Suboptimality in perception

Dobromir Rahnev[1*] & Rachel Denison[2*]

[1] Department of Psychology, Georgia Institute of Technology, Atlanta, GA
[2] Department of Psychology and Center for Neural Science, New York University, New York, NY
[*] Authors contributed equally to this work

Correspondence
Dobromir Rahnev
Department of Psychology
Georgia Institute of Technology
130 J.S. Coon Building
Atlanta, GA 30332
drahnev@gmail.com

and

Rachel Denison
Department of Psychology and Center for Neural Science
New York University
6 Washington Place
New York, NY 10003
rachel.denison@nyu.edu

Keywords: optimality, suboptimality, perception, review

ABSTRACT
Human perception is increasingly described as optimal. This view reflects recent successes of Bayesian approaches to perception but ignores an extensive literature documenting suboptimal performance in perceptual tasks. Here we review several classes of suboptimal perceptual decisions, including improper placement, maintenance, and adjustment of perceptual criteria, inadequate tradeoff between speed and accuracy, and inappropriate confidence ratings. We examine suboptimalities in the cue combination literature, which has often been taken as evidence for optimality in perception. We further discuss how findings regarding visual illusions, adaptation, and appearance relate to the concept of optimality. We extract a number of principles that account for suboptimal behavior across all of these studies. Finally, we outline an "Objectives-Constraints-Mechanisms" approach for guiding future investigations and discussions of optimal and suboptimal perception. In this approach, findings of optimality or suboptimality are not ends in themselves but serve to characterize the perceptual system's objectives (i.e., what it aims to achieve), constraints (i.e., what costs it incurs), and mechanisms (what processes it uses to trade off the objectives and constraints). We suggest that this conceptual framework, more than a focus on optimality per se, can advance our understanding of perception.

INTRODUCTION

How do people make perceptual judgments based on the available sensory information? This fundamental question has been a focus of psychological research from the 19th century on (Fechner, 1860; Helmholtz, 1856). Many perceptual tasks naturally lend themselves to what has traditionally been called "ideal observer" analysis, whereby the optimal behavior is mathematically determined and human behavior is compared to this standard (Green & Swets, 1966; Ulehla, 1966). The extensive literature on this topic includes many examples of humans performing similar to an ideal observer but also features many examples of suboptimal behavior. Perceptual science has a strong tradition of developing models and theories that attempt to account for the full range of empirical data on how humans perceive (Macmillan & Creelman, 2005).

Recent years have seen an impressive surge of Bayesian theories of human cognition and perception (Gershman, Horvitz, & Tenenbaum, 2015; Griffiths, Lieder, & Goodman, 2015; Tenenbaum, Kemp, Griffiths, & Goodman, 2011). These theories often depict humans as optimal decision-makers, especially in the area of perception. A number of high-profile papers have shown examples of human perceptual behavior that is close to optimal (Ernst & Banks, 2002; Körding & Wolpert, 2004), while other papers have attempted to explain apparently suboptimal behaviors as being in fact optimal (Weiss, Simoncelli, & Adelson, 2002). The joint influence of these factors have led many to claim that humans are essentially optimal in perceptual tasks:

> "Human performance on perceptual classification tasks approaches that of an ideal observer" (Summerfield & Tsetsos, 2015, p.27)
> "Across a wide range of tasks, people seem to act in a manner consistent with optimal Bayesian models" (Vul, Goodman, Griffiths, & Tenenbaum, 2014, p.1)
> "Humans have been shown to integrate prior knowledge and sensory information in a probabilistic manner to obtain optimal (or nearly so) estimates" (Acerbi, Vijayakumar, & Wolpert, 2014, p.1)
> "These studies with different approaches have shown that human perception is close to the Bayesian optimal" (Körding & Wolpert, 2006, p. 321)
> "... psychophysics is providing a growing body of evidence that human perceptual computations are 'Bayes' optimal'." (Knill & Pouget, 2004, p. 712)

Despite a number of recent criticisms of such assertions regarding human optimality (Bowers & Davis, 2012a, 2012b; Eberhardt & Danks, 2011; Jones & Love, 2011; Marcus & Davis, 2013, 2015), as well as statements from some of the most prominent Bayesian theorists that their goal is not to demonstrate optimality (Griffiths, Chater, Norris, & Pouget, 2012), the quotes above indicate that the view that humans are (close to) optimal in perceptual tasks has taken strong foothold.

To facilitate a more comprehensive view of human perceptual decisions, here we review a number of areas in which humans are suboptimal. We aim to cover as much ground as possible without discussing each finding in detail. Given the vast literature on the topic, our review is necessarily incomplete, but we hope that the numerous examples of suboptimality in perceptual decision making will lead to a more balanced view and facilitate a deeper understanding of human perception. We also discuss how findings of suboptimality can reveal the principles of the human perceptual system. We advocate for an Objectives-Constraints-Mechanisms approach to understanding perception and explore the implications of this approach for the

concept of perceptual optimality. Finally, we provide recommendations for discussing optimality in empirical studies of perception and sensory processing.

DEFINING OPTIMALITY

Optimality can be a difficult concept to define. Most research to date thus focuses on simple cases in which one of two stimulus categories is presented on each trial and observers make a perceptual judgment discriminating between the two possibilities. In such cases, optimal performance is usually defined as the response strategy that produces the highest level of reward. If reward is not explicitly provided, then it is usually assumed that observers attempt to maximize accuracy (which is equivalent to rewarding equally all correct responses and punishing equally all incorrect ones).

What is the strategy that maximizes reward? In the general case, on each trial an observer attempts to estimate the expected value (EV) of deciding on stimulus $\boldsymbol{s}$ based on the internal response $\boldsymbol{r}$ and reward for that stimulus $R(s)$:

$$EV(s) = P(s|r) * R(s) \tag{1}$$

which, by using Bayes' formula, can be further expanded to

$$EV(s) = P(r|s) * P(s) * R(s)/P(r) \tag{2}$$

where $P(s|r)$ is the posterior probability of s, $P(r|s)$ is the likelihood function that depends on the internal response, while $P(s)$ and $P(r)$ are the prior probability of occurrence for s and r. In the case of two stimulus classes s_1 and s_2, the optimal strategy is to respond s_2 when $EV(s_2) \geq EV(s_1)$, which, using equation 2, is equivalent to responding s_2 when:

$$\frac{P(r|s_2)}{P(r|s_1)} \geq \frac{P(s_1)}{P(s_2)} * \frac{R(s_1)}{R(s_2)} \tag{3}$$

In formula 3, $\frac{P(r|s_2)}{P(r|s_1)}$ is known as the "likelihood ratio", $\frac{P(s_1)}{P(s_2)}$ is the prior odds, and $\frac{R(s_1)}{R(s_2)}$ is the reward bias. Formulas 2 and 3 assume no penalty for incorrect responses. In cases in which a full reward matrix is provided such that $R_{i,j}$ is the reward for responding "s_i" when stimulus s_j was presented, then a straightforward computation shows that the reward bias term in equation 3 needs to be replaced by $\frac{R_{1,1}-R_{2,1}}{R_{2,2}-R_{1,2}}$.

Theoretically, the likelihood function $P(r|s)$ can take any shape, but in practice, $P(r|s)$ can almost always be approximated with a Gaussian distribution (Macmillan & Creelman, 2005; See, Warm, Dember, & Howe, 1997; Swets, 1986). See the first point in "Methodological considerations that can account for suboptimal behavior" below for further discussion of this distributional assumption.

EXAMPLES OF SUBOPTIMALITY

1. Criterion in simple 2-choice tasks

In the simplest and most ubiquitous case, only two stimuli s_1 and s_2 are presented with equal probability and equal reward (that is often not defined explicitly). From formula 3 we can derive that the location of the optimal criterion is the point where the two likelihood functions $P(r|s_1)$ and $P(r|s_2)$ intersect and the likelihood ratio is 1 (**Figure 1**).

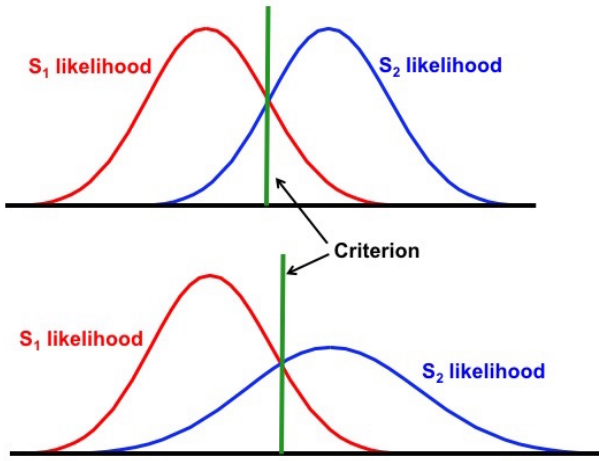

***Figure 1**. Depiction of optimal criteria in simple 2-choice tasks. The upper panel shows the likelihood functions for two stimuli S_1 and S_2 with equal variability. The green vertical line represents the location of the optimal criterion such that the region on the left of the criterion is categorized as "S_1" and the region on the right as "S_2". The lower panel shows the location of the optimal criterion when the variability of the two likelihood functions differs (in the case depicted here the optimal criterion results in a higher proportion of S_1 responses).*

1.1 Detection criteria

Many tasks involve the simple distinction between noise (s_1) and signal+noise (s_2). These are usually referred to as detection tasks. In most cases $P(r|s_1)$ is found to have smaller variance than $P(r|s_2)$ (Green & Swets, 1966; Macmillan & Creelman, 2005; Swets, Tanner, & Birdsall, 1961), from where it follows that an optimal observer would choose s_1 more often than s_2 even when the two stimuli are presented at equal rates (**Figure 1**). Indeed, many detection studies find that observers are "conservative" (i.e., choosing the noise distribution s_1 more than half of the time; Gorea & Sagi, 2000; Green & Swets, 1966; Macmillan & Creelman, 2005; Rahnev et al., 2011; Reckless et al., 2014; Solovey, Graney, & Lau, 2015; Swets et al., 1961) thus suggesting that observers do have access to their internal uncertainty. However, most studies do not allow for the estimation of the likelihood functions for individual observers and thus it is an open question how optimal observers in those studies actually are. A few studies have reported "liberal" detection criteria (i.e., choosing the signal+noise distribution s_2 more than half of the time; Morales et al., 2015; Rahnev et al., 2011; Solovey et al., 2015) thus providing examples of clearly suboptimal strategies.

1.2 Discrimination criteria

Detection tasks feature an inherent asymmetry between the noise vs. signal+noise stimuli but other tasks require observers to discriminate between two roughly equivalent stimuli. For example, observers might discriminate left vs. rightward motion or clockwise vs. counterclockwise grating orientation. For these types of stimuli, the likelihood functions for each stimulus category can safely be assumed to have approximately equal variability (Macmillan & Creelman, 2005; See et al., 1997). Such studies find that the average criterion location across the whole group of observers is usually close to the optimal (likelihood ratio = 1) but individual observers can still exhibit substantial biases in either direction (e.g., Whiteley & Sahani, 2008). For example, we re-analyzed the data from a recent study in which observers discriminated between a grating tilted 45 degrees clockwise or counterclockwise from vertical (Rahnev, Nee, Riddle, Larson, & D'Esposito, 2016). Seventeen observers came for four sessions on different

days completing 480 trials each time. Using a binomial test, we found that only 11 of the 68 total sessions did not exhibit significant deviation from unbiased responding of clockwise or counterclockwise. Further, observers tended to have relatively stable biases as demonstrated by a positive criterion correlation across all pairs of sessions (all p's < .003). Thus, even if the performance of the group appears to be close to optimal, individual observers often deviate substantially from optimality.

1.3 Two-stimulus tasks

The biases observed in detection and discrimination experiments led to the development of the popular two-alternative forced-choice (2AFC) task, in which both stimulus categories are presented on each trial, in order to reduce individual bias (Macmillan & Creelman, 2005). 2AFC tasks separate the two stimuli either temporally (these tasks are also commonly referred to as 2-interval-forced-choice or 2IFC tasks) or spatially. Note that in recent years many researchers have begun to use the term "2AFC" for tasks in which only one stimulus is presented. To avoid confusion, we adopt the term "2-stimulus tasks" to refer to tasks where two stimuli are presented (the original meaning of 2AFC) and the term "1-stimulus tasks" to refer to the common single-stimulus tasks such as detection and discrimination tasks discussed in 1.1 and 1.2.

Even though 2-stimulus tasks were designed to remove observer bias, significant biases have been observed for them, too (Macmillan & Creelman, 2005; Yaffa Yeshurun, Carrasco, & Maloney, 2008). For example, early research suggested that if the two stimuli in a trial differ in intensity then the second one is more often selected as the one of higher intensity, a phenomenon called *time-order errors* (Fechner, 1860; Osgood, 1953). More recently Yeshurun et al. (2008) re-analyzed 2IFC data from seventeen previous experiments and found significant choice biases such that observers did not choose the first and second interval equally. The direction of the bias varied between the different experiments, suggesting that the specific experimental design has an influence on observers' bias.

1.4 Explaining suboptimality in simple 2-choice tasks

Why do people have trouble setting appropriate criteria in simple 2-choice tasks? One possibility is that they have a tendency to give the same response when uncertain. For example, a given observer may respond that they saw left (rather than right) motion every time they get distracted or had very low evidence for either choice. This could be due to a preference for one of the two stimuli or one of the two motor response options. Re-analysis of another previous study (Rahnev, Lau, & De Lange, 2011) where we withheld the stimulus-response mapping until after the stimulus presentation still found that 12 of the 21 observers revealed a significant response bias for motion direction. This suggests that a preference in motor behavior cannot fully account for this type of suboptimality. Thus, it appears that many observers automatically develop a preference for one of the stimulus categories, and this preference leads to suboptimal behavior. Nevertheless, it is possible that this bias does not arise from an inappropriate decision strategy but rather from biases in the sensory system. For example, for some observers left vs. rightward motion may generate likelihood functions with different variability, similar to detection tasks in which the noise and noise+signal distributions have different variability (see **Figure 1**).

2. Maintaining stable criteria

Above we considered observers' average criterion in simple cases when the optimal criterion should be placed at the point at which the likelihood ratio equals 1. We now turn our attention to whether factors other than the likelihood functions have an impact on the perceptual decision. An optimal observer would be insensitive to any other factors (**Figure 2**).

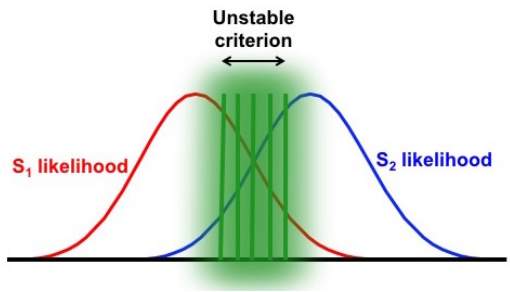

Figure 2*. Depiction of a failure to maintain a stable criterion. The optimal criterion is shown in Figure 1 but observers often fail to maintain that criterion over the course of the experiment, resulting in a criterion that effectively varies over trials.*

2.1 Sequential effects

Optimality requires that judgments are made based on the evidence from the current stimulus independently of previous stimuli. However, sequential effects are ubiquitous in perceptual tasks (Fischer & Whitney, 2014; Fründ, Wichmann, & Macke, 2014; Kaneko & Sakai, 2015; Liberman, Fischer, & Whitney, 2014; T. A. Tanner, Haller, & Atkinson, 1967; Treisman & Faulkner, 1984; Ward & Lockhead, 1970; Yu & Cohen, 2009). The general finding is that observers' responses are positively autocorrelated such that the response on the current trial is likely to be the same as on the previous trial, though in some cases negative autocorrelations have also been reported (T. A. Tanner et al., 1967; Ward & Lockhead, 1970).

2.2 Switching between different criteria

Another factor that has been found to influence optimal criterion placement is interleaving trials that require different criteria. Gorea & Sagi (2000) demonstrated that when high-contrast stimuli (optimally requiring a relatively liberal detection criterion) and low-contrast stimuli (optimally requiring a relatively conservative detection criterion) were interleaved, observers tended to use the same compromised detection criterion that was suboptimal for both the high- and low-contrast stimuli. This happened despite clear cues indicating the high- and low-contrast stimuli. Similar effects have been shows in a variety of paradigms that involved using stimuli of different contrasts (Gorea, Caetta, & Sagi, 2005; Gorea & Sagi, 2001, 2002; Zak, Katkov, Gorea, & Sagi, 2012), attended vs. unattended stimuli (Morales et al., 2015; Rahnev, Maniscalco, et al., 2011), and central vs. peripheral stimuli (Solovey et al., 2015).

2.3 Irrelevant reward influencing the criterion

Several lines of research suggest that observers change their criteria based on factors that should optimally be ignored. For example, maximizing one's payoff necessitates using the same (unbiased) criterion whether a large or small reward is offered on a particular trial. However, both monetary rewards and punishments lead observers to adopt a more liberal detection criterion such that more stimuli are identified as targets (Reckless et al., 2014; Reckless, Bolstad, Nakstad, Andreassen, & Jensen, 2013). Note that in these studies the rewards were given simply for responding correctly and thus should not have changed the criterion. Similar changes to response criterion due to monetary motivation are obtained in a variety of paradigms (Henriques, Glowacki, & Davidson, 1994; Taylor et al., 2004). To complicate matters, observers' personality traits interact with the type of monetary reward in altering response criteria (Markman, Baldwin, & Maddox, 2005). Thus, even though optimality necessitates that observers only use task-relevant information, it appears that a wide range of irrelevant factors are capable of shifting the response criterion.

2.4 Explaining suboptimality in maintaining stable criteria

Why do people shift their response criteria based on factors that should be irrelevant for the criterion placement? Some of the above examples can be explained as memory limitations. For example, maintaining two criteria for two different stimulus classes simultaneously may be too taxing to the system. On the other hand, sequential effects have been explained in terms of an automatic tendency to exploit the continuity in our normal environment, even though such continuity is not present in most experimental setups (Fischer & Whitney, 2014; Liberman et al., 2014). However, it is harder to explain why personality traits or task features such as the presence of monetary rewards that should be irrelevant to the response criterion change observers' criteria. It appears that in some situations observers may use additional factors besides what is suggested by Bayesian inference to make their perceptual decisions (Mueller & Weidemann, 2008). Very little research has focused on identifying such factors and explaining why they influence observers' responses.

3. Adjusting choice criteria

One of the most common ways to assess optimality in perceptual decision making is to manipulate the prior probability of the stimulus classes and/or provide unequal payoffs that bias responses towards one of the stimulus categories (Macmillan & Creelman, 2005). As can be seen from formula 3, the two manipulations have an equivalent effect on the optimal response strategy: both require observers to shift their criterion in likelihood space by a factor dictated by the specific prior probability and reward structure (**Figure 3**).

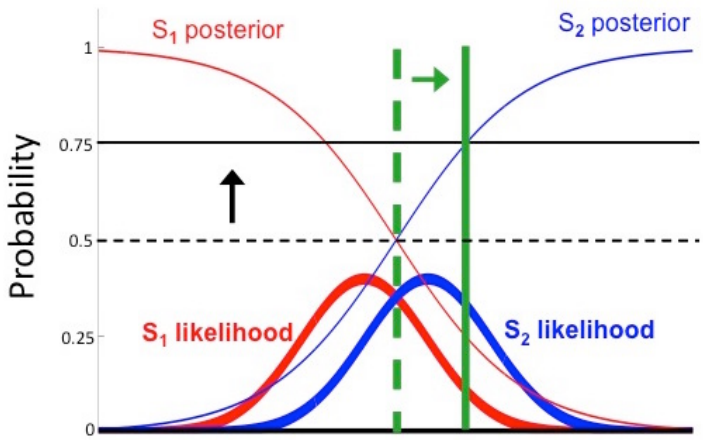

***Figure 3**. Depiction of optimal adjustment of choice criteria. In addition to the S_1 and S_2 likelihood functions (in thick red and blue lines), the figure shows the corresponding posterior functions (in thin red and blue lines). The vertical criteria in likelihood space (thick green lines) correspond to the horizontal thresholds in posterior probability space (thin black lines). Optimal criterion and threshold for equal prior probabilities or payoffs are shown in dashed lines. If unequal prior probability or unequal payoff is provided such that S_1 ought to be chosen three times as often as S_2, then the threshold would optimally be shifted to 0.75, corresponding to a shift in the criterion such that the horizontal threshold and vertical criterion intersect on the S_2 posterior.*

3.1 Priors

Two main approaches have been used to determine whether observers can optimally adjust their criterion when one of two stimuli has a higher probability of occurrence. In base-rate manipulations, long blocks of the same occurrence frequency are used, and often observers are

not told the probabilities of occurrence in advance (e.g., Maddox, 1995). Most studies find that observers adjust their criterion to account for the unequal base rate, but this adjustment is smaller than what is required for optimal performance, resulting in a conservative criterion placement (Bohil & Maddox, 2003a; Green & Swets, 1966; Maddox, Bohil, & Dodd, 2003; Maddox & Bohil, 2001, 2003, 2005; Maddox & Dodd, 2001; T. A. Tanner et al., 1967; W. P. Tanner, 1956). Some studies have suggested that observers become progressively more suboptimal as the base-rate becomes progressively more extreme (Bohil & Maddox, 2003a; Green & Swets, 1966). However, a few studies have reported that certain conditions result in extreme criterion placement such that observers rely more on base-rate information than is optimal (Maddox & Bohil, 1998b). Finally, other studies found that with extensive training approximately half of the observers are able to adjust the criterion to a near optimal level (Maddox, 1995).

A second way to manipulate the probability of occurrence is to do it on a trial-by-trial basis and explicitly inform the observers about the stimulus probabilities before each trial. Research that has used this method also finds conservative criterion placement such that observers do not adjust their criterion enough (Ackermann & Landy, 2014; de Lange, Rahnev, Donner, & Lau, 2013; Rahnev, Lau, et al., 2011; Summerfield & Koechlin, 2010; Ulehla, 1966).

3.2 Payoffs

The decision criterion can also be manipulated by giving different payoffs for different responses. The general finding with this manipulation is that observers, again, do not adjust their criterion enough (Ackermann & Landy, 2014; Bohil & Maddox, 2001, 2003a, 2003b; Busemeyer & Myung, 1992; Maddox et al., 2003; Maddox & Bohil, 1998a, 2000, 2001, 2003, 2005; Maddox & Dodd, 2001; Markman et al., 2005; Taylor et al., 2004; Ulehla, 1966) and, as with base rates, become more suboptimal for more extreme payoffs (Bohil & Maddox, 2003a). Nevertheless, one study that involved a very large number of sessions with two monkeys reported extreme criterion changes (Feng, Holmes, Rorie, & Newsome, 2009).

Criterion adjustments in response to unequal payoffs are usually found to be more suboptimal compared to adjustments in response to unequal base-rates (Ackermann & Landy, 2014; Bohil & Maddox, 2001, 2003a; Busemeyer & Myung, 1992; Healy & Kubovy, 1981; Maddox & Bohil, 1998a; Maddox & Dodd, 2001; Maddox, 2002) though the opposite pattern was found by Green and Swets (1966). Different types of perceptual judgments that went beyond choosing one of two possible stimulus categories, as well as different modes of presenting the payoff structure, lead to similar observations: observers can use uncertainty in the data and in their internal estimates but fall short of optimality (P. A. Warren, Graf, Champion, & Maloney, 2012). For example, Landy, Goutcher, Trommershäuser, & Mamassian (2007) asked both naive and experienced observers to judge the average orientation of a set of line segments and included reward and cost regions; all observers showed suboptimal shifts in the presence of large costs. Finally, the exact payoff structure may also influence observers' optimality. For instance, introducing a cost for incorrect answers leads to more suboptimal criterion placement compared to conditions with the same optimal criterion shift but without a cost for incorrect answers (Maddox et al., 2003; Maddox & Bohil, 2000; Maddox & Dodd, 2001).

3.3 Explaining suboptimality in choice criterion

Why are observers unable to adjust their decision criteria optimally in response to priors and rewards? One possibility is that they do not have an accurate internal representation of the relevant probability (Acerbi et al., 2014; Ackermann & Landy, 2014; Zhang & Maloney, 2012). For example, Zhang & Maloney (2012) proposed that observers represent the logarithm of a

given probability rather than the probability itself. A related possibility is that observers set their criteria directly on the likelihood function without properly computing the posterior probability (A. E. Dusoir, 1975; T. Dusoir, 1983; Ingham, 1970; Macmillan & Creelman, 1990; Matthews, Davies, & Holley, 1993; See et al., 1997; Swets, 1986).

Another possible explanation is the "flat-maxima" hypothesis, according to which the observer adjusts the decision criterion based on the change in reward and has trouble finding its optimal value if other criterion positions result in similar reward rates (Bohil & Maddox, 2003b; Busemeyer & Myung, 1992; Maddox et al., 2003; Maddox & Bohil, 2001, 2003, 2004, 2005; Maddox & Dodd, 2001; von Winterfeldt & Edwards, 1982).

When the criterion-reward function has flat regions, large deviations in criterion can be seen as only mildly suboptimal because of the relatively small losses in reward. In fact, some authors have argued that observers in their studies should be considered basically optimal since they achieved close to maximal reward even though their decision criteria were clearly suboptimal (Feng et al., 2009; Whiteley & Sahani, 2008). However, optimal behavior would not lead to the observed systematic deviations in criterion placement, and therefore mechanisms beyond optimal computations are needed to fully account for the data.

4. Adjusting tradeoff between speed and accuracy

In the examples above, the only variable of interest has been observers' choice irrespective of their reaction times (RTs). However, if instructed, observers can provide responses faster at lower accuracy, a phenomenon known as speed-accuracy tradeoff (SAT; Fitts, 1966; Heitz, 2014). An important question here is whether observers can adjust their decision process optimally in response to a particular payoff structure that includes reaction time (**Figure 4**).

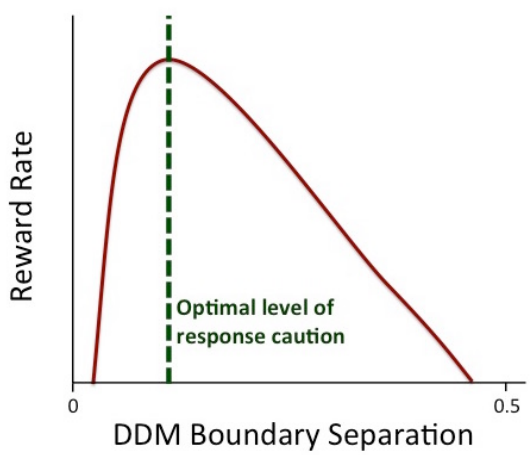

Figure 4*. Depiction of the reward rate curve for different boundary separations in the drift-diffusion model (DDM) framework (Starns & Ratcliff, 2010). A larger separation means more evidence is needed to make a response, so responses are more accurate but take longer. The optimal level of response caution - the amount of boundary separation that maximizes the reward per unit time - is depicted with the dashed line.*

4.1 Trading off speed and accuracy

A number of studies that explored this question found that while observers are able to adjust their behavior to account for both accuracy and RT, they cannot do this optimally (Balci et al.,

2011; Bogacz, Hu, Holmes, & Cohen, 2010; Simen et al., 2009; Starns & Ratcliff, 2010, 2012; Tsetsos, Pfeffer, Jentgens, & Donner, 2015). In most cases, observers set their decision threshold more conservatively than optimal, leading to slightly higher accuracy but substantially slower responses than optimal (Bogacz et al., 2010; Simen et al., 2009; Starns & Ratcliff, 2010, 2012). This is true when observers have a fixed period of time to complete as many trials as possible (Bogacz et al., 2010; Simen et al., 2009; Starns & Ratcliff, 2010, 2012), and in the more familiar design with a fixed number of trials per block (Starns & Ratcliff, 2010, 2012). Further, observers set more conservative decision criteria for more difficult conditions when optimality demanded that they do the opposite (Starns & Ratcliff, 2012). Older adults are even more suboptimal than college-age participants by this measure (Starns & Ratcliff, 2010, 2012). Similar to adjusting one's criterion based on rewards, extensive training reduces suboptimal behavior but does not eliminate it (Balci et al., 2011). Finally, recent research shows that when speed is emphasized, observers' usage of sensory information becomes suboptimal (Ho et al., 2012; Rae, Heathcote, Donkin, Averell, & Brown, 2014).

4.2 Keeping a low error rate under implicit time pressure

Even though observers tend to overemphasize accuracy, they are also suboptimal in tasks that require an extreme emphasis on accuracy. This conclusion comes from a line of research on visual search in which observers are typically given unlimited amount of time to decide whether a target is present or not (Eckstein, 2011). In certain situations, such as airport checkpoints or detecting tumors in mammograms, the goal is to keep very low miss rate, because misses can have dire consequences (Evans, Birdwell, & Wolfe, 2013; Wolfe, Brunelli, Rubinstein, & Horowitz, 2013). However, such situations typically feature very low target prevalence, so an observer may need to adjust both the criterion for target detection and a quitting threshold that dictates when to stop searching (Wolfe & Van Wert, 2010). A series of studies by Wolfe and colleagues found that observers, even trained doctors and airport checkpoint screeners, are suboptimal in such tasks in that they allow overly high rates of misses (Evans et al., 2013; Evans, Tambouret, Evered, Wilbur, & Wolfe, 2011; Wolfe et al., 2013; Wolfe, Horowitz, & Kenner, 2005; Wolfe & Van Wert, 2010). Further, this effect is robust and resistant to a variety of methods designed to help observers set more appropriate criteria (Wolfe et al., 2007) or correct motor errors (Van Wert, Horowitz, & Wolfe, 2009). An explanation of this suboptimality based on capacity limits is rejected by two studies that found that observers use a relatively more optimal criterion after a block of high prevalence targets accompanied with feedback (Wolfe et al., 2007, 2013).

4.3 Explaining suboptimality in speed-accuracy tradeoff

Why are observers unable to trade off speed and accuracy optimally? It is possible to account for overly conservative decision criteria by postulating that, in addition to maximizing their reward rate, observers place a premium on being accurate (Balci et al., 2011; Bogacz et al., 2010). Another possibility is that observers' judgments of elapsed time are noisy, and placing the threshold higher than the optimal value leads to a higher reward rate than setting it lower than optimal by the same amount (Simen et al., 2009; Zacksenhouse, Bogacz, & Holmes, 2010). Finally, observers may be unable or unwilling to set extreme criteria, making it impossible to keep a very low error rate (Wolfe et al., 2013). More than one of these factors may play a role in each of the demonstrations of suboptimality discussed above.

5. Confidence in one's decision

Up to this point we have considered how observers place, maintain, and adjust their perceptual criteria in order to maximize their task performance. Observers are also able to provide metacognitive confidence ratings of their subjective belief that each of their decisions was

correct. We now turn our attention to the question of whether these confidence judgments are optimal (**Figure 5**).

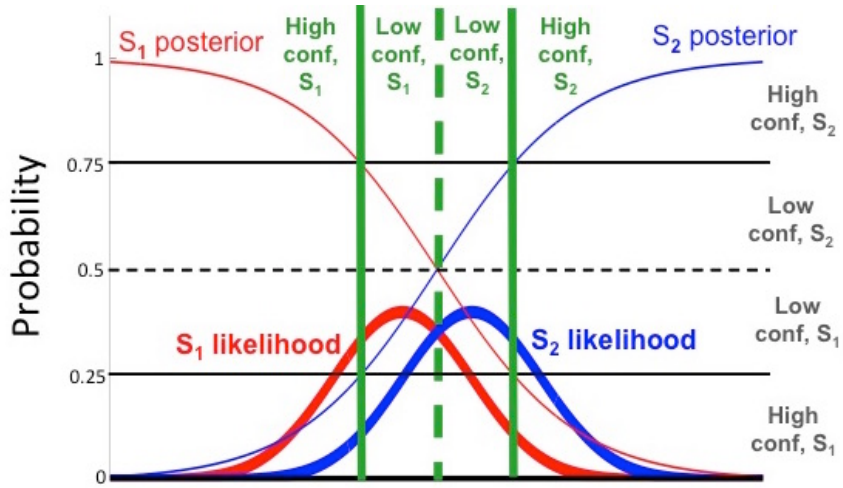

Figure 5*. Depiction of how an observer should give confidence ratings. Similar to Figure 3, both the likelihood and posterior functions are depicted. Confidence thresholds are optimally given on the posterior probability space (depicted as thin black lines). These thresholds correspond to criteria in likelihood space (depicted as thick green lines). This horizontal thresholds and vertical criteria intersect on the S_2 posterior.*

5.1 Over- and under-confidence (confidence calibration)

The most straightforward test of the optimality of observers' confidence ratings is to determine whether their stated probability of being correct matches the actual probability of being correct. For example, if we consider all trials in which an optimal observer has 70% confidence of being correct, then we would expect the average accuracy on those trials to be 70%. This logic applies when an observer chooses between two equally likely options without a significant bias for one over the other (though does not hold in the presence of unequal prior probabilities or choice biases, Drugowitsch, Moreno-Bote, & Pouget, 2014). This type of relationship between confidence and accuracy is often referred to as "confidence calibration" (Baranski & Petrusic, 1994). Studies of confidence have found that for certain tasks observers are overconfident (i.e., they overestimate their accuracy) (Adams, 1957; Baranski & Petrusic, 1994; Dawes, 1980; Harvey, 1997; Keren, 1988; Koriat, 2011) while for other tasks observers are underconfident (i.e., they underestimate their accuracy) (Baranski & Petrusic, 1994; Björkman, Juslin, & Winman, 1993; Dawes, 1980; Harvey, 1997; Winman & Juslin, 1993). One pattern that emerges consistently is that overconfidence often occurs for difficult tasks while underconfidence appears in easy tasks (Baranski & Petrusic, 1994, 1995, 1999), a phenomenon known as the *hard-easy effect* (Gigerenzer, Hoffrage, & Kleinbölting, 1991). Similar results are seen for tasks outside of the perceptual domain such as answering general knowledge questions (Griffin & Tversky, 1992). Over- and under-confidence are stable over different tasks (Ais, Zylberberg, Barttfeld, & Sigman, 2015; C. Song et al., 2011) and depend on non-perceptual factors such as one's optimism bias (Ais et al., 2015).

5.2 Dissociations of confidence and accuracy

Miscalibration of confidence, as with over- and under-confidence findings, can arise from a variety of causes such as misrepresentation of probabilities or observer-specific factors like shyness about giving high confidence. However, regardless of such factors, one would predict

that an observer who performs at a similar level in two different experimental conditions would have similar confidence for those conditions. However, despite the intuitiveness of such a proposition, many studies have demonstrated dissociations between confidence and accuracy. For example, a requirement to provide quick responses decreases accuracy while leaving confidence unchanged (Baranski & Petrusic, 1994; Vickers & Packer, 1982). A similar effect was obtained by Kiani, Corthell, & Shadlen (2014), who showed that a stimulus manipulation that increases RT but does not affect accuracy leads to a decrease in confidence. Dissociations between confidence and accuracy have also been found in conditions that differ in attention (Rahnev, Bahdo, de Lange, & Lau, 2012; Rahnev, Maniscalco, et al., 2011; Wilimzig, Tsuchiya, Fahle, Einhäuser, & Koch, 2008), the variability of the perceptual signal (de Gardelle & Mamassian, 2015; Koizumi, Maniscalco, & Lau, 2015; A. Song, Koizumi, & Lau, 2015; Spence, Dux, & Arnold, 2015; Zylberberg, Roelfsema, & Sigman, 2014), the stimulus-onset asynchrony in metacontrast masking (Lau & Passingham, 2006), the presence of unconscious information (Vlassova, Donkin, & Pearson, 2014), and the relative timing of a concurrent saccade (Navajas, Sigman, & Kamienkowski, 2014). Further, some of these biases seem to arise from individual differences that are stable across multiple sessions (de Gardelle & Mamassian, 2015). Finally, dissociations between confidence and accuracy have been found in studies that applied transcranial magnetic stimulation (TMS) to the visual (Rahnev, Maniscalco, Luber, Lau, & Lisanby, 2012), premotor (Fleming et al., 2015), or frontal cortex (Chiang, Lu, Hsieh, Chang, & Yang, 2014), possibly indicating disruptions to the normal circuits that compute confidence.

5.3 Metacognitive sensitivity (confidence resolution)

The sections above were concerned with the average magnitude of confidence ratings over many trials. Another measure of interest is the degree of correspondence between confidence and accuracy on individual trials (Fleming & Lau, 2014; Metcalfe & Shimamura, 1994). The degree to which the two go together on a trial-by-trial basis is often taken as a measure of metacognitive sensitivity (Fleming & Lau, 2014) and has also been referred to as "confidence resolution" (Baranski & Petrusic, 1994).

Research in this domain finds that metacognitive sensitivity is often imperfect (Metcalfe & Shimamura, 1994; Nelson & Narens, 1990). Recently, Maniscalco & Lau (2012) developed a method that reveals how optimal an observer's metacognitive sensitivity is. Their method computes *meta-d'*, a measure of how much information is available for metacognition, which can then be compared with the actual *d'* value. An optimal observer would have a *meta-'d*/*d'* ratio of 1. Maniscalco & Lau obtained a ratio of .77, suggesting a 23% loss of information for confidence judgments. Even though some studies that used the same measure but different perceptual paradigms found values close to 1 (Fleming, Ryu, Golfinos, & Blackmon, 2014), many others arrived at values substantially lower than 1 (Maniscalco & Lau, 2015; Maniscalco, Peters, & Lau, 2016; Massoni, 2014; McCurdy et al., 2013; Schurger, Kim, & Cohen, 2015; Sherman, Seth, Barrett, & Kanai, 2015; Vlassova et al., 2014). Interestingly, at least one study has reported values significantly above 1, suggesting that in certain cases the metacognitive system has more information than was used for the primary decision (Charles, Van Opstal, Marti, & Dehaene, 2013).

5.4 Other factors influencing confidence ratings

Confidence judgments are influenced by a host of factors unrelated to the perceptual signal at hand. Maniscalco and Lau demonstrated that working memory load (Maniscalco & Lau, 2015) affects the relationship between confidence and accuracy. Emotional states also have an influence; for instance, worry increases metacognitive performance (Massoni, 2014). Other

factors, such as eye gaze stability (Schurger et al., 2015) and age (Weil et al., 2013) also correlate with the relationship between confidence and accuracy.

Sequential effects have also been reported for confidence judgments such that a high confidence rating is more likely to follow a high, rather than low, confidence rating (Mueller & Weidemann, 2008). Confidence dependencies exist even between different tasks, such as letter and color discrimination, that depend on different neural populations in the visual cortex (Rahnev, Koizumi, McCurdy, D'Esposito, & Lau, 2015). This effect was dubbed "confidence leak" and was shown to be negatively correlated with observers' metacognitive sensitivity.

Confidence has also been shown to exhibit a "positive evidence" bias (Maniscalco et al., 2016; Zylberberg, Barttfeld, & Sigman, 2012). In 2-choice tasks, one can distinguish between evidence supporting the correct response (positive evidence) from the evidence supporting the alternative response (negative evidence). Even though the perceptual decisions usually follow the optimal strategy of weighting equally both of these sources of evidence, confidence ratings are suboptimal in depending more heavily on the positive evidence (Koizumi et al., 2015; Maniscalco et al., 2016; A. Song et al., 2015; Zylberberg et al., 2012).

5.5 Explaining suboptimality in confidence ratings

Why do observers give inappropriate confidence ratings? Most modeling approaches - such as signal detection theory (Green & Swets, 1966; Macmillan & Creelman, 2005), drift diffusion models (Ratcliff & Starns, 2009; Vickers, 1979), and Bayesian theories of population coding (Drugowitsch & Pouget, 2012) - assume that subjective reports of confidence are based directly on the perceptual signal. However, even though these approaches can sometimes account for particular types of suboptimal behavior (King & Dehaene, 2014; Rahnev, Maniscalco, et al., 2011), it is hard to see how they can account for the full array of suboptimalities reviewed above. Instead, other theories postulate the existence of either different processing streams that contribute differentially to the perceptual decision and the subjective confidence judgment (Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009; Jolij & Lamme, 2005; Weiskrantz, 1996) or a second processing stage that determines the confidence judgment, and which builds upon the information in an earlier processing stage responsible for the perceptual decision (Lau & Rosenthal, 2011; Maniscalco & Lau, 2010, 2016; Pleskac & Busemeyer, 2010). Both types of models could be used to explain the various findings of suboptimal behavior.

6. Comparing sensitivity in different tasks

The above sections discussed observers' performance on a single task. Another way of examining optimality is to compare the performance on two related tasks. If the two tasks have a formal relationship, then an optimal observers' sensitivity on the two tasks would follow that relationship.

6.1 Comparing performance in 1-stimulus and 2-stimulus tasks

Visual sensitivity has traditionally been measured by employing either (1) a 1-stimulus (detection or discrimination) task in which a single stimulus from one of two stimulus classes is presented on each trial, or (2) a 2-stimulus task in which both stimulus classes are presented on each trial (see 1.3 above). Intuitively, 2-stimulus tasks are easier because the final decision is based on two, rather than one, stimulus. In fact, assuming independent processing of each stimulus, the relationship between sensitivity on these two types of tasks can be mathematically defined: the sensitivity on the 2-stimulus task should be $\sqrt{2}$ times higher than on the detection task (Macmillan & Creelman, 2005; **Figure 6**). Nevertheless, empirical studies have often contradicted this predicted relationship, suggesting that one or both tasks were performed in a

suboptimal manner. Some studies found sensitivity ratios larger than $\sqrt{2}$ (Creelman & Macmillan, 1979; Jesteadt, 1974; Leshowitz, 1969; Markowitz & Swets, 1967; Pynn, 1972; Schulman & Mitchell, 1966; Swets & Green, 1961; Viemeister, 1970; Watson, Kellogg, Kawanishi, & Lucas, 1973; Yaffa Yeshurun et al., 2008), while others have found ratios smaller than $\sqrt{2}$ (Leshowitz, 1969; Markowitz & Swets, 1967; Swets & Green, 1961).

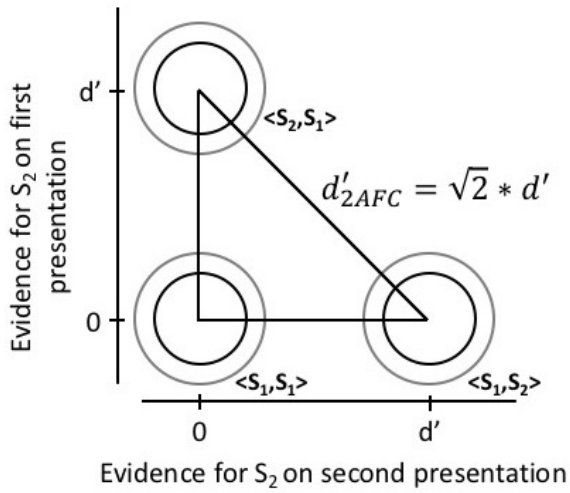

***Figure 6**. Depiction of the relationship between 1-stimulus and 2-stimulus tasks. The three sets of concentric circles represent 2D circular Gaussian distributions corresponding to presenting two stimuli in a row (e.g., $<S_2,S_1>$ means that S_2 was presented first and S_1 was presented second). If the discriminability between S_1 and S_2 is d' (1-stimulus task), then the Pythagorean theorem gives us the expected discriminability between $<S_1,S_2>$ and $<S_2,S_1>$ (2-stimulus task).*

6.2 Comparing performance in other tasks

Many other comparisons between tasks have been performed in the literature. For example, Creelman and Macmillan (1979) compared the sensitivity on 9 different psychophysical tasks and found a complex pattern of dependencies, many of which were at odds with optimal performance. Yeshurun et al. (2008) found that observers performed better in the first of two consecutive detection tasks, suggesting an inability to distribute resources optimally between the two stimulus intervals. Other studies find that longer inter-stimulus intervals in 2IFC tasks lead to decreases in sensitivity (Berliner & Durlach, 1973; Kinchla & Smyzer, 1967; W. P. Tanner, 1961), presumably due to memory limitations.

An alternative approach to comparing an observer's performance on different tasks is allowing observers to choose which tasks they prefer to complete and analyzing the optimality of these decisions. In particular, one can test for the presence of transitivity: if an observer prefers task A to task B and task B to task C, then the observer should choose task A to task C. Human observers, however, have been shown to violate the transitivity principle (Zhang, Morvan, & Maloney, 2010).

6.3 Explaining suboptimality in between-task comparisons

Why does perceptual sensitivity violate the expected relationship between different tasks? One possibility is that observers face certain capacity limits in one but not the other task. For example, compared to 1-stimulus tasks, the more complex 2-stimulus task requires the simultaneous processing of two stimuli. If limited resources hamper the processing of the two

stimuli, then sensitivity in that task would fall short of what is predicted based on the single-stimulus task. Nevertheless, in some experiments observers performed worse than expected on the detection, rather than on the 2-stimulus task. A possible explanation of this effect is the presence of a larger "criterion jitter" in the detection task, i.e., a larger variability in the decision criterion from trial to trial (see **Figure 2**). Since 2-stimulus tasks involve the comparison of two stimuli on each trial, these tasks are less susceptible to criterion jitter. Such criterion variability, which could stem from sequential dependencies or even random criterion fluctuations, decreases the estimated sensitivity (Mueller & Weidemann, 2008).

7. Cue combination

Studies of cue combination have been fundamental to the view that sensory perception is optimal (Trommershäuser, Körding, & Landy, 2011). Cue combination (also called cue integration) is needed whenever different sensory features provide separate pieces of information about a single physical quantity. For example, auditory and visual signals can separately inform about the location of an object. Each cue provides imperfect information about the physical world, but different cues have different sources of variability. As a result, integrating them can provide a more accurate and reliable estimate of the physical quantity of interest.

Cue combination lends itself to ideal observer modeling and tests of optimality by focusing on the question of whether a perceptual estimate formed from two cues is the best estimate one could make given the estimates available from each cue individually. The optimal estimate is typically taken to be the one that maximizes precision (minimizes variability) across trials, which is called the minimum-variance unbiased estimator. When the variability for each cue is Gaussian and independent of the other cues, the minimum-variance unbiased estimator is a linear combination of the estimates from each cue, weighted by their individual reliabilities (Landy, Banks, & Knill, 2011). This is equivalent to maximum likelihood estimation (MLE) and is optimal in the sense that it is the maximum a posteriori estimate when the prior over estimates is uniform. Whether this weighted sum formula holds for a given cue integration task can be readily tested psychophysically, and a large number of studies have done exactly this for different types of cues and tasks (see Ma, 2010 and Trommershauser et al., 2011 for reviews).

In particular, the optimal mean perceptual estimate (μ) after observing cue 1 (with feature estimate μ_1 and variance of σ_1^2) and cue 2 (with feature estimate μ_2 and variance of σ_2^2) is:

$$\mu = \frac{\mu_1}{\sigma_1^2} / (\frac{1}{\sigma_1^2} + \frac{1}{\sigma_2^2}) + \frac{\mu_2}{\sigma_2^2} / (\frac{1}{\sigma_1^2} + \frac{1}{\sigma_2^2})$$

and the optimal variance of the perceptual estimate (σ^2) is:

$$\sigma^2 = \frac{\sigma_1^2 * \sigma_2^2}{\sigma_1^2 + \sigma_2^2}$$

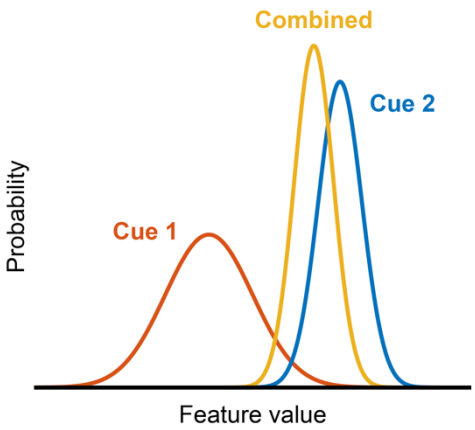

Figure 7*. Optimal cue integration. Two cues that give independent information about the value of a sensory feature (red and blue curves) are combined to form a single estimate of the feature value (green curve). The combined cue distribution is narrower than both individual cue distributions, and its mean is closer to the more certain cue (cue 2).*

7.1 Examples of optimality in cue combination

A classic example of this approach is a study of visual-haptic cue combination by Ernst & Banks (2002). In this study, observers estimated the height of a rectangle that they could 1) only see, 2) only touch, or 3) both see and touch. Performance in the visual-haptic condition was well described by the MLE formula: the single cue measurements predicted both the reliability of visual-haptic estimates and the weights given to the two cue types for these estimates. Many studies have observed similar optimal cue combination behavior in a range of tasks estimating different physical quantities. These studies have investigated integration across two modalities (including vision, touch, audition, the vestibular sense, and proprioception; e.g., Alais & Burr, 2004; Ernst & Banks, 2002; Gu, Angelaki, & DeAngelis, 2008; van Beers, Sittig, & Denier van der Gon, 1996) and across two features in the same modality, such as various visual cues to depth (e.g., (Jacobs, 1999; Landy, Maloney, Johnston, & Young, 1995). Common among these experiments is that trained observers complete many trials of a psychophysical task, and the two cues provide similar estimates of the quantity of interest. Optimal cue combination has also been observed during sensory-motor integration (Maloney & Zhang, 2010; K. Wei & Körding, 2011; Yaffa Yeshurun et al., 2008).

7.2 Examples of suboptimality in cue combination

Because optimality is often the hypothesized outcome in cue integration studies, findings of suboptimality may be underreported or underemphasized in the literature (Rosas & Wichmann, 2011). Still, a number of studies have demonstrated suboptimal cue combination behavior that violates some part of the MLE formula. These violations fall into two categories: 1) those in which the cues are integrated but are not weighted according to their independently measured reliabilities, and 2) those in which the reliability of estimates from two cues is no better than those from a single cue.

In the first category are findings from a wide range of combined modalities: visual-auditory (Battaglia, Jacobs, & Aslin, 2003; Burr, Banks, & Morrone, 2009; Maiworm & Röder, 2011), visual-vestibular (Fetsch, Pouget, Deangelis, & Angelaki, 2012; Prsa, Gale, & Blanke, 2012), visual-haptic (Battaglia, Kersten, & Schrater, 2011; Rosas, Wagemans, Ernst, & Wichmann, 2005), and visual-visual (Knill & Saunders, 2003; Rosas, Wichmann, & Wagemans, 2007). For example, auditory and visual cues were not integrated according to the MLE rule in a

localization task; instead, observers treated the visual cue as though it were more reliable than it really was (Battaglia et al., 2003). Similarly, visual and haptic depth cues were integrated according to their reliabilities, but observers underweighted the visual texture cue (Rosas et al., 2005). In some of these studies, cue misweighting was restricted to low-reliability cues: In a visual-vestibular heading task, observers overweighted vestibular cues when visual reliability was low (Fetsch et al., 2012), and in a visual-auditory temporal order judgment task, observers overweighted auditory cues when auditory reliability was low (Maiworm & Röder, 2011). However, overweighting does not only occur within a limited range of reliabilities (e.g., Battaglia et al., 2003; Prsa et al., 2012).

Several studies have failed to find optimal cue integration in the temporal domain. In an audio-visual rate combination task, observers only partially integrated the auditory and visual cues, and they did not integrate them at all when the rates were very different (Roach, Heron, & McGraw, 2006). Observers also overweight auditory cues in temporal order judgment tasks (Maiworm & Röder, 2011) and temporal bisection tasks (Burr et al., 2009). It is well-established that when two cues give very different estimates, observers tend to discount one of them (Gepshtein, Burge, Ernst, & Banks, 2005; Jack & Thurlow, 1973; Körding et al., 2007; Roach et al., 2006; D. H. Warren & Cleaves, 1971), an effect which has been called "robust fusion" (Maloney & Landy, 1989). However, in most of these studies, suboptimal cue combination was observed even when the cues gave similar estimates.

In the second category of suboptimal cue combination findings, two cues are no better than one (Chen & Tyler, 2015; Drugowitsch, DeAngelis, Klier, Angelaki, & Pouget, 2014; Landy & Kojima, 2001; Oruç, Maloney, & Landy, 2003; Rosas et al., 2005, 2007; Saarela & Landy, 2015). Picking the best cue is known as a "veto" type of cue combination (Bülthoff & Mallot, 1988) and is considered a case of "strong fusion" (Clark & Yullie, 1990; Landy et al., 1995). This is an even more serious violation of optimal cue combination, since it is as though no integration has taken place at all -- the system either picks the best cue or in some cases does *worse* with two cues than with one. In one demonstration of cue integration impairing performance, observers integrated multiple cues to letter identity even when the optimal strategy was to use only a single cue (Saarela & Landy, 2015).

7.3 Combining stimuli of the same type

So far we have only considered cue combination studies in which the two cues come from different sensory modalities or dimensions. Suboptimal behavior has also been observed when combining cues from the same dimension. For example, Summerfield and colleagues have recently shown that observers do not weight every sample stimulus equally in a decision (Summerfield & Tsetsos, 2015). For simultaneous samples, observers underweight "outlier" stimuli lying far from the mean of the sample (de Gardelle & Summerfield, 2011; Michael, de Gardelle, & Summerfield, 2014). For sequential samples, observers overweight stimuli toward the end of the sequence (a recency effect) as well as stimuli that are similar to recently presented items (Cheadle et al., 2014).

7.4 Combining sensory and motor cues

Suboptimal cue integration has also been found in sensory-motor tasks. For example, when integrating the path of a pointing movement with online visual feedback, observers tend to underestimate the uncertainty indicated by the feedback (Körding & Wolpert, 2004). In a pointing task in which observers were rewarded for hitting the correct visual target, observers tended to underweight the difficulty of the motor task (the size of the target), attempting to hit the target consistent with their perceptual decision even when that decision was based on uncertain

sensory information (Fleming, Maloney, & Daw, 2013). Within the action domain (and so beyond our focus on perception), Maloney and Zhang (2010) have reviewed studies showing both optimal and suboptimal behavior.

7.5 Explaining suboptimal cue combination

Why do observers sometimes combine cues suboptimally? One possible explanation is that people do not have accurate representations of the reliability of the cues. (Knill & Saunders, 2003; Rosas et al., 2005). This might be a particular problem in unnatural tasks. For example, in one task for which cue combination was suboptimal, observers haptically explored a surface with a single finger to estimate its slant. However, observers may have little experience with single-finger slant estimation, since multiple fingers or the whole hand might ordinarily be used for such a task (Rosas et al., 2005). Reliability estimation might also be difficult when the reliability is very low. This possibility may apply to studies in which observers were optimal within a range of sensory reliability, but not outside it (Fetsch et al., 2012; Maiworm & Röder, 2011).

Some authors suggest that another reason for over- or under-weighting a certain cue could be prior knowledge about how cues ought to be combined. This could include a prior assumption about how likely a cue is to be related to the desired physical property (Battaglia et al., 2011), how likely two cue types are to correspond to one another (and thus be beneficial to integrate) (Roach et al., 2006), or a general preference to rely on a particular modality, such as audition in a timing task (Maiworm & Röder, 2011).

For certain tasks, some researchers question the assumptions of the MLE model, such as Gaussian noise (Burr et al., 2009) or the independence of the neural representations of the two cues (Rosas et al., 2007). Nevertheless, worse performance with two cues than with one is difficult to reconcile with any normative cue integration model in the absence of other constraints.

Sometimes suboptimality in cue combination can depend on task requirements and observers' strategies for performing the task. The importance of these factors was revealed in the finding that observers' accuracy was suboptimal unless reaction time was taken into account (Drugowitsch, DeAngelis, et al., 2014) and the demonstration that observers can be optimal in one task but suboptimal in another with the same stimuli (Saarela & Landy, 2015). These examples show how assumptions about task demands and the particular task tested can influence conclusions drawn about optimality.

"Robust averaging," or down-weighting of outliers, has been observed when observers must combine multiple pieces of information that give very different perceptual estimates. It has been suggested that these suboptimal behaviors can be explained by adaptive gain changes that result in highest sensitivity to stimuli close to the mean of the sample (or in the sequential case, the subset of the sample that has been presented so far; Summerfield & Tsetsos, 2015). This adaptive gain mechanism is similar to models of sensory adaptation (Barlow, 1990; Carandini & Heeger, 2012; Wark, Lundstrom, & Fairhall, 2007). By following principles of efficient coding that place the largest dynamic range at the center of the sample (Barlow, 1961; Brenner, Bialek, & de Ruyter van Steveninck, 2000; Wainwright, 1999), different stimuli receive unequal weightings, leading to suboptimality. Note that psychophysical studies in which stimulus variability is low would not be expected to show this kind of suboptimality, because all the stimuli would have high gain (Cheadle et al., 2014).

8. Other examples of suboptimality

Thus far we have specifically focused on tasks where the optimal behavior can be specified mathematically in a relatively uncontroversial manner. However, the issue of optimality has been discussed in a variety of other contexts. Often these discussions center on cases in which perception is not veridical. From the perspective that the visual system should represent the true state of the world, such perception is suboptimal. While veridicality and optimality need not go hand in hand, we still review the relevant research and later use it to discuss some of the difficulties in defining optimality.

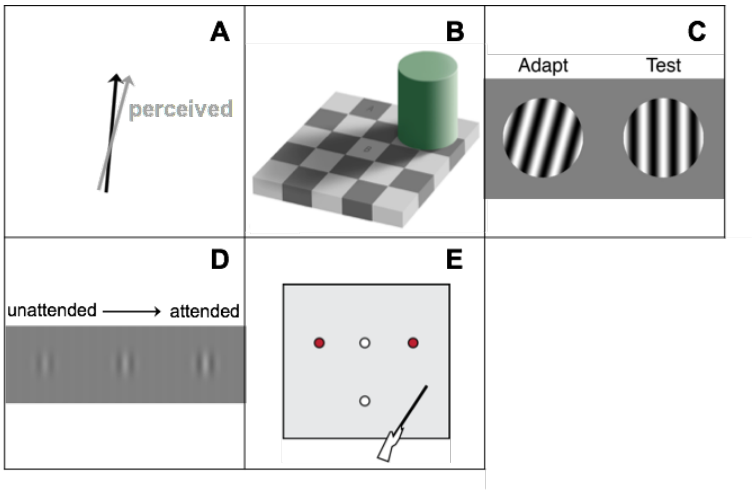

Figure 8*. Examples of adaptation, illusions, and biases. A) Cardinal repulsion. A nearly vertical (or horizontal) line looks more tilted away from the cardinal axis than it is. B) Adelson's checkerboard lightness illusion. Square 2 appears to be lighter than square 1, even though the two squares have the same luminance. Figure courtesy of Michael Bach (http://www.michaelbach.de/ot/lum-adelsonCheckShadow/index.html). C) Tilt aftereffect. After viewing a tilted adapting grating, observers perceive a vertical test grating to be tilted away from the adaptor. D) Effects of spatial attention on contrast appearance (Carrasco, Ling, & Read, 2004). An attended grating appears to have higher contrast than the same grating when it is unattended. E) Effects of action affordances on perceptual judgments* (Witt, 2011)*. Observers judge an object to be closer (far white circle compared to near white circle) relative to the distance between two landmark objects (red circles) when they are holding a tool that allows them to reach that object than when they have no tool.*

8.1 Perceptual biases, illusions, and improbabilities

A number of basic visual biases have been documented. Some examples include repulsion of orientation or motion direction estimates away from cardinal directions (**Figure 8A**; Jastrow, 1892; Rauber & Treue, 1998), a bias to perceive speeds as slower than they are when stimuli are low contrast (Stone & Thompson, 1992; Thompson, 1982; but see Thompson, Brooks, & Hammett, 2006), a bias to perceive surfaces as convex (Langer & Bülthoff, 2001; Sun & Perona, 1997), and a bias to perceive visual stimuli closer to fixation than they are (whereas the opposite is true for auditory stimuli; Odegaard, Wozny, & Shams, 2015).

When biases, context, or other factors lead to something looking dramatically different from its physical reality, we might call it a visual illusion. A classic example is the lightness illusion (**Figure 8B**) in which two squares on a checkerboard appear to be different shades of gray even

though they actually have the same luminance (Adelson, 1993). Perceptual illusions persist even when the observer knows about the illusion and even after thousands of trials of exposure (Gold, Murray, Bennett, & Sekuler, 2000).

Some illusions are difficult to reconcile with existing theories of optimal perception. Anderson, O'Vari, & Barth (2011), for example, reported strong percepts of illusory surfaces that were improbable according to optimal frameworks for contour synthesis. In the size-weight illusion, smaller objects are perceived as heavier than larger objects of the same weight, even though the prior expectation is that smaller objects are lighter (Brayanov & Smith, 2010).

8.2 Adaptation

Adaptation is a widespread phenomenon in sensory systems in which responsiveness to prolonged or repeated stimuli is reduced (Webster, 2015). Adaptation can be seen as suboptimal from a Bayesian perspective because subsequent perceptual estimates tend to diverge from rather than conform to the prior stimulus. For example, after prolonged viewing of a line tilted slightly away from vertical, a vertical line looks tilted in the opposite direction (the "tilt aftereffect", **Figure 8C**; Gibson & Radner, 1937). Or, after viewing motion in a certain direction, a stationary stimulus appears to drift in the opposite direction (Wohlgemuth, 1911). After adapting to a certain color, perception is biased toward the complementary color (Sabra, 1989; Turnbull, 1961), and after adapting to a specific face, another face appears more different from that face than it would have otherwise (Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & MacLeod, 2011). In all of these examples, perception is repelled away from the prior stimulus.

8.3 Appearance changes due to visual attention

The same physical stimulus can also be perceived in different ways depending on the state of visual attention. Directing spatial attention to a stimulus can make it appear higher contrast (**Figure 8D**; (Carrasco et al., 2004; Liu, Abrams, & Carrasco, 2009; Störmer, Mcdonald, & Hillyard, 2009), larger (Anton-Erxleben, Henrich, & Treue, 2007), faster (Anton-Erxleben, Herrmann, & Carrasco, 2013; Fuller, Park, & Carrasco, 2009; Turatto, Vescovi, & Valsecchi, 2007), brighter (Tse, 2005), and higher spatial frequency (Abrams, Barbot, & Carrasco, 2010; Gobell & Carrasco, 2005) than it would otherwise. Often attentional effects improve performance on a visual task, but sometimes they make performance worse (Ling & Carrasco, 2006; Y Yeshurun & Carrasco, 1998).

8.4 Cognition-based biases

Other studies have documented visual biases associated with more cognitive factors, including action affordances (Witt, 2011), motivation (Balcetis, 2015), and language (Lupyan, 2012). For example, when people will be reaching for an object with a tool that allows them to reach further, they report the object as looking closer than when they will be reaching without the tool (**Figure 8E**; Witt, Proffitt, & Epstein, 2005). In the linguistic domain, calling an object a "triangle" leads observers to report the object as having more equal sides than when the object is called "three-sided" (Lupyan, 2016). How much these more cognitive factors affect perception *per se*, as opposed to post-perceptual judgments, and to what extent the observed visual biases are mediated by attention, remain controversial questions (Firestone & Scholl, 2015).

8.5 Explaining these other examples of suboptimality

How can one explain these findings that are often seen as examples of suboptimality? Some biases and illusions have been explained as arising from priors in the visual system. Misperceptions of motion direction (Weiss et al., 2002) and biases in reporting the speed of low contrast stimuli (Stocker & Simoncelli, 2006a; Thompson, 1982; Vintch & Gardner, 2014) have

been explained as optimal percepts for a visual system with a prior for slow motion (Stocker & Simoncelli, 2006a; Weiss et al., 2002), because natural objects tend to be still or move slowly. The suggestion is that these priors have been made stable over a lifetime and influence perception even when they do not apply (i.e., in a laboratory task).

Optimal decoding of sensory representations in one task can also lead to suboptimal biases in another task using the same stimuli. For example, optimal computation in a motion direction discrimination task should lead to suboptimal perceptual biases in an estimation task -- which is exactly what was observed when these two tasks were interleaved in a single experiment (Jazayeri & Movshon, 2007).

Various efforts have been made to reconcile adaptation with Bayesian optimality (Grzywacz & Balboa, 2002; Hohwy, Roepstorff, & Friston, 2008; Schwiedrzik et al., 2014; Snyder, Schwiedrzik, Vitela, & Melloni, 2015). One of the most well-developed lines of work explains the repulsive effects of adaptation as a consequence of efficient coding (Stocker & Simoncelli, 2006b). In this framework, a sensory system adapts to maximize its dynamic range around the value of previous input. This change in coding does not affect the prior (as might be expected in a Bayesian treatment of adaptation) but rather affects the likelihood function that relates the system's measurement of the stimulus to the true stimulus value. Specifically, it skews likelihoods away from the adapted stimulus, giving rise to repulsive aftereffects. A similar principle has been suggested to explain why perceptual estimates are repelled from long-term priors, such as those determined by the statistics of natural images (X.-X. Wei & Stocker, 2012, 2015).

COMMON CAUSES OF SUBOPTIMALITY

We have so far described a number of examples of suboptimal behavior. Now we discuss several common causes of suboptimality that emerge from the findings we reviewed. These include general perceptual principles as well as methodological considerations that could account for some findings of suboptimal behavior.

Perceptual principles associated with suboptimality

1. Probability transformation

In order to optimally incorporate prior information into their perceptual decisions, observers need to be able to accurately represent this information. However, it appears that they can't always do this. Researchers commonly find S-shaped distortions of probability and frequency such that small values are overestimated while large values are underestimated (Brooke & MacRae, 1977; Varey, Mellers, & Birnbaum, 1990). Zhang and Maloney (2012) argued for the presence of "ubiquitous log odds" that systematically distort people's judgments.

2. Wrong priors

Observers have many priors that help them behave in their natural environment. If these priors are not flexibly changed in a new environment, such as a laboratory experiment, the behavior in that environment will be suboptimal (Brainard et al., 2006; Girshick, Landy, & Simoncelli, 2011; Glennerster, Tcheang, Gilson, Fitzgibbon, & Parker, 2006). Priors that are wrong for a given task can lead to visual illusions, as discussed in Section 8.1. Priors acquired during an experiment can also lead to suboptimal behavior when stimulus statistics are non-stationary (Raviv, Ahissar, & Loewenstein, 2012). The question of how different kinds of priors are learned is still relatively open (Seriès & Seitz, 2013).

3. Hard-to-learn priors

Some priors are inherently complex. Even though most research uses or assumes Gaussian priors, some studies have asked observers to use priors from more complex distributions, such as bimodal functions. Observers are usually suboptimal with such priors (Acerbi, Wolpert, & Vijayakumar, 2012; Gekas, Chalk, Seitz, & Series, 2013). Acerbi et al. (2014) tested observers' optimality when the priors are explicitly represented on each trial and found no difference in the degree of suboptimality for Gaussian and bimodal distributions. Thus, suboptimal implementation of complex priors appears to be due to inability to acquire and maintain the prior rather than in the ability to use it correctly. In some cases the priors are hard or impossible to calculate even for the experimenter let alone for the observer (Beck, Ma, Pitkow, Latham, & Pouget, 2012; Geisler & Najemnik, 2013).

4. Wrong likelihoods

If an observer does not have an accurate representation of his or her own likelihood function, it can lead to under- or over-weighting the sensory evidence relative to the prior. Inaccurate likelihoods could explain suboptimal behavior in some cue combination tasks (as discussed in Section 7.2). Observers can also fail to optimally use explicitly presented likelihood information (Körding & Wolpert, 2004), as described in Section 7.4.

5. Non-random guesses

It is possible that when the difference in the posterior probability between two options is small, observers "guess" between the two. If such guesses were not random (e.g., an observer is more likely to choose one stimulus category over another when uncertain), then this would lead to suboptimal performance. As discussed in Section 1, such guesses are one possible reason for biased criteria in 2-choice tasks. Many descriptive models of behavior include a separate parameter to account for guessing, though the guesses are usually assumed to be completely random (Acerbi et al., 2014; Garcia-Perez & Alcala-Quintana, 2010; Whiteley & Sahani, 2008; Wichmann & Hill, 2001).

6. Memory limitations

Most perceptual tasks do not have high memory demands and thus memory limitations are not regularly considered. However, many tasks involve non-trivial memory requirements. For example, in temporal 2-stimulus tasks (that is, 2IFC tasks), the first target may not be remembered perfectly while processing the second one. Similarly, in cases when observers should maintain separate criteria for different classes of stimuli, these criteria may attract each other (Gorea & Sagi, 2000, 2001, 2002; Morales et al., 2015; Rahnev, Maniscalco, et al., 2011; Solovey et al., 2015). Finally, in tasks that involve confidence ratings, observers need to maintain the location of several confidence criteria, which may again create larger memory demands. Phenomena like the "contraction bias", in which size comparisons of two successive stimuli depend on how large they are relative to the sample, have been explained as a stronger influence of a prior on the first of two successive stimuli due to a noisier representation of that stimulus in memory (Ashourian & Loewenstein, 2011).

7. Suboptimal confidence ratings

As discussed in Section 5, it is likely that subjective confidence ratings are based on partially different information than the perceptual decisions themselves (Del Cul et al., 2009; Jolij & Lamme, 2005; Lau & Rosenthal, 2011; Maniscalco & Lau, 2010; Pleskac & Busemeyer, 2010; Weiskrantz, 1996), leading to an imperfect relationship between these two quantities.

8. Suboptimal biases

The above principles postulate various hard limitations that could lead to suboptimal behavior. In other words, these limitations may be (nearly) insurmountable for observers despite their best efforts. However, it is likely that in some situations observers are suboptimal despite a potentially intact ability for optimality. For example, Stocker & Simoncelli (2008) suggest the presence of *self-consistency bias*: once observers decide on a model for how sensory input was generated, they no longer consider alternative models. Stocker and Simoncelli show how this bias can account for suboptimality in a second perceptual decision since observers may only consider scenarios consistent with their first decision. Similarly, Fleming, Maloney, & Daw (2013) propose that in certain cases observers may make a categorical commitment to one or other state of the world and discard probabilistic information about the likelihood of each state. A similar selection of evidence is seen in the "positive evidence bias" discussed in Section 5.4.

9. Efficient coding

Influential theories of brain function, such as the *efficient coding hypothesis* (Barlow, 1961; Simoncelli, 2003; Summerfield & Tsetsos, 2015), posit that the brain is optimized for efficient rather than optimal coding. Efficient coding is a strategy to use a limited number of neurons to encode a large stimulus space. Suboptimal behavior arising from adaptation, a pervasive feature of sensory processing, has begun to be explained in this framework, as discussed in Section 8.2. A related mechanism - neural normalization (Reynolds & Heeger, 2009) - also postulates that sensory information is transformed in a way that leads to partial loss of information. All strategies that involve partial information loss necessarily lead to suboptimal behavior on tasks that require the lost original information.

Methodological considerations that can account for suboptimal behavior

1. Experimenters making wrong distributional assumptions

Many of the examples of suboptimality above have relied on the assumption that the likelihood function $P(r|s)$ has a Gaussian distribution. This is a reasonable assumption in many common cases (Macmillan & Creelman, 2005; See et al., 1997; Swets, 1986) but, if incorrect, can make otherwise optimal behavior appear suboptimal (Healy & Kubovy, 1981; Kubovy, 1977; Maloney & Thomas, 1991). Nevertheless, inferences about suboptimality related to, among others, sequential effects, speed-accuracy tradeoffs, confidence-accuracy dissociations, perceptual illusions, and perception for action do not rely on distributional assumptions. On the flip side, most demonstrations of optimal behavior (e.g., Ernst & Banks, 2002) also rely on assumptions of Gaussian variability.

2. Lack of motivation to be optimal

One reason noted by many researchers as to why observers may not adjust their criterion in studies with unequal rewards is a desire to be accurate that competes with the desire for maximal reward (the optimal strategy). For example, Maddox & Bohil (1998a) posited the COmpetition Between Reward and Accuracy maximization (COBRA) hypothesis according to which observers attempt to maximize reward but also place a premium on accuracy (Maddox & Bohil, 2004, 2005). Placing a premium on accuracy in addition to reward can also be an issue in studies on the speed-accuracy tradeoff. Similarly, the overly conservative criterion in some detection studies could be due to observers not wanting to make false alarms, which can be seen as lying.

3. Insufficient training with the task

A potential explanation for suboptimal behavior is that observers did not receive sufficient training with the task. Indeed, trial-by-trial feedback does make behavior more optimal in the majority of cases (e.g., Baranski & Petrusic, 1994; Maddox & Bohil, 2005), so it is tempting to

blame insufficient training for suboptimal behavior. Nevertheless, a large number of studies have shown that trial-by-trial feedback does not make observers more optimal in a number of specific tasks (Björkman et al., 1993; Keren, 1988; Maddox & Bohil, 2001; Winman & Juslin, 1993). Further, some studies featured continuous trial-by-trial feedback for months and still found suboptimal behavior (e.g., Feng et al., 2009). Thus, even though meaningful feedback appears necessary for proper learning, in many cases it is not sufficient for observers to achieve optimality.

4. Task specification

An otherwise optimal observer may appear suboptimal if her assumptions about the task do not match the assumptions of the experimenter or the analysis. For instance, many experiments use a range of different stimulus intensities and then analyze each intensity separately as if it were the only one presented. A potential problem in this approach is that observers develop a prior over all intensities presented. Drugowitsch et al. (2014) showed how this design flaw may exacerbate the hard-easy effect in which observers are overconfident in hard tasks and underconfident in easy tasks. Similarly, observers may change their beliefs about a task and corresponding response criteria due to random variability during the experiment -- for example, inferring that the reliability of a predictive cue has decreased after several invalid trials. These scenarios highlight the notion that great care needs to be taken that observers' assumptions in performing a task match exactly the assumptions implicit in the analysis.

OPTIMALITY AND APPROACHES TO UNDERSTANDING THE PERCEPTUAL SYSTEM

Overarching theory vs. bag of tricks

One attraction of the idea that human perception is optimal is the promise that this approach can lead to an overarching theory of brain processing (Griffiths et al., 2012). Such a theory would allow us to describe diverse perceptual phenomena under the same theoretical framework. Nevertheless, whether an overarching theory of brain function can be constructed is a purely empirical question. The long list of examples of suboptimality in this review should be a cautionary tale about the plausibility of an overarching theory based on optimality alone.

Another extreme view is to see the brain as a "bag of tricks" (Ramachandran, 1990). In this view, the brain has adopted a new trick to deal with each new environmental demand over the course of evolution, thus turning itself into a collection of heuristic solutions. Compiling a list of these solutions, no matter how extensive, will likely never add up to a coherent theory.

The Objectives-Constraints-Mechanisms (OCM) approach

We suggest that the way forward is to find middle ground between these extreme positions. In particular, we can retain an overarching theoretical *framework*, without ignoring the messiness of human behavior.

We advocate for an Objectives-Constraints-Mechanisms (OCM) approach to understanding the perceptual systems of the brain. In our view, the perceptual system is trying to solve a loosely-defined optimization problem: how to maximize the value of its representations, while minimizing the cost of the resources expended. Therefore, it is critical to specify what types of representations are beneficial (i.e., define the objectives of the system) and what kinds of costs are associated with them (i.e., define the constraints of the system). Critically, these benefits and costs need to be optimized on several, possibly competing, timescales: from the immediate situation to the lifetime of the organism and even the species. Specific examples of each component are listed in Box 1.

Objectives
The first step in the OCM approach is to specify explicitly the objectives of the perceptual system. It is natural to assume that the objective of the system is simply to represent the world as it is. However, it is much more likely that the perceptual system's objective is to produce "useful" rather than veridical representations of the world (Gigerenzer & Brighton, 2009; Juslin, Nilsson, & Winman, 2009; Simon, 1956). Specifying what "useful" means is one of the great challenges that need to be addressed in order to understand brain function.

Constraints
The flip side of the positive value achieved by satisfying its objectives is that the perceptual system necessarily incurs costs. These costs need to be specified and quantified in order to understand the optimization problem that the brain needs to solve. A mechanism that falls short of fully achieving the brain's objectives but saves considerably on costs is likely to be selected over a mechanism that produces optimal representations at a great cost (Beck et al., 2012; Bowers & Davis, 2012a).

Mechanisms
Finally, there could be a number of ways for the perceptual system to maximize its value (i.e., satisfy its objectives) while minimizing its costs (i.e., remain within its constraints). Thus the final step in the OCM approach is to specify the mechanisms that the perceptual system has selected for its computations. Specifying the computational mechanisms used by the brain is at the heart of understanding perception.

BOX 1
Here we compile a short (non-exhaustive) list of objectives, constraints, and well-established mechanisms used by the visual system, to illustrate these concepts.

Objectives

1. Faithful representations

The perceptual system needs to be able to represent the outside world faithfully. Expected objects may be given extra weight but completely new and unexpected objects should still be represented with fidelity.

2. Relevant representations

Objects that are irrelevant to the current goals of the organism do not need to be represented with high fidelity. On the other hand, highly relevant objects (e.g., faces) should receive more resources.

3. Fast representations

In a dynamic world, accurate representations are of little value unless they are also fast. It is likely that the perceptual system is wired for quick decision even in situations when more time is available.

Constraints

1. Metabolic energy

One cost incurred by the perceptual system is the use of metabolic energy (Carrasco, 2011; Lennie, 2003). Mechanisms that save metabolic energy may be preferred even if they are suboptimal.

2. Cortical territory

The number of cortical neurons, the number of connections between them, the number of dendrites and axonal length of each neuron, etc. are structurally constrained (Franconeri, Alvarez, & Cavanagh, 2013).

3. Physical variability ("noise")

Several physical and biological factors lead to variability in the properties of neurons, circuits, and their responses. In addition, neurons die, neurotransmitter levels vary, and nutrients fluctuate. The perceptual system needs to build representations that are robust to such factors but is inherently limited by the physical hardware available.

4. Computing with neurons

Brain computations are carried by neurons and thus inherit all of neurons' limitations such as relatively slow information transfer, limits on firing rate and frequency, etc.

Mechanisms

The brain implements a number of mechanisms that balance objectives and constraints by prioritizing some information and discarding other information.

1. Higher-level mechanisms

At this relatively more conceptual level, the brain employs mechanisms like spatial and feature-based attention, memory and learning, predictive coding, and efficient coding to prioritize, process efficiently, and retain information.

2. Lower-level mechanisms

At this relatively more computational level, the brain uses mechanisms like normalization (Reynolds & Heeger, 2009), adaptation, summary statistics (Alvarez, 2011), and biased competition (Desimone & Duncan, 1995) to implement the mechanisms from the higher, more conceptual level.

IMPLICATIONS OF THE OBJECTIVES-CONSTRAINTS-MECHANISMS APPROACH FOR OPTIMALITY

The Objectives-Constraints-Mechanisms approach clarifies that optimality is only meaningfully defined *conditional* on objectives and constraints. On the other hand, most research in the field, including the studies reviewed above, tacitly assume a single objective (performing the task at hand) and do not generally incorporate constraints, with the exception of some kind of noise. Thus, while the brain is optimizing performance in a multidimensional space of objectives and constraints, most research attempts to evaluate the performance based on a thin slice of this space. Any specific finding of optimality or suboptimality therefore provides little to no information about the optimality of the system *as a whole*.

Consider the visual system's strategy of creating relative rather than absolute representations of luminance. Such representations can be achieved through normalization (Reynolds & Heeger, 2009), efficient coding (Barlow, 1961; Simoncelli, 2003; Summerfield & Tsetsos, 2015), etc. This is a reasonable strategy: the absolute luminance is almost never needed, so the brain discards it, presumably to conserve resources. However, throwing away absolute luminance leads to poor performance whenever this information is actually needed, as in the checkerboard illusion.

Indeed, illusions are often framed as a suboptimality that arises because of a more general optimality in the perceptual system. Some have criticized such explanations as “just so stories”, able to claim, post-hoc, that any suboptimality is in fact optimal (Bowers & Davis, 2012a). In our view, there is a powerful duality between suboptimality and optimality in a Bayesian framework: any prior is, in effect, a bias, which under some circumstances must be suboptimal.

These considerations should lead us away from making any statements that could imply that the perceptual system as a whole is optimal (“the brain is optimal”, “people are optimal”, “perception is optimal”, etc.) or suboptimal. Instead, we should emphasize the objectives, constraints, and mechanisms implied by experimental findings of optimality or suboptimality in specific tasks.

RECOMMENDATIONS FOR FUTURE STUDIES

Optimal models as starting points

It is reasonable to assume that people want to perform as well as possible on any task. Thus, an optimal model that incorporates relevant constraints will often be a good starting point in modeling behavior. Conversely, assuming a strong heuristic will often fail to describe human behavior across a variety of tasks. For example, Ma, Shen, Dziugaite, & van den Berg (2015) recently demonstrated that optimal models are as good or better than the max rule (a rule in which the observer only considers the maximum of N inputs) across a range of different tasks. Nevertheless, the countless examples of suboptimality in human perception should serve as a warning that pure optimal models, especially ones that do not take into consideration the objectives, constraints, and mechanisms of the visual system, will often be most useful as starting points rather than as the ultimate description of human behavior.

According to some Bayesian theorists, models that assume optimal behavior are intrinsically preferable to models that do not (e.g., Drugowitsch & Pouget, 2012). The argument is usually that because people can approximate optimal behavior on some tasks, they must possess the machinery for fully optimal decisions. However, close-to-optimal behavior can also be produced by non-optimal models (Bowers & Davis, 2012a). On the other hand, the ubiquity of suboptimal perceptual decisions argues against such a strong Bayesian view. It is generally agreed that evolutionary pressures likely produced heuristic but useful, rather than normative, behavior (Gigerenzer & Brighton, 2009; Juslin et al., 2009; Simon, 1956). Thus, when comparing specific implementational models, optimal ones should not be given more or less weight *a priori*.

How (not) to demonstrate optimality

Many phenomena in visual perception have been explained as optimal inference. Often these explanations necessitate postulating additional parameters for attentional lapses (Whiteley & Sahani, 2008), observers’ prior beliefs (Stocker & Simoncelli, 2006a), etc. While these extra parameters are usually well justified and are needed to incorporate relevant constraints, the fact that they are treated as free parameters, rather than being estimated separately, can easily lead to overfitting such that an optimal model appears to fit the data better than it should (Bowers & Davis, 2012a). The ability of an optimal model containing free parameters to fit the data should not be taken as a *demonstration* that human behavior is indeed optimal; independent tests of the new model should be performed.

Box 2
Recommendations for discussing optimality in experimental research

1. Describe assumptions about what information the observer is using to perform the task (e.g., stimulus properties, training, experimenter's instructions, feedback, explicit vs. implicit rewards, response time pressure, etc.).
2. Specify the objectives, constraints, and/or mechanisms (OCM) being tested.
3. State predictions for optimal performance conditioned on the task assumptions and hypothesized OCM.
4. Interpret data with respect to the OCM hypotheses, not optimality per se.
5. Discuss any task assumptions that may be incorrect and how different assumptions might affect the interpretation of the results.

CONCLUSION

As this review demonstrates, suboptimal behavior is the rule rather than the exception in perception. Suboptimal behavior appears in practically every task in which optimality can be mathematically defined.

In our view, this widespread suboptimality, together with the difficulties in even defining what optimal behavior is outside of constrained laboratory tasks, should steer the field away from arguing that observers are optimal. To be clear, we are not against testing the optimality of performance in well-defined tasks -- such studies are critical in uncovering the principles that govern the perceptual system. Rather, we advocate a shift of emphasis in the framing and discussion of such studies. Psychology has a long history of using ideal observer models to investigate such questions, which we believe has been somewhat obscured in recent years by an increased emphasis on demonstrating optimality. In the framework of our Objectives-Constraints-Mechanisms (OCM) approach, findings should be interpreted as advancing our understanding of one or more of these three components, rather than the presence of optimality per se.

References

Abrams, J., Barbot, A., & Carrasco, M. (2010). Voluntary attention increases perceived spatial frequency. *Attention, Perception, & Psychophysics*, *72*(6), 1510–1521. doi:10.3758/APP.72.6.1510

Acerbi, L., Vijayakumar, S., & Wolpert, D. M. (2014). On the origins of suboptimality in human probabilistic inference. *PLoS Computational Biology*, *10*(6), e1003661. doi:10.1371/journal.pcbi.1003661

Acerbi, L., Wolpert, D. M., & Vijayakumar, S. (2012). Internal representations of temporal statistics and feedback calibrate motor-sensory interval timing. *PLoS Computational Biology*, *8*(11), e1002771. doi:10.1371/journal.pcbi.1002771

Ackermann, J. F., & Landy, M. S. (2014). Suboptimal decision criteria are predicted by subjectively weighted probabilities and rewards. *Attention, Perception & Psychophysics*. doi:10.3758/s13414-014-0779-z

Adams, J. K. (1957). A confidence scale defined in terms of expected percentages. *The American Journal of Psychology*, *70*(3), 432–6.

Adelson, E. H. (1993). Perceptual organization and the judgment of brightness. *Science*, *262*(5142), 2042–2044.

Ais, J., Zylberberg, A., Barttfeld, P., & Sigman, M. (2015). Individual consistency in the accuracy and distribution of confidence judgments. *Cognition*, *146*, 377–386. doi:10.1016/j.cognition.2015.10.006

Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology*, *14*(3), 257–62. doi:10.1016/j.cub.2004.01.029

Alvarez, G. A. (2011). Representing multiple objects as an ensemble enhances visual cognition. *Trends in Cognitive Sciences*, *15*(3), 122–31. doi:10.1016/j.tics.2011.01.003

Anderson, B. L., O'Vari, J., & Barth, H. (2011). Non-Bayesian Contour Synthesis. *Current Biology*, *21*(6), 492–496. doi:10.1016/j.cub.2011.02.011

Anton-Erxleben, K., Henrich, C., & Treue, S. (2007). Attention changes perceived size of moving visual patterns. *Journal of Vision*, *7*(11), 5.1–9. doi:10.1167/7.11.5

Anton-Erxleben, K., Herrmann, K., & Carrasco, M. (2013). Independent effects of adaptation and attention on perceived speed. *Psychological Science*, *24*(2), 150–159. doi:10.1177/0956797612449178

Ashourian, P., & Loewenstein, Y. (2011). Bayesian inference underlies the contraction bias in delayed comparison tasks. *PLoS ONE*, *6*(5), e19551. doi:10.1371/journal.pone.0019551

Balcetis, E. (2015). Approach and avoidance as organizing structures for motivated distance perception. *Emotion Review*.

Balci, F., Simen, P., Niyogi, R., Saxe, A., Hughes, J. A., Holmes, P., & Cohen, J. D. (2011). Acquisition of decision making criteria: reward rate ultimately beats accuracy. *Attention, Perception & Psychophysics*, *73*(2), 640–57. doi:10.3758/s13414-010-0049-7

Baranski, J. V, & Petrusic, W. M. (1994). The calibration and resolution of confidence in perceptual judgments. *Perception & Psychophysics*, *55*(4), 412–28.

Baranski, J. V, & Petrusic, W. M. (1995). On the calibration of knowledge and perception. *Canadian Journal of Experimental Psychology*, *49*(3), 397–407.

Baranski, J. V, & Petrusic, W. M. (1999). Realism of confidence in sensory discrimination. *Perception & Psychophysics*, *61*(7), 1369–83.

Barlow, H. B. (1961). Possible principles underlying the transformation of sensory messages. In W. A. Rosenblith (Ed.), *Sensory Communication*. MIT Press.

Barlow, H. B. (1990). A theory about the functional role and synaptic mechanism of visual after-effects. *Vision: Coding and Efficiency*.

Battaglia, P. W., Jacobs, R. A., & Aslin, R. N. (2003). Bayesian integration of visual and auditory signals for spatial localization. *Journal of the Optical Society of America A, Optics and Image Science*, *20*(7), 1391–1397.

Battaglia, P. W., Kersten, D., & Schrater, P. R. (2011). How haptic size sensations improve distance perception. *PLoS Computational Biology*, *7*(6), e1002080. doi:10.1371/journal.pcbi.1002080

Beck, J. M., Ma, W. J., Pitkow, X., Latham, P. E., & Pouget, A. (2012). Not noisy, just wrong: the role of suboptimal inference in behavioral variability. *Neuron*, *74*(1), 30–9. doi:10.1016/j.neuron.2012.03.016

Berliner, J. E., & Durlach, N. I. (1973). Intensity perception. IV. Resolution in roving-level discrimination. *The Journal of the Acoustical Society of America*, *53*(5), 1270–87.

Björkman, M., Juslin, P., & Winman, A. (1993). Realism of confidence in sensory discrimination: the underconfidence phenomenon. *Perception & Psychophysics*, *54*(1), 75–81.

Bogacz, R., Hu, P. T., Holmes, P. J., & Cohen, J. D. (2010). Do humans produce the speed-accuracy trade-off that maximizes reward rate? *Quarterly Journal of Experimental Psychology (2006)*, *63*(5), 863–91. doi:10.1080/17470210903091643

Bohil, C. J., & Maddox, W. T. (2001). Category discriminability, base-rate, and payoff effects in perceptual categorization. *Perception & Psychophysics*, *63*(2), 361–76.

Bohil, C. J., & Maddox, W. T. (2003a). A test of the optimal classifier's independence assumption in perceptual categorization. *Perception & Psychophysics*, *65*(3), 478–93.

Bohil, C. J., & Maddox, W. T. (2003b). On the generality of optimal versus objective classifier feedback effects on decision criterion learning in perceptual categorization. *Memory & Cognition*, *31*(2), 181–98.

Bowers, J. S., & Davis, C. J. (2012a). Bayesian just-so stories in psychology and neuroscience. *Psychological Bulletin*, *138*(3), 389–414. doi:10.1037/a0026450

Bowers, J. S., & Davis, C. J. (2012b). Is that what Bayesians believe? Reply to Griffiths, Chater, Norris, and Pouget (2012). *Psychological Bulletin*, *138*(3), 423–426. doi:10.1037/a0027750

Brainard, D. H., Longère, P., Delahunt, P. B., Freeman, W. T., Kraft, J. M., & Xiao, B. (2006). Bayesian model of human color constancy. *Journal of Vision*, *6*(11), 1267–1281. doi:10.1167/6.11.10

Brayanov, J. B., & Smith, M. A. (2010). Bayesian and "Anti-Bayesian" Biases in Sensory Integration for Action and Perception in the Size-Weight Illusion. *Journal of Neurophysiology*, *103*(3), 1518–1531. doi:10.1152/jn.00814.2009

Brenner, N., Bialek, W., & de Ruyter van Steveninck, R. (2000). Adaptive rescaling maximizes information transmission. *Neuron*, *26*(3), 695–702.

Brooke, J. B., & MacRae, A. W. (1977). Error patterns in the judgment and production of numerical proportions. *Perception & Psychophysics*, *21*(4), 336–340. doi:10.3758/BF03199483

Bülthoff, H. H., & Mallot, H. A. (1988). Integration of depth modules: stereo and shading. *Journal of the Optical Society of America A, Optics and Image Science*, *5*(10), 1749–1758.

Burr, D., Banks, M. S., & Morrone, M. C. (2009). Auditory dominance over vision in the perception of interval duration. *Experimental Brain Research*, *198*(1), 49–57. doi:10.1007/s00221-009-1933-z

Busemeyer, J. R., & Myung, I. J. (1992). An adaptive approach to human decision making: Learning theory, decision theory, and human performance. *Journal of Experimental Psychology: General*, *121*(2), 177–194. doi:10.1037/0096-3445.121.2.177

Carandini, M., & Heeger, D. J. (2012). Normalization as a canonical neural computation. *Nature Reviews. Neuroscience*, *13*(1), 51–62. doi:10.1038/nrn3136

Carrasco, M. (2011). Visual attention: the past 25 years. *Vision Research*, *51*(13), 1484–525. doi:10.1016/j.visres.2011.04.012

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, *7*(3), 308–13. doi:10.1038/nn1194

Charles, L., Van Opstal, F., Marti, S., & Dehaene, S. (2013). Distinct brain mechanisms for conscious versus subliminal error detection. *NeuroImage*, *73*, 80–94.

doi:10.1016/j.neuroimage.2013.01.054
Cheadle, S., Wyart, V., Tsetsos, K., Myers, N., de Gardelle, V., Herce Castañón, S., & Summerfield, C. (2014). Adaptive Gain Control during Human Perceptual Choice. *Neuron*, *81*(6), 1429–1441. doi:10.1016/j.neuron.2014.01.020
Chen, C.-C., & Tyler, C. W. (2015). Shading Beats Binocular Disparity in Depth from Luminance Gradients: Evidence against a Maximum Likelihood Principle for Cue Combination. *PloS One*, *10*(8), e0132658. doi:10.1371/journal.pone.0132658
Chiang, T.-C., Lu, R.-B., Hsieh, S., Chang, Y.-H., & Yang, Y.-K. (2014). Stimulation in the Dorsolateral Prefrontal Cortex Changes Subjective Evaluation of Percepts. *PloS One*, *9*(9), e106943. doi:10.1371/journal.pone.0106943
Clark, J. J., & Yullie, A. L. (1990). *Data Fusion for Sensory Information Processing*. Boston: Kluwer Academic Publishers.
Creelman, C. D., & Macmillan, N. A. (1979). Auditory phase and frequency discrimination: a comparison of nine procedures. *Journal of Experimental Psychology. Human Perception and Performance*, *5*(1), 146–56.
Dawes, R. M. (1980). Confidence in intellectual vs. confidence in perceptual judgments. In E. D. Lantermann & H. Feger (Eds.), *Similarity and choice: Papers in honor of Clyde Coombs* (pp. 327–345). Bern: Han Huber.
de Gardelle, V., & Mamassian, P. (2015). Weighting Mean and Variability during Confidence Judgments. *PloS One*, *10*(3), e0120870. doi:10.1371/journal.pone.0120870
de Gardelle, V., & Summerfield, C. (2011). Robust averaging during perceptual judgment. *Proceedings of the National Academy of Sciences*, *108*(32), 13341–13346. doi:10.1073/pnas.1104517108
de Lange, F. P., Rahnev, D., Donner, T. H., & Lau, H. (2013). Prestimulus Oscillatory Activity over Motor Cortex Reflects Perceptual Expectations. *The Journal of Neuroscience*, *33*(4), 1400–10. doi:10.1523/JNEUROSCI.1094-12.2013
Del Cul, a, Dehaene, S., Reyes, P., Bravo, E., & Slachevsky, A. (2009). Causal role of prefrontal cortex in the threshold for access to consciousness. *Brain*, *132*(Pt 9), 2531–40. doi:10.1093/brain/awp111
Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222. doi:10.1146/annurev.ne.18.030195.001205
Drugowitsch, J., DeAngelis, G. C., Klier, E. M., Angelaki, D. E., & Pouget, A. (2014). Optimal multisensory decision-making in a reaction-time task. *eLife*, *3*, e03005. doi:10.7554/eLife.03005
Drugowitsch, J., Moreno-Bote, R., & Pouget, A. (2014). Relation between Belief and Performance in Perceptual Decision Making. *PloS One*, *9*(5), e96511. doi:10.1371/journal.pone.0096511
Drugowitsch, J., & Pouget, A. (2012). Probabilistic vs. non-probabilistic approaches to the neurobiology of perceptual decision-making. *Current Opinion in Neurobiology*, *22*(6), 963–9. doi:10.1016/j.conb.2012.07.007
Dusoir, A. E. (1975). Treatments of bias in detection and recognition models: A review. *Perception & Psychophysics*, *17*(2), 167–178. doi:10.3758/BF03203882
Dusoir, T. (1983). Isobias curves in some detection tasks. *Perception & Psychophysics*, *33*(5), 403–412. doi:10.3758/BF03202890
Eberhardt, F., & Danks, D. (2011). Confirmation in the Cognitive Sciences: The Problematic Case of Bayesian Models. *Minds and Machines*, *21*(3), 389–410. doi:10.1007/s11023-011-9241-3
Eckstein, M. P. (2011). Visual search: A retrospective. *Journal of Vision*, *11*(5), 14–14. doi:10.1167/11.5.14
Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–33. doi:10.1038/415429a

Evans, K. K., Birdwell, R. L., & Wolfe, J. M. (2013). If you don't find it often, you often don't find it: why some cancers are missed in breast cancer screening. *PloS One*, *8*(5), e64366. doi:10.1371/journal.pone.0064366

Evans, K. K., Tambouret, R. H., Evered, A., Wilbur, D. C., & Wolfe, J. M. (2011). Prevalence of abnormalities influences cytologists' error rates in screening for cervical cancer. *Archives of Pathology & Laboratory Medicine*, *135*(12), 1557–60. doi:10.5858/arpa.2010-0739-OA

Fechner, G. T. (1860). *Elemente der Psychophysik*. Leipzig: Breitkopf und Härtel.

Feng, S., Holmes, P., Rorie, A., & Newsome, W. T. (2009). Can monkeys choose optimally when faced with noisy stimuli and unequal rewards? *PLoS Computational Biology*, *5*(2), e1000284. doi:10.1371/journal.pcbi.1000284

Fetsch, C. R., Pouget, A., Deangelis, G. C., & Angelaki, D. E. (2012). Neural correlates of reliability-based cue weighting during multisensory integration. *Nature Neuroscience*, *15*(1), 146–154. doi:10.1038/nn.2983

Firestone, C., & Scholl, B. J. (2015). Cognition does not affect perception: Evaluating the evidence for "top-down" effects. *The Behavioral and Brain Sciences*, 1–77. doi:10.1017/S0140525X15000965

Fischer, J., & Whitney, D. (2014). Serial dependence in visual perception. *Nature Neuroscience*, *17*(5), 738–43. doi:10.1038/nn.3689

Fitts, P. M. (1966). Cognitive aspects of information processing: III. Set for speed versus accuracy. *Journal of Experimental Psychology*, *71*(6), 849–857.

Fleming, S. M., & Lau, H. (2014). How to measure metacognition. *Frontiers in Human Neuroscience*, *8*. doi:10.3389/fnhum.2014.00443

Fleming, S. M., Maloney, L. T., & Daw, N. D. (2013). The Irrationality of Categorical Perception. *Journal of Neuroscience*, *33*(49), 19060–19070. doi:10.1523/JNEUROSCI.1263-13.2013

Fleming, S. M., Maniscalco, B., Ko, Y., Amendi, N., Ro, T., & Lau, H. (2015). Action-Specific Disruption of Perceptual Confidence. *Psychological Science*, *26*(1), 89–98. doi:10.1177/0956797614557697

Fleming, S. M., Ryu, J., Golfinos, J. G., & Blackmon, K. E. (2014). Domain-specific impairment in metacognitive accuracy following anterior prefrontal lesions. *Brain*. doi:10.1093/brain/awu221

Franconeri, S. L., Alvarez, G. A., & Cavanagh, P. (2013). Flexible cognitive resources: competitive content maps for attention and memory. *Trends in Cognitive Sciences*, *17*(3), 134–41. doi:10.1016/j.tics.2013.01.010

Fründ, I., Wichmann, F. A., & Macke, J. H. (2014). Quantifying the effect of intertrial dependence on perceptual decisions. *Journal of Vision*, *14*(7). doi:10.1167/14.7.9

Fuller, S., Park, Y., & Carrasco, M. (2009). Cue contrast modulates the effects of exogenous attention on appearance. *Vision Research*, *49*(14), 1825–1837. doi:10.1016/j.visres.2009.04.019

Garcia-Perez, M. A., & Alcala-Quintana, R. (2010). The difference model with guessing explains interval bias in two-alternative forced-choice detection procedures. *Journal of Sensory Studies*, *25*(6), 876–898. doi:10.1111/j.1745-459X.2010.00310.x

Geisler, W. S., & Najemnik, J. (2013). Optimal and non-optimal fixation selection in visual search. *Perception ECVP Abstract*, *42*, 226. doi:10.1068/v130805

Gekas, N., Chalk, M., Seitz, A. R., & Series, P. (2013). Complexity and specificity of experimentally-induced expectations in motion perception. *Journal of Vision*, *13*(4), 8–8. doi:10.1167/13.4.8

Gepshtein, S., Burge, J., Ernst, M. O., & Banks, M. S. (2005). The combination of vision and touch depends on spatial proximity. *Journal of Vision*, *5*(11), 1013–1023. doi:10.1167/5.11.7

Gershman, S. J., Horvitz, E. J., & Tenenbaum, J. B. (2015). Computational rationality: A converging paradigm for intelligence in brains, minds, and machines. *Science*, *349*(6245),

273–278. doi:10.1126/science.aac6076
Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, *20*(5), 453–467. doi:10.1037/h0059826
Gigerenzer, G., & Brighton, H. (2009). Homo Heuristicus: Why Biased Minds Make Better Inferences. *Topics in Cognitive Science*, *1*(1), 107–143. doi:10.1111/j.1756-8765.2008.01006.x
Gigerenzer, G., Hoffrage, U., & Kleinbölting, H. (1991). Probabilistic mental models: a Brunswikian theory of confidence. *Psychological Review*, *98*(4), 506–28.
Girshick, A. R., Landy, M. S., & Simoncelli, E. P. (2011). Cardinal rules: visual orientation perception reflects knowledge of environmental statistics. *Nature Neuroscience*, *14*(7), 926–32. doi:10.1038/nn.2831
Glennerster, A., Tcheang, L., Gilson, S. J., Fitzgibbon, A. W., & Parker, A. J. (2006). Humans ignore motion and stereo cues in favor of a fictional stable world. *Current Biology*, *16*(4), 428–432. doi:10.1016/j.cub.2006.01.019
Gobell, J., & Carrasco, M. (2005). Attention alters the appearance of spatial frequency and gap size. *Psychological Science*, *16*(8), 644–651. doi:10.1111/j.1467-9280.2005.01588.x
Gold, J. M., Murray, R. F., Bennett, P. J., & Sekuler, A. B. (2000). Deriving behavioural receptive fields for visually completed contours. *Current Biology*, *10*(11), 663–666. doi:10.1016/S0960-9822(00)00523-6
Gorea, A., Caetta, F., & Sagi, D. (2005). Criteria interactions across visual attributes. *Vision Research*, *45*(19), 2523–32. doi:10.1016/j.visres.2005.03.018
Gorea, A., & Sagi, D. (2000). Failure to handle more than one internal representation in visual detection tasks. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(22), 12380–4. doi:10.1073/pnas.97.22.12380
Gorea, A., & Sagi, D. (2001). Disentangling signal from noise in visual contrast discrimination. *Nature Neuroscience*, *4*(11), 1146–50. doi:10.1038/nn741
Gorea, A., & Sagi, D. (2002). Natural extinction: A criterion shift phenomenon. *Visual Cognition*, *9*(8), 913–936. doi:10.1080/13506280143000638
Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: John Wiley & Sons Ltd.
Griffin, D., & Tversky, A. (1992). The weighing of evidence and the determinants of confidence. *Cognitive Psychology*, *24*(3), 411–435. doi:10.1016/0010-0285(92)90013-R
Griffiths, T. L., Chater, N., Norris, D., & Pouget, A. (2012). How the Bayesians got their beliefs (and what those beliefs actually are): comment on Bowers and Davis (2012). *Psychological Bulletin*, *138*(3), 415–422. doi:10.1037/a0026884
Griffiths, T. L., Lieder, F., & Goodman, N. D. (2015). Rational Use of Cognitive Resources: Levels of Analysis Between the Computational and the Algorithmic. *Topics in Cognitive Science*, *7*(2), 217–229. doi:10.1111/tops.12142
Grzywacz, N. M., & Balboa, R. M. (2002). A Bayesian framework for sensory adaptation. *Neural Computation*, *14*(3), 543–559. doi:10.1162/089976602317250898
Gu, Y., Angelaki, D. E., & DeAngelis, G. C. (2008). Neural correlates of multisensory cue integration in macaque MSTd. *Nature Neuroscience*, *11*(10), 1201–1210. doi:10.1038/nn.2191
Harvey, N. (1997). Confidence in judgment. *Trends in Cognitive Sciences*, *1*(2), 78–82. doi:10.1016/S1364-6613(97)01014-0
Healy, A. F., & Kubovy, M. (1981). Probability matching and the formation of conservative decision rules in a numerical analog of signal detection. *Journal of Experimental Psychology: Human Learning and Memory*, *7*(5), 344–354.
Heitz, R. P. (2014). The speed-accuracy tradeoff: history, physiology, methodology, and behavior. *Frontiers in Neuroscience*, *8*, 150. doi:10.3389/fnins.2014.00150

Helmholtz, H. L. F. (1856). *Treatise on physiological optics*. Bristol: Thoemmes Continuum.
Henriques, J. B., Glowacki, J. M., & Davidson, R. J. (1994). Reward fails to alter response bias in depression. *Journal of Abnormal Psychology*, *103*(3), 460–6.
Ho, T., Brown, S., van Maanen, L., Forstmann, B. U., Wagenmakers, E.-J., & Serences, J. T. (2012). The optimality of sensory processing during the speed-accuracy tradeoff. *The Journal of Neuroscience*, *32*(23), 7992–8003. doi:10.1523/JNEUROSCI.0340-12.2012
Hohwy, J., Roepstorff, A., & Friston, K. (2008). Predictive coding explains binocular rivalry: an epistemological review. *Cognition*, *108*(3), 687–701. doi:10.1016/j.cognition.2008.05.010
Ingham, J. G. (1970). Individual differences in signal detection. *Acta Psychologica*, *34*, 39–50. doi:10.1016/0001-6918(70)90003-X
Jack, C. E., & Thurlow, W. R. (1973). Effects of degree of visual association and angle of displacement on the "ventriloquism" effect. *Perceptual and Motor Skills*, *37*(3), 967–979. doi:10.2466/pms.1973.37.3.967
Jacobs, R. A. (1999). Optimal integration of texture and motion cues to depth. *Vision Research*, *39*(21), 3621–3629.
Jastrow, J. (1892). Studies from the University of Wisconsin: On the Judgment of Angles and Positions of Lines. *The American Journal of Psychology*, *5*(2), 214. doi:10.2307/1410867
Jazayeri, M., & Movshon, J. A. (2007). A new perceptual illusion reveals mechanisms of sensory decoding. *Nature*, *446*(7138), 912–915. doi:10.1038/nature05739
Jesteadt, W. (1974). Intensity and frequency discrimination in one- and two-interval paradigms. *The Journal of the Acoustical Society of America*, *55*(6), 1266. doi:10.1121/1.1914696
Jolij, J., & Lamme, V. A. F. (2005). Repression of unconscious information by conscious processing: evidence from affective blindsight induced by transcranial magnetic stimulation. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(30), 10747–51. doi:10.1073/pnas.0500834102
Jones, M., & Love, B. C. (2011). Bayesian Fundamentalism or Enlightenment? On the explanatory status and theoretical contributions of Bayesian models of cognition. *Behavioral and Brain Sciences*, *34*(04), 169–188. doi:10.1017/S0140525X10003134
Juslin, P., Nilsson, H., & Winman, A. (2009). Probability theory, not the very guide of life. *Psychological Review*, *116*(4), 856–874. doi:10.1037/a0016979
Kaneko, Y., & Sakai, K. (2015). Dissociation in decision bias mechanism between probabilistic information and previous decision. *Frontiers in Human Neuroscience*, *9*. doi:10.3389/fnhum.2015.00261
Keren, G. (1988). On the ability of monitoring non-veridical perceptions and uncertain knowledge: Some calibration studies. *Acta Psychologica*, *67*(2), 95–119. doi:10.1016/0001-6918(88)90007-8
Kiani, R., Corthell, L., & Shadlen, M. N. (2014). Choice Certainty Is Informed by Both Evidence and Decision Time. *Neuron*, *84*(6), 1329–1342. doi:10.1016/j.neuron.2014.12.015
Kinchla, R. A., & Smyzer, F. (1967). A diffusion model of perceptual memory. *Perception & Psychophysics*, *2*(6), 219–229. doi:10.3758/BF03212471
King, J.-R., & Dehaene, S. (2014). A model of subjective report and objective discrimination as categorical decisions in a vast representational space. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *369*(1641), 20130204. doi:10.1098/rstb.2013.0204
Knill, D. C., & Pouget, A. (2004). The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends in Neurosciences*, *27*(12), 712–9. doi:10.1016/j.tins.2004.10.007
Knill, D. C., & Saunders, J. A. (2003). Do humans optimally integrate stereo and texture information for judgments of surface slant? *Vision Research*, *43*(24), 2539–2558.
Koizumi, A., Maniscalco, B., & Lau, H. (2015). Does perceptual confidence facilitate cognitive control? *Attention, Perception & Psychophysics*. doi:10.3758/s13414-015-0843-3
Körding, K. P., Beierholm, U., Ma, W. J., Quartz, S., Tenenbaum, J. B., & Shams, L. (2007).

Causal Inference in Multisensory Perception. *PLoS ONE*, *2*(9), e943. doi:10.1371/journal.pone.0000943
Körding, K. P., & Wolpert, D. M. (2004). Bayesian integration in sensorimotor learning. *Nature*, *427*(6971), 244–7. doi:10.1038/nature02169
Körding, K. P., & Wolpert, D. M. (2006). Bayesian decision theory in sensorimotor control. *Trends in Cognitive Sciences*, *10*(7), 319–26. doi:10.1016/j.tics.2006.05.003
Koriat, A. (2011). Subjective confidence in perceptual judgments: a test of the self-consistency model. *Journal of Experimental Psychology: General*, *140*(1), 117–139. doi:10.1037/a0022171
Kubovy, M. (1977). A possible basis for conservatism in signal detection and probabilistic categorization tasks. *Perception & Psychophysics*, *22*(3), 277–281. doi:10.3758/BF03199690
Landy, M. S., Banks, M. S., & Knill, D. C. (2011). Ideal-Observer Models of Cue Integration. In J. Trommershäuser, K. P. Körding, & M. S. Landy (Eds.), *Sensory Cue Integration* (pp. 5–29). New York: Oxford University Press.
Landy, M. S., Goutcher, R., Trommershäuser, J., & Mamassian, P. (2007). Visual estimation under risk. *Journal of Vision*, *7*(6), 4. doi:10.1167/7.6.4
Landy, M. S., & Kojima, H. (2001). Ideal cue combination for localizing texture-defined edges. *Journal of the Optical Society of America A, Optics and Image Science*, *18*(9), 2307–2320.
Landy, M. S., Maloney, L., Johnston, E. B., & Young, M. (1995). Measurement and modeling of depth cue combination: in defense of weak fusion. *Vision Research*, *35*(3), 389–412.
Langer, M. S., & Bülthoff, H. H. (2001). A prior for global convexity in local shape-from-shading. *Perception*, *30*(4), 403–410.
Lau, H., & Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(49), 18763–8. doi:10.1073/pnas.0607716103
Lau, H., & Rosenthal, D. (2011). Empirical support for higher-order theories of conscious awareness. *Trends in Cognitive Sciences*, *15*(8), 365–73. doi:10.1016/j.tics.2011.05.009
Lennie, P. (2003). *The Cost of Cortical Computation*. *Current Biology* (Vol. 13). doi:10.1016/S0960-9822(03)00135-0
Leshowitz, B. (1969). Comparison of ROC Curves from One- and Two-Interval Rating-Scale Procedures. *The Journal of the Acoustical Society of America*, *46*(2B), 399. doi:10.1121/1.1911703
Liberman, A., Fischer, J., & Whitney, D. (2014). Serial Dependence in the Perception of Faces. *Current Biology*, *24*(21), 2569–74. doi:10.1016/j.cub.2014.09.025
Ling, S., & Carrasco, M. (2006). When sustained attention impairs perception. *Nature Neuroscience*, *9*(10), 1243–1245. doi:10.1038/nn1761
Liu, T., Abrams, J., & Carrasco, M. (2009). Voluntary attention enhances contrast appearance. *Psychological Science*, *20*(3), 354–362. doi:10.1111/j.1467-9280.2009.02300.x
Lupyan, G. (2012). Linguistically modulated perception and cognition: the label-feedback hypothesis. *Frontiers in Psychology*, *3*, 54. doi:10.3389/fpsyg.2012.00054
Lupyan, G. (2016). The paradox of the universal triangle: concepts, language, and prototypes. *Quarterly Journal of Experimental Psychology (2006)*, 1–69. doi:10.1080/17470218.2015.1130730
Ma, W. J. (2010). Signal detection theory, uncertainty, and Poisson-like population codes. *Vision Research*, *50*(22), 2308–2319. doi:10.1016/j.visres.2010.08.035
Ma, W. J., Shen, S., Dziugaite, G., & van den Berg, R. (2015). Requiem for the max rule? *Vision Research*. doi:10.1016/j.visres.2014.12.019
Macmillan, N. A., & Creelman, C. D. (1990). Response bias: Characteristics of detection theory, threshold theory, and “nonparametric” indexes. *Psychological Bulletin*, *107*(3), 401–413. doi:10.1037/0033-2909.107.3.401

Macmillan, N. A., & Creelman, C. D. (2005). *Detection Theory: A User's Guide* (2nd ed.). Mahwah, NJ: Erlbaum.

Maddox, W. T. (1995). Base-rate effects in multidimensional perceptual categorization. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *21*(2), 288–301.

Maddox, W. T. (2002). Toward a unified theory of decision criterion learning in perceptual categorization. *Journal of the Experimental Analysis of Behavior*, *78*(3), 567–595. doi:10.1901/jeab.2002.78-567

Maddox, W. T., & Bohil, C. J. (1998a). Base-rate and payoff effects in multidimensional perceptual categorization. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *24*(6), 1459–82.

Maddox, W. T., & Bohil, C. J. (1998b). Overestimation of base-rate differences in complex perceptual categories. *Perception & Psychophysics*, *60*(4), 575–92.

Maddox, W. T., & Bohil, C. J. (2000). Costs and benefits in perceptual categorization. *Memory & Cognition*, *28*(4), 597–615.

Maddox, W. T., & Bohil, C. J. (2001). Feedback effects on cost-benefit learning in perceptual categorization. *Memory & Cognition*, *29*(4), 598–615.

Maddox, W. T., & Bohil, C. J. (2003). A theoretical framework for understanding the effects of simultaneous base-rate and payoff manipulations on decision criterion learning in perceptual categorization. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *29*(2), 307–20.

Maddox, W. T., & Bohil, C. J. (2004). Probability matching, accuracy maximization, and a test of the optimal classifier's independence assumption in perceptual categorization. *Perception & Psychophysics*, *66*(1), 104–18.

Maddox, W. T., & Bohil, C. J. (2005). Optimal classifier feedback improves cost-benefit but not base-rate decision criterion learning in perceptual categorization. *Memory & Cognition*, *33*(2), 303–19.

Maddox, W. T., Bohil, C. J., & Dodd, J. L. (2003). Linear transformations of the payoff matrix and decision criterion learning in perceptual categorization. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *29*(6), 1174–93. doi:10.1037/0278-7393.29.6.1174

Maddox, W. T., & Dodd, J. L. (2001). On the relation between base-rate and cost-benefit learning in simulated medical diagnosis. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *27*(6), 1367–84.

Maiworm, M., & Röder, B. (2011). Suboptimal Auditory Dominance in Audiovisual Integration of Temporal Cues. *Tsinghua Science & Technology*.

Maloney, L. T., & Landy, M. S. (1989). A Statistical Framework for Robust Fusion of Depth Information. In W. A. Pearlman (Ed.), *Proceedings of SPIE* (pp. 1154–1163). doi:10.1117/12.970125

Maloney, L. T., & Thomas, E. A. . (1991). Distributional assumptions and observed conservatism in the theory of signal detectability. *Journal of Mathematical Psychology*, *35*(4), 443–470. doi:10.1016/0022-2496(91)90043-S

Maloney, L. T., & Zhang, H. (2010). Decision-theoretic models of visual perception and action. *Vision Research*, *50*(23), 2362–74. doi:10.1016/j.visres.2010.09.031

Maniscalco, B., & Lau, H. (2010). Comparing signal detection models of perceptual decision confidence. *Journal of Vision*, *10*(7), 213–213. doi:10.1167/10.7.213

Maniscalco, B., & Lau, H. (2012). A signal detection theoretic approach for estimating metacognitive sensitivity from confidence ratings. *Consciousness and Cognition*, *21*(1), 422–30. doi:10.1016/j.concog.2011.09.021

Maniscalco, B., & Lau, H. (2015). Manipulation of working memory contents selectively impairs metacognitive sensitivity in a concurrent visual discrimination task. *Neuroscience of Consciousness*, *2015*(1), niv002. doi:10.1093/nc/niv002

Maniscalco, B., & Lau, H. (2016). The signal processing architecture underlying subjective reports of sensory awareness. *Neuroscience of Consciousness*, (November 2015), 1–17. doi:10.1093/nc/niw002

Maniscalco, B., Peters, M. A. K., & Lau, H. (2016). Heuristic use of perceptual evidence leads to dissociation between performance and metacognitive sensitivity. *Attention, Perception & Psychophysics*. doi:10.3758/s13414-016-1059-x

Marcus, G. F., & Davis, E. (2013). How robust are probabilistic models of higher-level cognition? *Psychological Science*, *24*(12), 2351–60. doi:10.1177/0956797613495418

Marcus, G. F., & Davis, E. (2015). Still Searching for Principles: A Response to Goodman et al. (2015). *Psychological Science*, *26*(4), 542–544. doi:10.1177/0956797614568433

Markman, A. B., Baldwin, G. C., & Maddox, W. T. (2005). The interaction of payoff structure and regulatory focus in classification. *Psychological Science*, *16*(11), 852–5. doi:10.1111/j.1467-9280.2005.01625.x

Markowitz, J., & Swets, J. A. (1967). Factors affecting the slope of empirical ROC curves: Comparison of binary and rating responses. *Perception & Psychophysics*, *2*(3), 91–100. doi:10.3758/BF03210301

Massoni, S. (2014). Emotion as a boost to metacognition: How worry enhances the quality of confidence. *Consciousness and Cognition*, *29*, 189–198. doi:10.1016/j.concog.2014.08.006

Matthews, G., Davies, D. R., & Holley, P. J. (1993). Cognitive predictors of vigilance. *Human Factors*, *35*(1), 3–24.

McCurdy, L. Y., Maniscalco, B., Metcalfe, J., Liu, K. Y., de Lange, F. P., & Lau, H. (2013). Anatomical Coupling between Distinct Metacognitive Systems for Memory and Visual Perception. *The Journal of Neuroscience*, *33*(5), 1897–906. doi:10.1523/JNEUROSCI.1890-12.2013

Metcalfe, J., & Shimamura, A. P. (1994). *Metacognition: Knowing about Knowing*. Cambridge, MA: MIT Press.

Michael, E., de Gardelle, V., & Summerfield, C. (2014). Priming by the variability of visual information. *Proceedings of the National Academy of Sciences*, *111*(21), 7873–7878. doi:10.1073/pnas.1308674111

Morales, J., Solovey, G., Maniscalco, B., Rahnev, D., de Lange, F. P., & Lau, H. (2015). Low attention impairs optimal incorporation of prior knowledge in perceptual decisions. *Attention, Perception & Psychophysics*, *77*(6), 2021–36. doi:10.3758/s13414-015-0897-2

Mueller, S. T., & Weidemann, C. T. (2008). Decision noise: An explanation for observed violations of signal detection theory. *Psychonomic Bulletin & Review*, *15*(3), 465–494. doi:10.3758/PBR.15.3.465

Navajas, J., Sigman, M., & Kamienkowski, J. E. (2014). Dynamics of visibility, confidence, and choice during eye movements. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(3), 1213–1227. doi:10.1037/a0036321

Nelson, T. O., & Narens, L. (1990). Metamemory: A theoretical framework and some new findings. In G. Bower (Ed.), *The Psychology of Learning and Motivation* (pp. 125–141). New York: Academic Press.

Odegaard, B., Wozny, D. R., & Shams, L. (2015). Biases in Visual, Auditory, and Audiovisual Perception of Space. *PLoS Computational Biology*, *11*(12), e1004649. doi:10.1371/journal.pcbi.1004649

Oruç, I., Maloney, L. T., & Landy, M. S. (2003). Weighted linear cue combination with possibly correlated error. *Vision Research*, *43*(23), 2451–2468.

Osgood, C. E. (1953). *Method and theory in experimental psychology*. Oxford University Press.

Pleskac, T. J., & Busemeyer, J. R. (2010). Two-stage dynamic signal detection: a theory of choice, decision time, and confidence. *Psychological Review*, *117*(3), 864–901. doi:10.1037/a0019737

Prsa, M., Gale, S., & Blanke, O. (2012). Self-motion leads to mandatory cue fusion across sensory modalities. *Journal of Neurophysiology*, *108*(8), 2282–2291. doi:10.1152/jn.00439.2012

Pynn, C. T. (1972). Intensity Perception. III. Resolution in Small-Range Identification. *The Journal of the Acoustical Society of America*, *51*(2B), 559. doi:10.1121/1.1912878

Rae, B., Heathcote, A., Donkin, C., Averell, L., & Brown, S. (2014). The hare and the tortoise: emphasizing speed can change the evidence used to make decisions. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *40*(5), 1226–43. doi:10.1037/a0036801

Rahnev, D., Bahdo, L., de Lange, F. P., & Lau, H. (2012). Prestimulus hemodynamic activity in dorsal attention network is negatively associated with decision confidence in visual perception. *Journal of Neurophysiology*, *108*(5), 1529–36. doi:10.1152/jn.00184.2012

Rahnev, D., Koizumi, A., McCurdy, L. Y., D'Esposito, M., & Lau, H. (2015). Confidence Leak in Perceptual Decision Making. *Psychological Science*, *26*(11), 1664–1680. doi:10.1177/0956797615595037

Rahnev, D., Lau, H., & De Lange, F. P. (2011). Prior expectation modulates the interaction between sensory and prefrontal regions in the human brain. *Journal of Neuroscience*, *31*(29), 10741–10748.

Rahnev, D., Maniscalco, B., Graves, T., Huang, E., De Lange, F. P., & Lau, H. (2011). Attention induces conservative subjective biases in visual perception. *Nature Neuroscience*, *14*(12), 1513–1515. doi:10.1038/nn.2948

Rahnev, D., Maniscalco, B., Luber, B., Lau, H., & Lisanby, S. H. (2012). Direct injection of noise to the visual cortex decreases accuracy but increases decision confidence. *Journal of Neurophysiology*, *107*(6), 1556–63. doi:10.1152/jn.00985.2011

Rahnev, D., Nee, D. E., Riddle, J., Larson, A. S., & D'Esposito, M. (2016). Causal evidence for frontal cortex organization for perceptual decision making. *Proceedings of the National Academy of Sciences*. doi:10.1073/pnas.1522551113

Ramachandran, V. (1990). Interactions between motion, depth, color and form: The utilitarian theory of perception. In C. Blakemore (Ed.), *Vision: Coding and efficiency* (pp. 346–360). Cambridge, England: Cambridge University Press.

Ratcliff, R., & Starns, J. J. (2009). Modeling confidence and response time in recognition memory. *Psychological Review*, *116*(1), 59–83. doi:10.1037/a0014086

Rauber, H. J., & Treue, S. (1998). Reference repulsion when judging the direction of visual motion. *Perception*, *27*(4), 393–402.

Raviv, O., Ahissar, M., & Loewenstein, Y. (2012). How recent history affects perception: the normative approach and its heuristic approximation. *PLoS Computational Biology*, *8*(10), e1002731. doi:10.1371/journal.pcbi.1002731

Reckless, G. E., Bolstad, I., Nakstad, P. H., Andreassen, O. a, & Jensen, J. (2013). Motivation alters response bias and neural activation patterns in a perceptual decision-making task. *Neuroscience*, *238*, 135–147. doi:10.1016/j.neuroscience.2013.02.015

Reckless, G. E., Ousdal, O. T., Server, A., Walter, H., Andreassen, O. A., & Jensen, J. (2014). The left inferior frontal gyrus is involved in adjusting response bias during a perceptual decision-making task. *Brain and Behavior*, *4*(3), 398–407. doi:10.1002/brb3.223

Reynolds, J. H., & Heeger, D. J. (2009). The normalization model of attention. *Neuron*, *61*(2), 168–85. doi:10.1016/j.neuron.2009.01.002

Roach, N. W., Heron, J., & McGraw, P. V. (2006). Resolving multisensory conflict: a strategy for balancing the costs and benefits of audio-visual integration. *Proceedings Biological Sciences / The Royal Society*, *273*(1598), 2159–2168. doi:10.1098/rspb.2006.3578

Rosas, P., Wagemans, J., Ernst, M. O., & Wichmann, F. A. (2005). Texture and haptic cues in slant discrimination: reliability-based cue weighting without statistically optimal cue combination. *Journal of the Optical Society of America A, Optics and Image Science*, *22*(5),

801–809.
Rosas, P., & Wichmann, F. A. (2011). Cue Combination: Beyond Optimality. In J. Trommershäuser, K. P. Körding, & M. S. Landy (Eds.), *Sensory Cue Integration* (pp. 144–152). New York: Oxford University Press.
Rosas, P., Wichmann, F. A., & Wagemans, J. (2007). Texture and object motion in slant discrimination: failure of reliability-based weighting of cues may be evidence for strong fusion. *Journal of Vision*, *7*(6), 3. doi:10.1167/7.6.3
Saarela, T. P., & Landy, M. S. (2015). Integration trumps selection in object recognition. *Current Biology*, *25*(7), 920–7. doi:10.1016/j.cub.2015.01.068
Sabra, A. I. (1989). The Optics of Ibn Al-Haytham. Books I-III. On Direct Vision. London: The Warburg Institute.
Schulman, A. I., & Mitchell, R. R. (1966). Operating characteristics from yes-no and forced-choice procedures. *The Journal of the Acoustical Society of America*, *40*(2), 473–7.
Schurger, A., Kim, M.-S., & Cohen, J. D. (2015). Paradoxical Interaction between Ocular Activity, Perception, and Decision Confidence at the Threshold of Vision. *PloS One*, *10*(5), e0125278. doi:10.1371/journal.pone.0125278
Schwiedrzik, C. M., Ruff, C. C., Lazar, A., Leitner, F. C., Singer, W., & Melloni, L. (2014). Untangling perceptual memory: hysteresis and adaptation map into separate cortical networks. *Cerebral Cortex*, *24*(5), 1152–1164. doi:10.1093/cercor/bhs396
See, J. E., Warm, J. S., Dember, W. N., & Howe, S. R. (1997). Vigilance and Signal Detection Theory: An Empirical Evaluation of Five Measures of Response Bias. *Human Factors*, *39*(1), 14–29. doi:10.1518/001872097778940704
Seriès, P., & Seitz, A. R. (2013). Learning what to expect (in visual perception). *Frontiers in Human Neuroscience*, *7*, 668. doi:10.3389/fnhum.2013.00668
Sherman, M. T., Seth, A. K., Barrett, A. B., & Kanai, R. (2015). Prior expectations facilitate metacognition for perceptual decision. *Consciousness and Cognition*, *35*, 53–65. doi:10.1016/j.concog.2015.04.015
Simen, P., Contreras, D., Buck, C., Hu, P., Holmes, P., & Cohen, J. D. (2009). Reward rate optimization in two-alternative decision making: empirical tests of theoretical predictions. *Journal of Experimental Psychology. Human Perception and Performance*, *35*(6), 1865–97. doi:10.1037/a0016926
Simon, H. A. (1956). Rational choice and the structure of the environment. *Psychological Review*, *63*(2), 129–138.
Simoncelli, E. P. (2003). Vision and the statistics of the visual environment. *Current Opinion in Neurobiology*, *13*(2), 144–149. doi:10.1016/S0959-4388(03)00047-3
Snyder, J. S., Schwiedrzik, C. M., Vitela, A. D., & Melloni, L. (2015). How previous experience shapes perception in different sensory modalities. *Frontiers in Human Neuroscience*, *9*, 594. doi:10.3389/fnhum.2015.00594
Solovey, G., Graney, G. G., & Lau, H. (2015). A decisional account of subjective inflation of visual perception at the periphery. *Attention, Perception & Psychophysics*, *77*(1), 258–71. doi:10.3758/s13414-014-0769-1
Song, A., Koizumi, A., & Lau, H. (2015). A Behavioral Method to Manipulate Metacognitive Awareness Independent of Stimulus Awareness. In M. Overgaard (Ed.), *Behavioral Methods in Consciousness Research*. Oxford: Oxford University Press. doi:http://dx.doi.org/10.1093/acprof:oso/9780199688890.003.0005
Song, C., Kanai, R., Fleming, S. M., Weil, R. S., Schwarzkopf, D. S., & Rees, G. (2011). Relating inter-individual differences in metacognitive performance on different perceptual tasks. *Consciousness and Cognition*, *20*(4), 1787–92. doi:10.1016/j.concog.2010.12.011
Spence, M. L., Dux, P. E., & Arnold, D. H. (2015). Computations Underlying Confidence in Visual Perception. *Journal of Experimental Psychology. Human Perception and Performance*. doi:10.1037/xhp0000179

Starns, J. J., & Ratcliff, R. (2010). The effects of aging on the speed-accuracy compromise: Boundary optimality in the diffusion model. *Psychology and Aging*, *25*(2), 377–390. doi:10.1037/a0018022

Starns, J. J., & Ratcliff, R. (2012). Age-related differences in diffusion model boundary optimality with both trial-limited and time-limited tasks. *Psychonomic Bulletin & Review*, *19*(1), 139–45. doi:10.3758/s13423-011-0189-3

Stocker, A. A., & Simoncelli, E. P. (2006a). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience*, *9*(4), 578–85. doi:10.1038/nn1669

Stocker, A. A., & Simoncelli, E. P. (2006b). Sensory Adaptation within a Bayesian Framework for Perception. *Advances in Neural Information Processing Systems 18*, *18*, 1291–1298.

Stocker, A. A., & Simoncelli, E. P. (2008). A Bayesian Model of Conditioned Perception. In J. C. Platt, D. Koller, Y. Singer, & S. Roweis (Eds.), *Advances in Neural Information Processing Systems* (Vol. 20, pp. 1409–1416). Cambridge, MA: MIT Press.

Stone, L. S., & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research*, *32*(8), 1535–49.

Störmer, V. S., Mcdonald, J. J., & Hillyard, S. A. (2009). Cross-modal cueing of attention alters appearance and early cortical processing of visual stimuli. *Proceedings of the National Academy of Sciences*, *106*(52), 22456–22461. doi:10.1073/pnas.0907573106

Summerfield, C., & Koechlin, E. (2010). Economic value biases uncertain perceptual choices in the parietal and prefrontal cortices. *Frontiers in Human Neuroscience*, *4*, 208. doi:10.3389/fnhum.2010.00208

Summerfield, C., & Tsetsos, K. (2015). Do humans make good decisions? *Trends in Cognitive Sciences*, *19*(1), 27–34. doi:10.1016/j.tics.2014.11.005

Sun, J., & Perona, P. (1997). Shading and stereo in early perception of shape and reflectance. *Perception*, *26*(4), 519–529.

Swets, J. A. (1986). Form of empirical ROCs in discrimination and diagnostic tasks: Implications for theory and measurement of performance. *Psychological Bulletin*, *99*(2), 181–198. doi:http://dx.doi.org/10.1037/0033-2909.99.2.181

Swets, J. A., & Green, D. M. (1961). Sequential observations by human observers of signals in noise. In C. Cherry (Ed.), *Information theory: Proceedings of the fourth London symposium* (pp. 177–195). London: Butterworth.

Swets, J. A., Tanner, W. P., & Birdsall, T. G. (1961). Decision processes in perception. *Psychological Review*, *68*(5), 301–340.

Tanner, T. A., Haller, R. W., & Atkinson, R. C. (1967). Signal recognition as influenced by presentation schedules. *Perception & Psychophysics*, *2*(8), 349–358. doi:10.3758/BF03210070

Tanner, W. P. (1956). Theory of recognition. *Journal of the Acoustical Society of America*, *28*, 882–888.

Tanner, W. P. (1961). Physiological implications of psychophysical data. *Annals of the New York Academy of Sciences*, *89*, 752–65.

Taylor, S. F., Welsh, R. C., Wager, T. D., Phan, K. L., Fitzgerald, K. D., & Gehring, W. J. (2004). A functional neuroimaging study of motivation and executive function. *NeuroImage*, *21*(3), 1045–54. doi:10.1016/j.neuroimage.2003.10.032

Tenenbaum, J. B., Kemp, C., Griffiths, T. L., & Goodman, N. D. (2011). How to grow a mind: statistics, structure, and abstraction. *Science*, *331*(6022), 1279–85. doi:10.1126/science.1192788

Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research*, *22*(3), 377–80.

Thompson, P., Brooks, K., & Hammett, S. T. (2006). Speed can go up as well as down at low contrast: implications for models of motion perception. *Vision Research*, *46*(6-7), 782–786. doi:10.1016/j.visres.2005.08.005

Treisman, M., & Faulkner, A. (1984). The setting and maintenance of criteria representing levels of confidence. *Journal of Experimental Psychology: Human Perception and Performance*, *10*(1), 119–139.

Trommershäuser, J., Körding, K. P., & Landy, M. S. (Eds.). (2011). *Sensory Cue Integration*. New York: Oxford University Press.

Tse, P. U. (2005). Voluntary attention modulates the brightness of overlapping transparent surfaces. *Vision Research*, *45*(9), 1095–1098. doi:10.1016/j.visres.2004.11.001

Tsetsos, K., Pfeffer, T., Jentgens, P., & Donner, T. H. (2015). Action Planning and the Timescale of Evidence Accumulation. *PloS One*, *10*(6), e0129473. doi:10.1371/journal.pone.0129473

Turatto, M., Vescovi, M., & Valsecchi, M. (2007). Attention makes moving objects be perceived to move faster. *Vision Research*, *47*(2), 166–178. doi:10.1016/j.visres.2006.10.002

Turnbull, W. H. (1961). *The Correspondence of Isaac Newton, Vol. 3, 1688–1694*. Cambridge: Cambridge University Press.

Ulehla, Z. J. (1966). Optimality of perceptual decision criteria. *Journal of Experimental Psychology*, *71*(4), 564–9.

van Beers, R. J., Sittig, A. C., & Denier van der Gon, J. J. (1996). How humans combine simultaneous proprioceptive and visual position information. *Experimental Brain Research*, *111*(2), 253–61.

Van Wert, M. J., Horowitz, T. S., & Wolfe, J. M. (2009). Even in correctable search, some types of rare targets are frequently missed. *Attention, Perception & Psychophysics*, *71*(3), 541–53. doi:10.3758/APP.71.3.541

Varey, C. A., Mellers, B. A., & Birnbaum, M. H. (1990). Judgments of proportions. *Journal of Experimental Psychology. Human Perception and Performance*, *16*(3), 613–25.

Vickers, D. (1979). *Decision Processes in Visual Perception*. New York: Academic Press.

Vickers, D., & Packer, J. (1982). Effects of alternating set for speed or accuracy on response time, accuracy and confidence in a unidimensional discrimination task. *Acta Psychologica*, *50*(2), 179–97. doi:<a data-auto="ep_link" href="http://dx.doi.org/10.1016/0001-6918(82)90006-3" target="_blank" id="linkhttp:dx.doi.org10.10160001-69188290006-3" title="http://dx.doi.org/10.1016/0001-6918(82)90006-3" data-title="http://dx.doi.org/10.1016/0001-6918(82)90006-3">http://dx.doi.org/10.1016/0001-6918(82)90006-3

Viemeister, N. F. (1970). Intensity discrilnination: Performance in three paradigms. *Perception & Psychophysics*, *8*(6), 417–419. doi:10.3758/BF03207037

Vintch, B., & Gardner, J. L. (2014). Cortical correlates of human motion perception biases. *Journal of Neuroscience*, *34*(7), 2592–2604. doi:10.1523/JNEUROSCI.2809-13.2014

Vlassova, A., Donkin, C., & Pearson, J. (2014). Unconscious information changes decision accuracy but not confidence. *Proceedings of the National Academy of Sciences*, *111*(45), 16214–16218. doi:10.1073/pnas.1403619111

von Winterfeldt, D., & Edwards, W. (1982). Costs and payoffs in perceptual research. *Psychological Bulletin*, *91*(3), 609–622.

Vul, E., Goodman, N., Griffiths, T. L., & Tenenbaum, J. B. (2014). One and done? Optimal decisions from very few samples. *Cognitive Science*, *38*(4), 599–637. doi:10.1111/cogs.12101

Wainwright, M. J. (1999). Visual adaptation as optimal information transmission. *Vision Research*, *39*(23), 3960–3974.

Ward, L. M., & Lockhead, G. R. (1970). Sequential effects and memory in category judgments. *Journal of Experimental Psychology*, *84*(1), 27–34.

Wark, B., Lundstrom, B. N., & Fairhall, A. (2007). Sensory adaptation. *Current Opinion in Neurobiology*, *17*(4), 423–429. doi:10.1016/j.conb.2007.07.001

Warren, D. H., & Cleaves, W. T. (1971). Visual-proprioceptive interaction under large amounts

of conflict. *Journal of Experimental Psychology*, *90*(2), 206–214.
Warren, P. A., Graf, E. W., Champion, R. A., & Maloney, L. T. (2012). Visual extrapolation under risk: human observers estimate and compensate for exogenous uncertainty. *Proceedings. Biological Sciences / The Royal Society*, *279*(1736), 2171–9. doi:10.1098/rspb.2011.2527
Watson, C. S., Kellogg, S. C., Kawanishi, D. T., & Lucas, P. A. (1973). The uncertain response in detection-oriented psychophysics. *Journal of Experimental Psychology*, *99*(2), 180–185.
Webster, M. A. (2015). Visual Adaptation. *Annual Review of Vision Science*, *1*, 547–567. doi:10.1146/annurev-vision-082114-035509
Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, *428*(6982), 557–561. doi:10.1038/nature02420
Webster, M. A., & MacLeod, D. I. A. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1571), 1702–1725. doi:10.1098/rstb.2010.0360
Wei, K., & Körding, K. P. (2011). Causal Inference in Sensorimotor Learning and Control. In J. Trommershäuser, K. Kording, & M. S. Landy (Eds.), *Sensory Cue Integration* (pp. 30–45). New York.
Wei, X.-X., & Stocker, A. A. (2012). Efficient coding provides a direct link between prior and likelihood in perceptual Bayesian inference. *Advances in Neural Information Processing Systems 25*, 1313–1321.
Wei, X.-X., & Stocker, A. A. (2015). A Bayesian observer model constrained by efficient coding can explain “anti-Bayesian” percepts. *Nature Neuroscience*, *18*(10), 1509–1517. doi:10.1038/nn.4105
Weil, L. G., Fleming, S. M., Dumontheil, I., Kilford, E. J., Weil, R. S., Rees, G., … Blakemore, S.-J. (2013). The development of metacognitive ability in adolescence. *Consciousness and Cognition*, *22*(1), 264–71. doi:10.1016/j.concog.2013.01.004
Weiskrantz, L. (1996). Blindsight revisited. *Current Opinion in Neurobiology*, *6*(2), 215–20.
Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience*, *5*(6), 598–604. doi:10.1038/nn858
Whiteley, L., & Sahani, M. (2008). Implicit knowledge of visual uncertainty guides decisions with asymmetric outcomes. *Journal of Vision*, *8*(3), 2.1–15. doi:10.1167/8.3.2
Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, *63*(8), 1293–313.
Wilimzig, C., Tsuchiya, N., Fahle, M., Einhäuser, W., & Koch, C. (2008). Spatial attention increases performance but not subjective confidence in a discrimination task. *Journal of Vision*, *8*(5), 1–10. doi:10.1167/8.5.7
Winman, A., & Juslin, P. (1993). Calibration of sensory and cognitive judgments: Two different accounts. *Scandinavian Journal of Psychology*, *34*(2), 135–148. doi:10.1111/j.1467-9450.1993.tb01109.x
Witt, J. K. (2011). Action's effect on perception. *Current Directions in Psychological Science*.
Witt, J. K., Proffitt, D. R., & Epstein, W. (2005). Tool use affects perceived distance, but only when you intend to use it. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(5), 880–888. doi:10.1037/0096-1523.31.5.880
Wohlgemuth, A. (1911). *On the After-effect of Seen Movement* (Vol. 1). Cambridge University Press.
Wolfe, J. M., Brunelli, D. N., Rubinstein, J., & Horowitz, T. S. (2013). Prevalence effects in newly trained airport checkpoint screeners: trained observers miss rare targets, too. *Journal of Vision*, *13*(3), 33. doi:10.1167/13.3.33
Wolfe, J. M., Horowitz, T. S., & Kenner, N. M. (2005). Cognitive psychology: rare items often missed in visual searches. *Nature*, *435*(7041), 439–40. doi:10.1038/435439a
Wolfe, J. M., Horowitz, T. S., Van Wert, M. J., Kenner, N. M., Place, S. S., & Kibbi, N. (2007).

Low target prevalence is a stubborn source of errors in visual search tasks. *Journal of Experimental Psychology. General*, *136*(4), 623–38. doi:10.1037/0096-3445.136.4.623

Wolfe, J. M., & Van Wert, M. J. (2010). Varying target prevalence reveals two dissociable decision criteria in visual search. *Current Biology*, *20*(2), 121–4. doi:10.1016/j.cub.2009.11.066

Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, *396*(6706), 72–75. doi:10.1038/23936

Yeshurun, Y., Carrasco, M., & Maloney, L. T. (2008). Bias and sensitivity in two-interval forced choice procedures: Tests of the difference model. *Vision Research*, *48*(17), 1837–1851. doi:10.1016/j.visres.2008.05.008

Yu, A. J., & Cohen, J. D. (2009). Sequential effects: Superstition or rational behavior? *Advances in Neural Information Processing Systems*, *21*, 1873–80.

Zacksenhouse, M., Bogacz, R., & Holmes, P. (2010). Robust versus optimal strategies for two-alternative forced choice tasks. *Journal of Mathematical Psychology*, *54*(2), 230–246. doi:10.1016/j.jmp.2009.12.004

Zak, I., Katkov, M., Gorea, A., & Sagi, D. (2012). Decision criteria in dual discrimination tasks estimated using external-noise methods. *Attention, Perception & Psychophysics*, *74*(5), 1042–55. doi:10.3758/s13414-012-0269-0

Zhang, H., & Maloney, L. T. (2012). Ubiquitous log odds: a common representation of probability and frequency distortion in perception, action, and cognition. *Frontiers in Neuroscience*, *6*, 1. doi:10.3389/fnins.2012.00001

Zhang, H., Morvan, C., & Maloney, L. T. (2010). Gambling in the visual periphery: a conjoint-measurement analysis of human ability to judge visual uncertainty. *PLoS Computational Biology*, *6*(12), e1001023. doi:10.1371/journal.pcbi.1001023

Zylberberg, A., Barttfeld, P., & Sigman, M. (2012). The construction of confidence in a perceptual decision. *Frontiers in Integrative Neuroscience*, *6*(September), 79. doi:10.3389/fnint.2012.00079

Zylberberg, A., Roelfsema, P. R., & Sigman, M. (2014). Variance misperception explains illusions of confidence in simple perceptual decisions. *Consciousness and Cognition*, *27*, 246–253. doi:10.1016/j.concog.2014.05.012