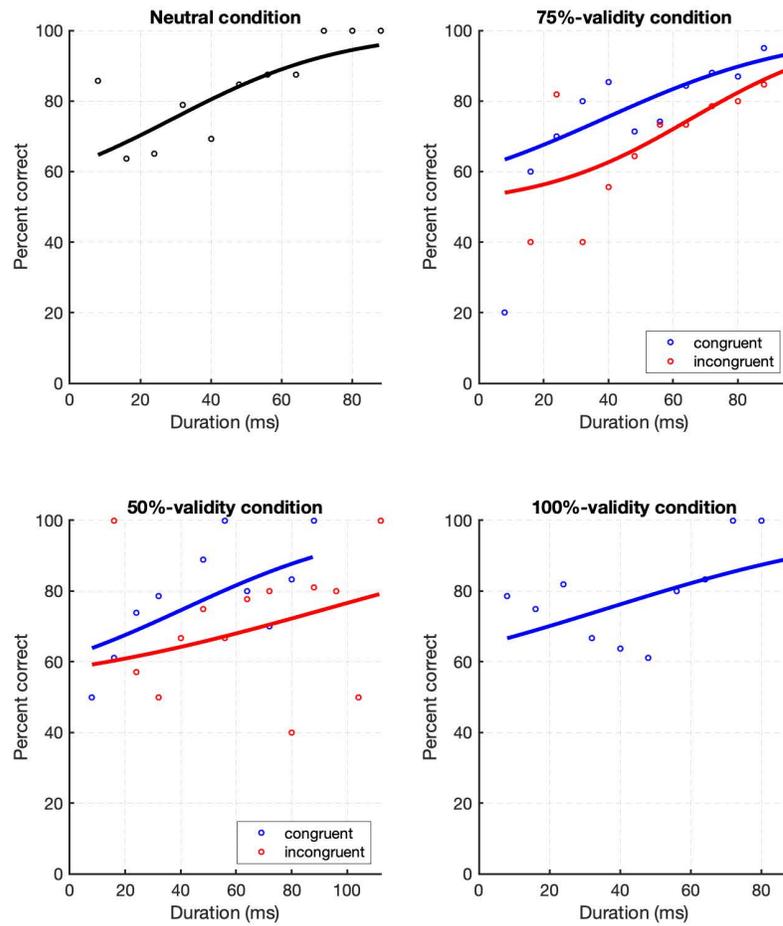


Figure A.5: Logistic function fits for a single participant (5) for each experimental condition in Experiment 1.

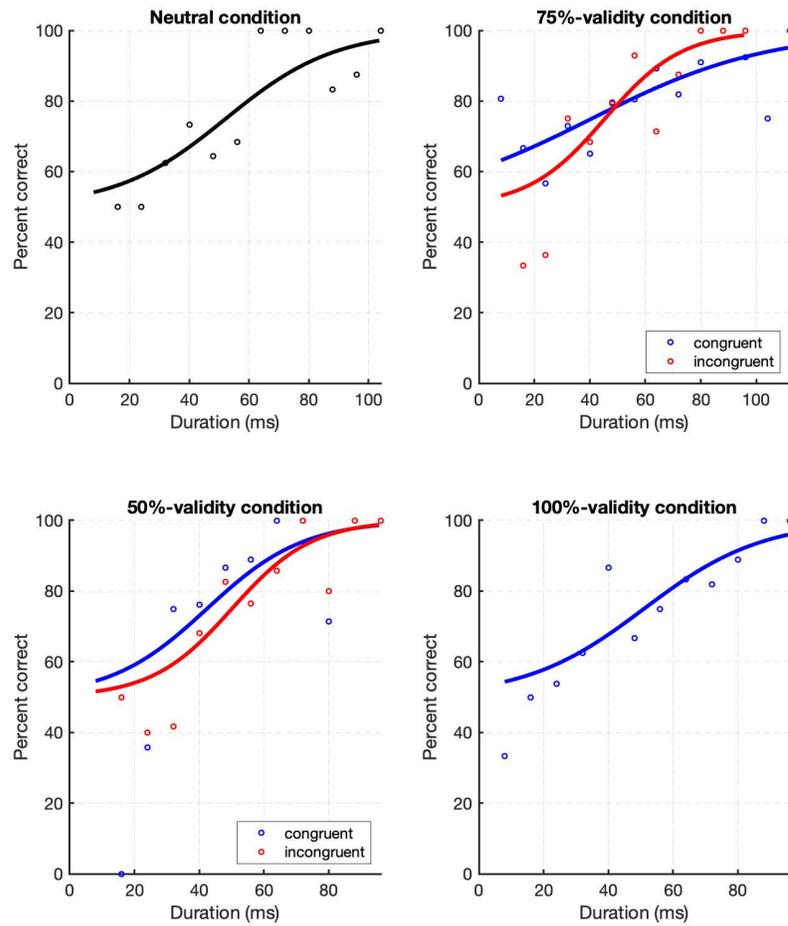


Figure A.6: Logistic function fits for a single participant (6) for each experimental condition in Experiment 1.

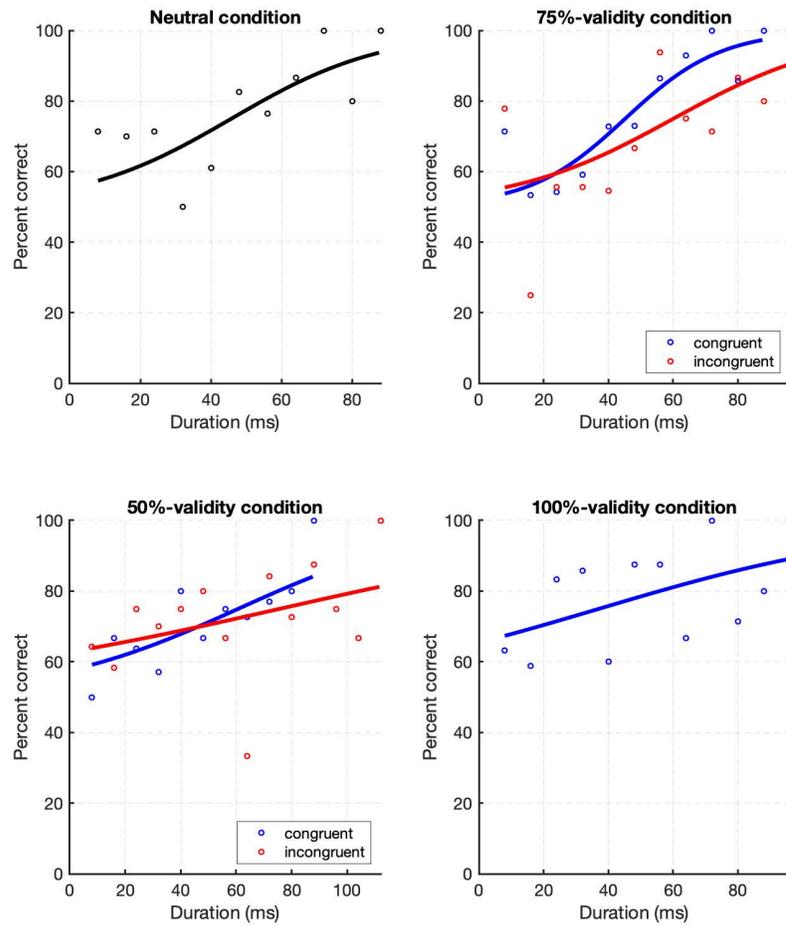


Figure A.7: Logistic function fits for a single participant (7) for each experimental condition in Experiment 1.

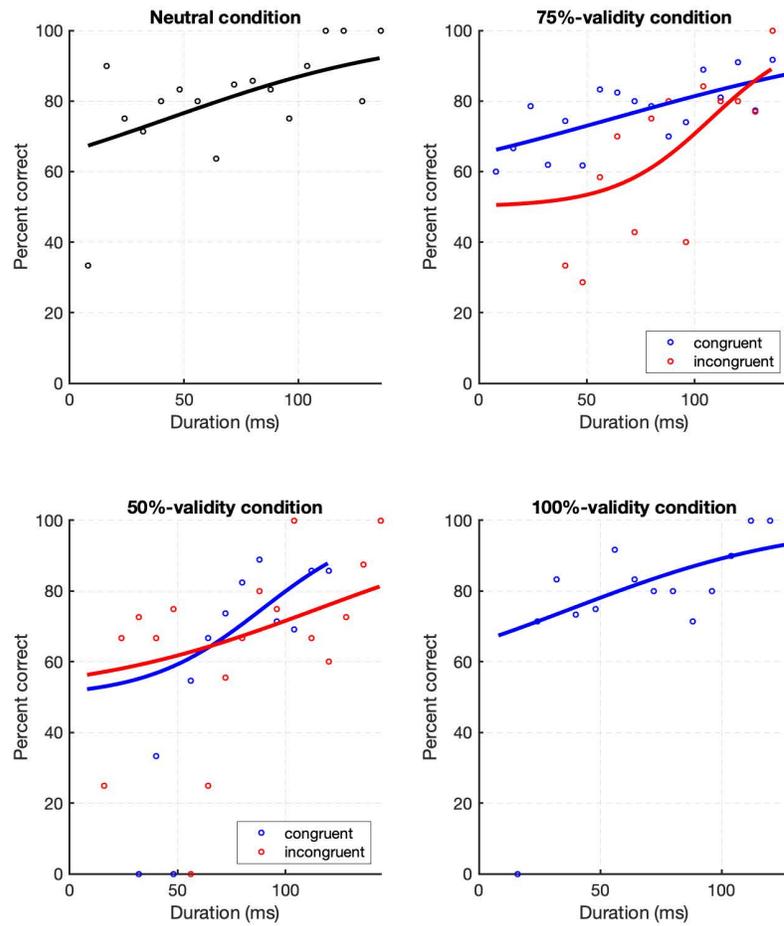


Figure A.8: Logistic function fits for a single participant (8) for each experimental condition in Experiment 1.

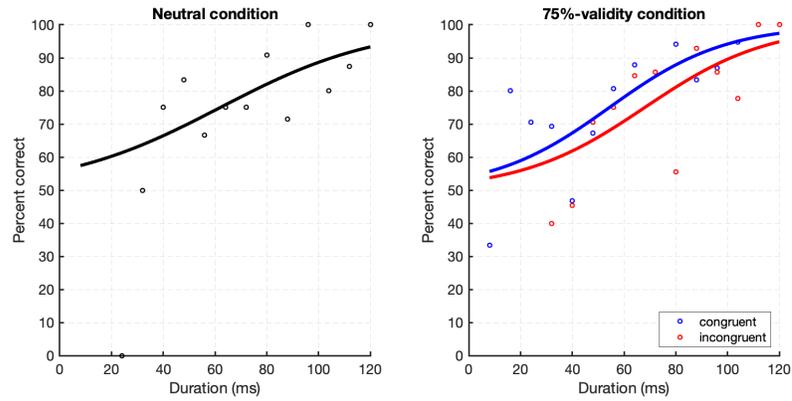


Figure A.9: Logistic function fits for a single participant (Group 1) for each experimental condition in Experiment 2.

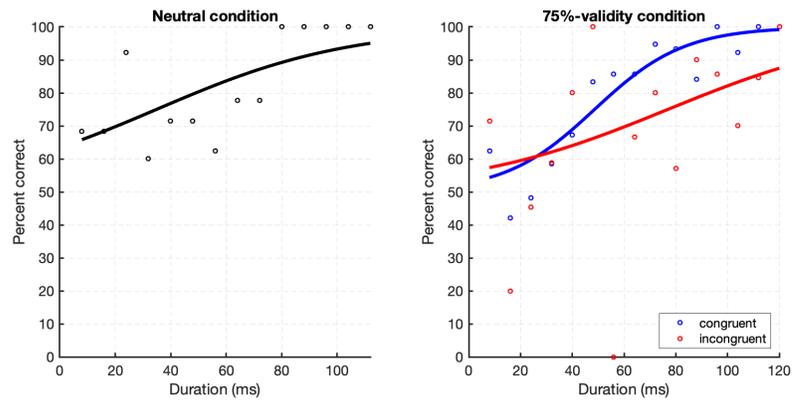


Figure A.10: Logistic function fits for a single participant (Group 1) for each experimental condition in Experiment 2.

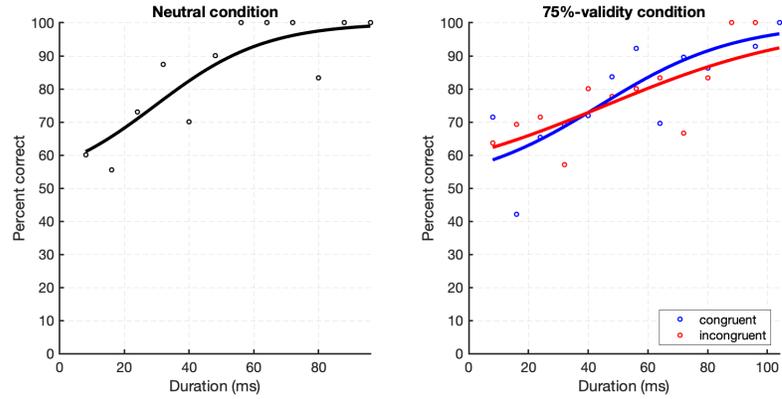


Figure A.11: Logistic function fits for a single participant (Group 1) for each experimental condition in Experiment 2.

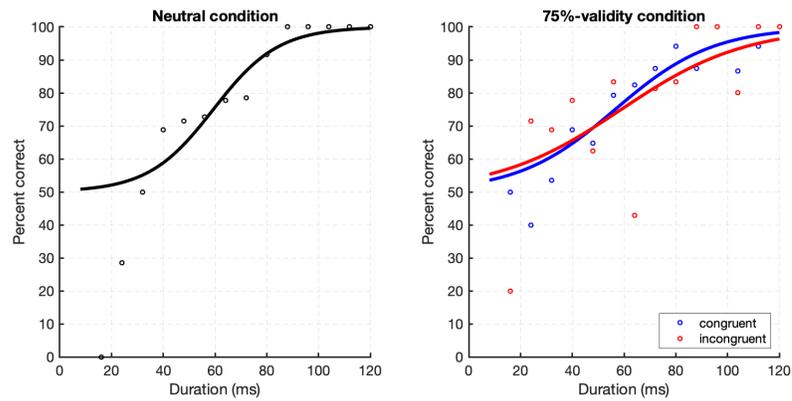


Figure A.12: Logistic function fits for a single participant (Group 1) for each experimental condition in Experiment 2.

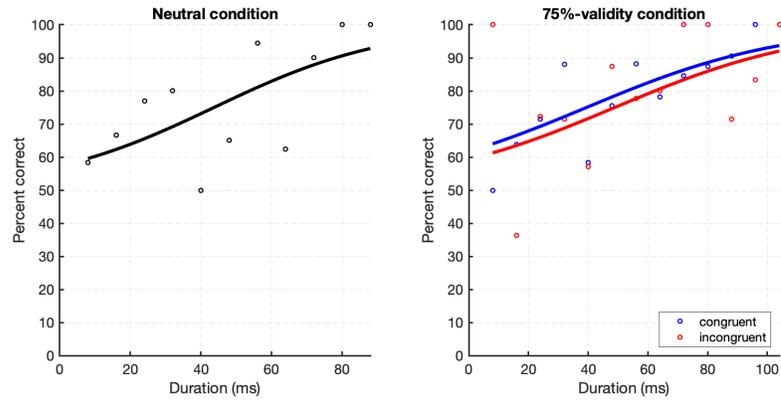


Figure A.13: Logistic function fits for a single participant (Group 1) for each experimental condition in Experiment 2.

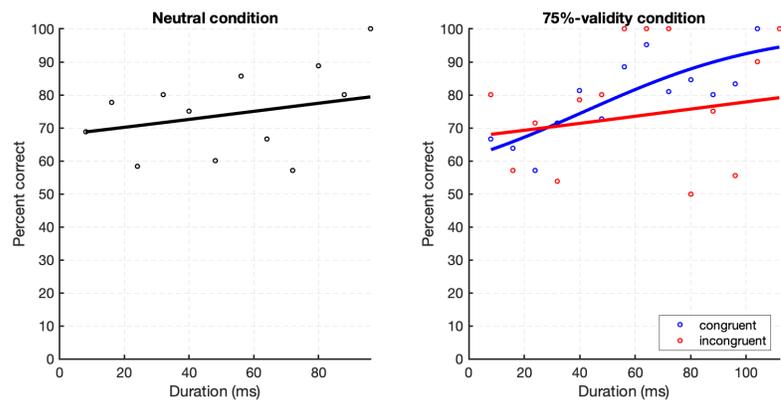


Figure A.14: Logistic function fits for a single participant (Group 1) for each experimental condition in Experiment 2.

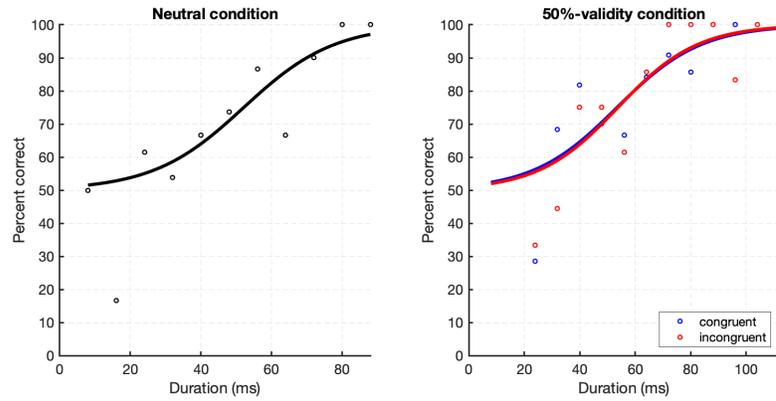


Figure A.15: Logistic function fits for a single participant (Group 2) for each experimental condition in Experiment 2.

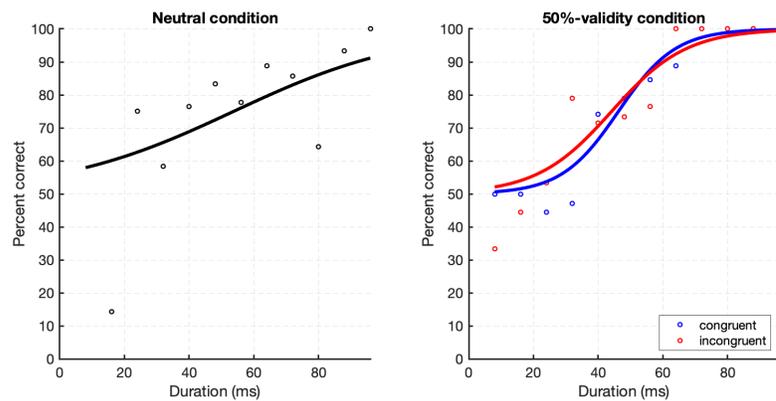


Figure A.16: Logistic function fits for a single participant (Group 2) for each experimental condition in Experiment 2.

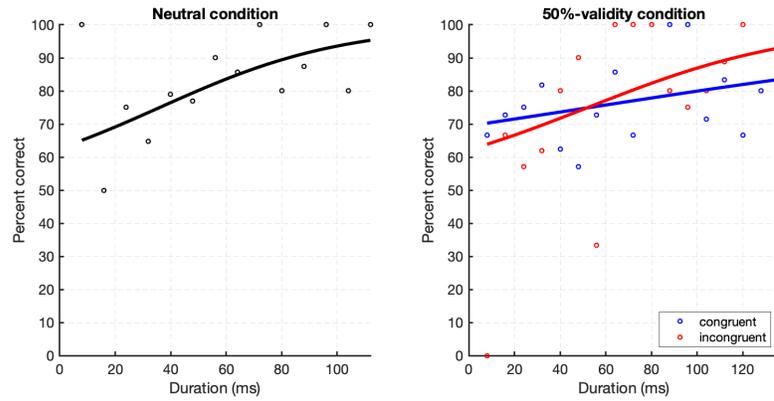


Figure A.17: Logistic function fits for a single participant (Group 2) for each experimental condition in Experiment 2.

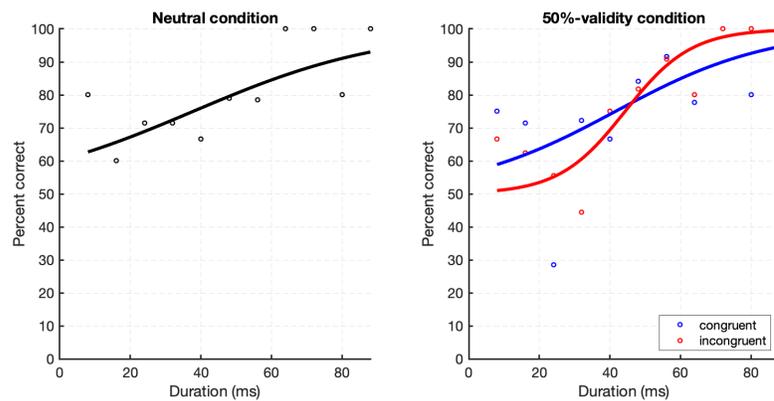


Figure A.18: Logistic function fits for a single participant (Group 2) for each experimental condition in Experiment 2.

# Appendix B

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3. **PNAS volume number, issue number, and issue date:** vol. 114 no. 8 1773-1782 (PNAS February 21, 2017 114 (8) 1773-1782; first published February 6, 2017) ( <https://www.pnas.org/content/114/8/1773> )
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### Unmet expectations delay sensory processes

**Author:** Buse M. Urgan,Huseyin Boyaci

**Publication:** Vision Research

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