Calibrating vision: Concepts and questions

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ABSTRACT

The idea that visual coding and perception are shaped by experience and adjust to changes in the environment or the observer is universally recognized as a cornerstone of visual processing, yet the functions and processes mediating these calibrations remain in many ways poorly understood. In this article we review a number of facets and issues surrounding the general notion of calibration, with a focus on plasticity within the encoding and representational stages of visual processing. These include how many types of calibrations there are – and how we decide; how plasticity for encoding is intertwined with other principles of sensory coding; how it is instantiated at the level of the dynamic networks mediating vision; how it varies with development or between individuals; and the factors that may limit the form or degree of the adjustments. Our goal is to give a small glimpse of an enormous and fundamental dimension of vision, and to point to some of the unresolved questions in our understanding of how and why ongoing calibrations are a pervasive and essential element of vision.

1. Introduction

Sensory systems are continuously evolving, developing, adjusting, learning, and repurposing to mold perception to the world and to the tasks and observer at hand. This "plasticity" is recognized as a core principle in neural coding, and one that continues to be a central topic of study. For example, in the 7 initial volumes of the recently launched Annual Review of Vision Science, we identified 25 out of 158 articles (16 %) that were focused on different forms of plasticity. These included reviews of normal and abnormal development (Mathôt, 2020; Norcia & Gerhard, 2015), compensation for impairments (Fine & Park, 2018; Legge & Chung, 2016; Morland, 2015), adaptation and learning (Berry & Nedivi, 2016; Dosher & Lu, 2017; Li, 2016; Weber et al., 2019; Webster, 2015; Xu, 2018), and flexibility in processing and decision making (Gold & Stocker, 2017; Roelfsema & de Lange, 2016). They vary over many levels of analysis and explanation, from computational theory and behavior to physiological, anatomical, and molecular measurements. This diversity is also evident among the wide range of topics in the current special issue on calibrating vision. Clearly the notion of calibration pervades most, if not all, aspects of vision.

But what does it mean to calibrate vision and how is it related to the broader concept of plasticity? How are the relevant measurements and phenomena related, and what do they reveal about the function and structure of vision? How do calibrations change through the lifespan or vary at different levels or in different streams of processing? Are there individual differences in the degrees or forms of these calibrations? And what are the constraints they operate under? The answers to these questions are surprisingly poorly understood. As noted, aspects of visual plasticity and its surrounding theoretical frameworks have been recently reviewed in detail many times.[1] In this article our aim is to provide an overview of the concept of calibrating vision and selected examples of how and why it is manifest in the visual system. But a larger aim is to

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[1] In addition to the Annual Review of Vision Science papers, e.g. see Weber and Fairhall (2019), and Młynarski and Hermundstad (2021) on adaptation and efficient coding; Gilbert and Li (2012) on plasticity in adult visual cortex; Simoncelli and Olshuasen (2001), Geisler (2007), and Snow et al. (2017) on experience-dependent tuning to natural scene statistics; Maurer (2017) and Maurer and Werker (2014) on plasticity during visual development; Seriès and Seitz (2013) on Bayesian models of visual perception; Sasaki et al. (2010) on perceptual learning; Kohn (2007), Solomon and Kohn (2014), and Whitmire and Stanley (2016) on physiological mechanisms of adaptation.

identify what is not known. We lack a clear and principled framework for characterizing the purpose and consequences and mechanisms of calibrations in visual coding, and we hope this review will point to some of the issues and questions that will need to be addressed to develop this framework.

In terms of scope, the focus of this article is primarily on regulatory and developmental adjustments that impact visual coding. We refer to these as visual calibrations, in part to emphasize that this review covers only a small part of the wider spectrum of sensory plasticity, which encompasses many important dimensions we do not address. These dimensions include the enormous literature on topics such as perceptual learning and memory, or on evolutionary adaptations. Our review also focuses on calibrations at a conceptual level and in terms of their consequences, with limited reference to the underlying mechanisms. However, as we describe below, the distinctions between different types of plasticity or levels of analysis can be very blurry, and the notion of "calibrations" itself is admittedly vague. We therefore begin by considering the problem of understanding calibrations within the broader framework of plasticity, and then explore a selected subset of questions about the form and effect of visual calibrations. The review is organized around the following topics:

- Section 2 discusses the general problem of how to define and characterize plasticity and how to distinguish its different forms and functions.
- Section 3 considers how the notion of calibration is intertwined with different computational design principles in sensory systems.
- Section 4 emphasizes the importance of characterizing calibrations at the level of visual networks.
- Section 5 explores the calibrations associated with visual development.
- Section 6 asks whether there are individual differences in these processes.
- Section 7 examines potential limits to visual calibrations.

Each section ends with a brief summary and important open questions related to understanding visual calibrations.

2. Challenges to understanding the number and nature of visual calibrations

2.1. Defining plasticity

The term plasticity is often narrowly applied to longer-term and often structural changes in neural circuitry, in part to distinguish it from short-term changes in sensitivity (e.g. Wandell & Smirnakis, 2009). One of the best known examples is that similar inputs are required from the two eyes early in life in order to establish normal binocular connections in the cortex. As we review in detail below, depriving one eye or misaligning the inputs during this early sensitive period can result in stereoblindness or amblyopia (see section 3.1). In contrast, the adult visual system shows much less capacity to rewire. However, a variety of neural strategies help offset the binocular deficits, including suppressing signals from the weaker eye or relying more on monocular depth cues. Moreover, monocular deprivation can still induce effects in adulthood (albeit weaker), and developmental impairments can still be influenced in adulthood (e.g. with visual training or even resetting the system by a period of darkness; Hensch & Quinlan, 2018). Similarly, there are many examples of visual adjustments that counteract the visual losses that accompany aging or disease. For instance, percepts remain stable despite visual sensitivity loss (Werner et al., 1990); or individuals with central visual loss may begin to use a peripheral part of the retina for fixating (Baker et al., 2005). There are also many forms of plasticity associated with normal processing in the adult visual system. These include regulating sensitivity (adaptation) or developing expertise (perceptual learning). If processes like these are included, then at a

general level plasticity encompasses almost any change in sensory processing designed to improve perception or performance in response to changes in the environment, the observer, or the perceptual goal. However, this definition becomes so broad and vague that the concept risks losing its utility.

A further conceptual problem in associating plasticity with any functional change is that vision is an intrinsically dynamic system. Even in the optics, the lens adjusts to changes in viewing distance; and as the light level changes, so too does the pupil diameter. Is it more helpful to think about the behavioural and neural consequences of these mechanisms as plasticity, or the "hard-wired" dynamics of the eye's response? Similarly, should we think of the younger lens as showing greater plasticity because of the accommodative losses with age? Throughout the brain, sensory responses are modulated by other neural signals (Carandini & Heeger, 2012). This leads to effects such as 'normalization', and means that a neuron's output strongly depends on context, but is this context-dependence a form of plasticity or simply a feature of the network? The answer is unclear, and more so because the consequences of context in the space domain are very similar to effects that are more often described as plasticity in the time domain, and the two closely interact (Solomon & Kohn, 2014). An example is that the appearance of many visual features is affected in similar ways by "simultaneous" or "successive" contexts (Schwartz et al., 2007).[2] Finally, we continuously reallocate our attention depending on our goals or salient properties of the visual scene. Attention can increase neural gain while repeated exposure to a stimulus tends to suppress it, and in this way attention and adaptation may both involve modulating vision but in opposite ways (Rezec et al., 2004). Yet it is adaptation that is more typically considered as a form of plasticity.

2.2. Distinguishing types of plasticity

How many distinct types of visual plasticity are there, and how should we decide the boundaries between them? It may be that some processes vary seamlessly and continuously, and that the categories we create are like the labels we use to carve up the colors of the spectrum. It is also hard to contain an analysis to sensory coding (though that is again the main focus of the current review). For example, plasticity is also at the core of learning and memory, and the processes and concepts of perception and memory are clearly closely connected. Similarly, perception and action are intimately connected, and thus at least some aspects of visual calibrations cannot be isolated from motor plasticity and sensory-motor processing.

Despite these caveats, there seem to be broad differences among the types of adaptive changes that are observed or assumed in the visual system, that suggest different underlying phenomena. The differences in part depend on the perspective they are viewed from, and are also limited by our understanding of the basic principles of visual coding. For example, given that we still do not know how vision works, we likely also do not know where to look for corrections when it is not working, or what their purposes are.

2.2.1. Operational definitions

The most common way to define visual plasticity is to measure changes in visual perception or performance. For example, observers who repeatedly train on a perceptual task often become better at that

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[2] Yet there may nevertheless also be important differences between space and time effects. For example, temporal and spatial normalization could impact a neuron's variability in different ways (Festa et al., 2021), and while contrast normalization may amplify differences between neurons (e.g. winner-take-all, Busse et al., 2009), adaptation may tend to equate the responses (homeostasis, Benucci et al., 2013). Moreover, perceptually, there are at least some visual attributes (e.g. faces) that show strong adaptation without the corresponding spatial contrast influences (Webster & MacLeod, 2011).

task, an observation that gave rise to the construct of perceptual learning (Dosher & Lu, 2017). During development, exposure to specific stimuli also leads to enhanced discrimination for these stimuli, and has been termed perceptual narrowing (Section 3.2). In cases where vision is compromised during development or later in life, perceptual processing is reconfigured to make up for the deficits, including greater reliance on other senses. These effects fall under an umbrella of compensation and crossmodal plasticity (Bavelier & Neville, 2002). Individuals with visual impairments can improve with training regimens or as they learn to use aids or prostheses. These effects are actively studied under the theme of rehabilitation and recovery of function (Bavelier et al., 2010). Repeated exposure to a stimulus can also lead to losses in sensitivity and biases in perception, which in different contexts have been described as adaptation or response suppression or habituation (Section 3.1; Krekelberg et al., 2006). In still other cases prior exposure can enhance salience, as in priming (Kristjánsson & Campana, 2010), or increase the perceived similarity between the current and preceding stimuli (as in serial dependence; Fischer & Whitney, 2014). An enormous amount of work has been done to reveal the consequences and mechanisms for all of these changes. But the changes themselves reflect effects that are observed under different experimental or natural contexts, and describe how perceptual capacities and biases change within those contexts. They are thus more of a post-hoc collection of manifestations of plasticity than a priori theoretically-motivated accounts. As such, we do not know whether some as yet untested paradigm will yield a new operational type of visual plasticity.

2.2.2. Functional definitions

A second approach has been to ask what the different goals of vision are and then to associate different kinds of plasticity with different functional outcomes. Common examples are recovery of function or compensation when there is a visual loss or impairment. Other examples include optimizing coding (Section 3.2), for example to maximize sensitivity or to increase coding efficiency for the prevailing stimulus context. In a related way, the changes may involve flexible reallocation of resources for changing task demands. Still others are focused on percepts and link plasticity to invariance and constancy and perceptual norms (Section 3.3). Finally, as we discuss in Section 3.5, in a Bayesian context plasticity has also been invoked to understand how perceptual inferences might be re-tuned in the face of changing expectations or evidence.

2.2.3. Mechanistic definitions

Further forms of plasticity may be identified by distinguishing the specific brain mechanisms that support them. These forms include cortical reorganization – for example when cortical areas that normally process one sense are recruited for other modalities when the primary input is lost (e.g. in vision or hearing impairments; Finney et al., 2001). Or they may involve structural changes in the connections within and between areas. As an example, white matter tracts vary as reading abilities develop, and the changes involve a number of mechanisms including pruning and changes in myelination (Yeatman et al., 2012). Finer scale structural and functional changes have also been widely studied in the context of synaptic reweighting and plasticity (Berry & Nedivi, 2016; Hofer et al., 2009; Humeau & Choquet, 2019; Magee & Grienberger, 2020). Recordings from single neurons also point to both extrinsic and intrinsic adjustments that alter the gain and contrast responses of cells and also their tuning or stimulus selectivity (Kohn, 2007; Solomon & Kohn, 2014; Whitmire & Stanley, 2016). These adjustments have also been explored in terms of the biochemical mechanisms mediating the changes (Disney, 2021). Finally, given that evolution is plasticity, adaptations have of course also been widely studied in terms of genetic and epigenetic mechanisms.

2.2.4. Processing stream definitions

Yet another example of how plasticity is thought of is in terms of where along the visual pathway the changes occur (see also Section 4). The processes needed to calibrate the retina may be very different from requirements in the cortex, and plastic processes that have been given different labels may loosely map onto different stages of the stimulus–response process. Sensory adaptation is thought to begin at a relatively early encoding stage but extend throughout the visual hierarchy (Webster, 2015), while learned changes in decision criterion (Herzog et al., 2006; Wenger et al., 2008) presumably have their effects at the decision or response stages. There is evidence that different types of feedback can target plasticity at different stages. For example, Aberg and Herzog (2012) found that block feedback affects sensitivity but not decision criterion, while changes in bias are induced by trial-wise reverse feedback. The term 'perceptual learning' implies a change in perception, i.e. involving an increase in the precision of representation of the stimulus, but alternatively it may involve learning to use existing task-relevant sensory signals (Dosher & Lu, 1999; Mollon & Danilova, 1996). Single unit recordings during and after perceptual learning have found alterations in the activities of sensory neurons (Yan et al., 2014), but also alterations in the activities of neurons in cortical regions involved in decision making (Law & Gold, 2008). In humans, results from neuroimaging during perceptual learning favor changes in early visual cortex (Bao et al., 2010; Jehee et al., 2012) and even LGN (Yu et al., 2016) (which could be enabled either via feedforward or via feedback connections), as well as later cortical areas involved in sensory decisions (Kahnt et al., 2011). Similarly there may be different types of plasticity associated with encoding versus decoding, or with perceptual versus post-perceptual stages. Correct or not, ideas about different kinds of plasticity are intimately linked with ideas about what the purposes of different processing stages are, and what would be required to calibrate them.

2.2.5. Timescale definitions

Another potential criterion for distinguishing types of plasticity is the timescales over which they operate (e.g. Dosher & Lu, 2020). Evolutionary adaptations involve very different mechanisms and adjustments from the calibrations during one's life, yet might serve similar roles (Geisler & Diehl, 2002). In vision a central focus of evolutionary design has been on how visual coding is matched to characteristic properties of natural visual environments. The statistics of natural images – coupled with principles of optimal coding schemes (Section 3) – have led to a number of remarkable successes in predicting the form of visual representations (Geisler, 2007; Simoncelli & Olshausen, 2001). These successes may reflect tuning for relatively stable and ubiquitous features (e. g. the roughly 1/f structure of images; Field, 1987), but can also be seen as indicating processes that adjust to image properties varying over generational timescales. As discussed in Section 5, specific forms of plasticity are engaged during development to fine tune visual representations. These reflect both basic requisite maturation processes and processes dependent on and shaped by visual experience, and may produce major structural as well as functional changes in the visual system. Finally, forms of plasticity such as adaptation appear to operate over shorter timescales and provide more online-like calibrations for the current context.

These broad distinctions disguise widely varying timescales within each domain. For example, different visual functions develop and depend on visual experience in very different ways, with some functions maturing well into adulthood (e.g. Germine et al., 2011) and some showing more or less dependence on normal visual input (e.g. Fine et al., 2003; Maurer, 2017). A number of studies have also identified a variety of distinct timescales for visual adaptation (e.g. Bao & Engel, 2012; Delahunt et al., 2004; Neitz et al., 2002; Patterson et al., 2013), with some approaching the relative permanence of learning (Vul et al., 2008). An intriguing hypothesis is that some calibrations are optimized to track and adjust for different rates of change in the environment (Kording et al., 2007; Shadmehr et al., 2010). Finally, an important temporal distinction is not only how long a change takes but how long it lasts. The

consequences of adaptation are continuous recalibration to stimulus context, and in this sense reflect calibrations that operate in "real time." This is very different from the adjustments involved in processes like learning, which instead require more permanent neural traces, that may lie dormant but available to draw on when the relevant context or task arises.

2.2.6. Context for change definitions

A final example of a potential basis for defining forms of plasticity is the type of context the system is adjusting for. Recalibrations occur in response to changes in the stimulus environment, the observer, or the perceptual task. It is possible that a distinct set of recalibrations is triggered by each of these contexts. Thus we might expect different mechanisms to adjust to a change in visual diet vs a visual injury, or even when the same observer samples the same environment but for different information. These mechanisms might also be distinguished by differences not only in sensitivity but metacognition (e.g. confidence about our percepts; Mamassian, 2016). For example, an observer may not be aware of their own state of adaptation, so that they attribute changes in sensory responses to changes in the stimulus (Schwartz et al., 2007; Seriès et al., 2009), while conversely cognizant of response changes resulting from an injury or disease, or from change in the information they are trying to acquire. Observer contexts also vary depending on whether the state is static or changes during one's life. For instance, common deficits in vision - such as color deficiency or prosopagnosia – can be congenital or acquired, and the onset of the deficit might engage very different forms of plasticity.

As with other classifications, here again the distinctions are murky. How the scene is sampled will determine the pattern of stimulation, which can in turn impact the states of adaptation, and changes in adaptation states can change confidence judgments (Gallagher et al., 2019). Similarly, in the case of a visual loss observers might compensate with a different sampling strategy, but because the goal remains the same. How the visual system adjusts to a change in the external or internal environment may be hard to disentangle. An interesting case is congenital color deficiencies, which is a focus of a number of articles in the accompanying special issue. These result from simple and stable alterations at the beginning of vision (in the cone photopigments). A number of studies have pointed to compensatory adjustments in color coding so that color-deficient observers encode and experience color more like normal trichromats than their photopigment sensitivities alone would predict (Bosten, 2019; Isherwood et al., 2020). However the mechanisms for these adjustments are not well understood, and it is an area of active current interest to reveal if these compensations reflect direct neural gain, more complex sensory adjustments, or post-perceptual adjustments involving how color is named or categorized (Boehm et al., 2021; Emery et al., 2021; Knoblauch et al., 2020; Lindsey et al., 2021; Tregillus et al., 2021; Vanston et al., 2021; Werner et al., 2020). It is likely that all of these changes are involved, again pointing to the multiple manifestations of plasticity. Yet with regard to the context for the change, it is not evident whether different calibrations would have occurred if the impoverished cone signals arose from the environment rather than the observer, or how the system could tell.

Summary and open questions: The concepts of calibration and plasticity refer to a diverse range of phenomena tied to the notion that sensory processing can and must be shaped by experience. However there is not yet a well-established system or approach for classifying the number or nature of distinct adjustments that the visual system can implement. Deciphering the types and functions of plasticity – along with the contexts that induce it and the constraints it operates under – thus remains a major challenge. Specifically, what is lacking is a comprehensive taxonomy for visual or sensory plasticity. In developing this, it is unclear which of the many different potential criteria will prove most insightful, or how the patterns or types of plasticity that emerge will depend on the different criteria. Moreover, little is known about how different nominal types of plasticity (e.g., perceptual learning and

adaptation; Censor et al., 2016; H. Harris et al., 2012; Y. Li et al., 2020; McGovern et al., 2012; Yehezkel et al., 2010) interact, and what these interactions mean for the underlying mechanisms and functions of the calibrations. Addressing these challenges will likely lead to new key insights into the roles that different calibrations and adjustments play in the operation of the visual system.

3. Calibration and design principles in sensory processing

One way to conceptually organize the mechanisms and consequences of visual calibrations is to ask how they map onto general design principles that have been identified in sensory systems. These principles can include both the rules governing how elements in the system respond and the logical stages of information processing. For example, sensory neurons at many stages and across modalities appear to carry out similar operations including selective filtering of the stimulus, characteristic nonlinearities, and modulation of individual neural responses by local activity. These generic processes have thus been deemed canonical computations that may be used throughout the system (Carandini & Heeger, 2012). Plasticity and "fine-tuning" of the neural response similarly represents a universal design principle, but depends on many different mechanisms impacting different levels and aspects of the system. To illustrate this we consider examples of how plasticity has been conceptualized within different foundational frameworks of visual coding (for a related approach see Weber et al., 2019). While these examples again focus on the role of plasticity in encoding and representation, a similar approach could be applied to understand plasticity in terms of how visual information is decoded and acted on, for example in learning and decision making (Dosher & Lu, 1999; Heekeren et al., 2008; Mulder et al., 2014; O'Connell & Kelly, 2021).

3.1. Sensitivity regulation

One of the most basic forms of calibration involves adjusting neural responses to match the current range of stimulus inputs, much as a camera must adjust its exposure for the current light intensity, and these adjustments begin at the earliest stages of vision. Natural variations in light intensity are enormous (a 10^9 range), but visual responses can vary only a few orders of magnitude. Without scaling sensitivity for the ambient level the system would be saturated or be unresponsive most of the time. A number of mechanisms contribute to these adjustments, including separate receptor systems (rods and cones) over different ranges. Yet the primary mechanisms involve intrinsic gain changes which allow the receptor responses to remain roughly centered on the mean stimulus level. To be effective, this light adaptation must be matched to the statistics of the visual environment (Mante et al., 2005; Rieke & Rudd, 2009). For example, light levels can vary widely even within a scene (e.g. in regions in direct light or shadow) and in turn will vary with each fixation. Thus sensitivity regulation must be localized in both space and time, and at photopic levels includes rapid gain changes within the individual cones. However, other adjustments reflect greater integration. For example, retinal adaptation also involves an additional class of receptors (intrinsically photosensitive retinal ganglion cells) that more coarsely sample the stimulus in both space and time to monitor the overall light level (Lucas et al., 2020). Similarly, the time-constants for receptor adaptation must be more sluggish than fixational changes or the world would fade to gray. Slower adaptation is also useful to allow calibration for the average rather than momentary stimulus. For example color constancy requires discounting the scene illumination. This is not possible for a single surface but could be facilitated by adapting to the average color signal sampled across multiple surfaces (D'Zmura & Lennie, 1986). The receptors themselves may even include multiple timescales of sensitivity regulation (Webster & Leonard, 2008). Color perception remains very similar between the fovea and near periphery despite a large difference in spectral sensitivity (e.g. because of macular pigment screening). Short-term color adaptation at these two

locations varies relative to the same physical stimulus rather than the same cone excitations, suggesting that the short-term adjustments ride atop a baseline calibration with a much longer memory (Webster & Leonard, 2008).

Adaptation is of course not limited to the retina but instead arises at all stages of visual coding and is arguably an intrinsic property of almost all neural responses. As a result, the signs of adaptation are ubiquitous, but vary depending on the information the channels encode (Webster, 2015). Thus while receptors adapt to the mean light level, later neurons encode and adapt to variations or patterns in the light. Some of these adjustments occur as early as the retina, where postreceptoral cells in some species adapt not only to contrast (variance in the light) but also to higher-order properties such as orientation and motion direction (Gollisch & Meister, 2010). In turn, adaptation at cortical sites reflects response changes to many visual attributes ranging from low-level features (e.g. local orientation or motion) to high-level entities (e.g. objects or faces). The properties of these adjustments also reflect the characteristics of coding at different cortical stages. For example, adaptation to faces show greater transfer across size, orientation, or retinal location, consistent with the idea that at least part of the response change occurs at stages which represent faces or objects in non-retinotopic coordinates (Webster & MacLeod, 2011).

What binds these diverse response changes in terms of a single concept (adaptation) is that they all reflect very similar patterns of short-term plasticity. In particular, exposure to a stimulus leads to perceptual aftereffects that are selective for properties of the stimulus, consistent with a selective change in responsiveness to the adapting stimulus. These response changes are manifest both as changes in sensitivity (e.g. higher detection thresholds and lower perceived contrast for the stimuli similar to the adaptor) and as changes in appearance (e.g. the adapting stimulus may appear more neutral or nearby stimuli may appear less like the adaptor). Classic examples of these appearance biases are that colors fade toward gray with exposure, and that adaptation to a tilted line biases the perceived orientation of other lines. The fact that very similar patterns of change occur for most visual attributes suggests that the visual system uses common coding schemes for representing different visual attributes, and that sensitivity regulation through adaptation is a fundamental process in these schemes (Webster, 2015).

However, these similarities may mask fundamental differences in the form or function of adaptation at different encoding stages. Compared to the changes in light intensity, temporal or spatial variations in most visual attributes may be modest. As a result, the priority for adaptation may shift from preventing saturated responses at the earliest stages to fine tuning and balancing responses across encoding mechanisms at later stages. There may also be important related differences in the degree of adaptation. While increasingly strong and sophisticated forms of adaptation continue to be revealed in the retina, in the mammalian visual system cortical responses appear more readily adaptable. For example, as noted below, cells in the parvocellular geniculate pathway exhibit little adaptation to color or luminance contrast, while such response changes are dramatic in V1 (Tailby, Solomon, Dhruv, et al., 2008). Moreover, the degree of adaptation may also vary systematically across cortical processing stages, which could reflect changes in the mechanisms or functions of plasticity (Haak & Beckmann, 2019; Mattar et al., 2016). Finally, the nature of the response changes can themselves vary depending on the context. Changes in the contrast response function (CRF) could reflect a change in response gain (the overall range of the channel response) or contrast gain (the range of stimuli over which the responses vary), and these have different functional consequences that could reflect maximizing sensitivity to changes in the ambient stimulus vs matching the operating range for the overall stimulus levels (Kwon et al., 2009).

3.2. Coding efficiency

Some of the most important insights into the design principles

governing encoding and representation in the visual system have come from applications of information theory (Attneave, 1954; Barlow, 1961), and this mathematical framework also makes precise predictions about the form and function of calibrations (Barlow & Földiák, 1989; Barlow, 1990; Wainwright, 1999). The amount of information that can be carried by neurons is constrained both by the limited operating range of any given channel and the limited number of channels. To maximize channel capacity, for a single neuron or channel, responses should be matched to the range of available inputs so that each response level occurs with equal frequency. This predicts that the CRF for the unit should reflect the cumulative probability distribution of the stimulus (Laughlin, 1981). Thus if the stimulus distribution is a Gaussian then the corresponding CRF would be sigmoidal, asymptoting at low or high values while changing most rapidly around the mean. This allows the channel to devote most of its capacity to signaling small changes around the mean, which are the most common, at the cost of reduced sensitivity to stimulus variations far from the mean, which are rare. This principle successfully predicts the form of the CRF at early stages including the relative sensitivity to different stimuli, such as luminance and chromatic signals: the wavelength sensitivities of the cones overlap substantially, so there is a much smaller range of chromatic contrasts than luminance contrasts in natural images, yet this is counterbalanced by a much higher sensitivity to chromatic contrast (von der Twer & MacLeod, 2001).

In this context adaptation can be seen as re-tuning the neural responses when the stimulus changes in order to maintain the channel efficiency. Exactly how the CRF changes should depend on the specific change in the stimulus distribution. However adaptation and other longer term adjustments may only be able to track some of these changes. In particular, while it is known that short-term adaptation can adjust responses for both the mean and the variance of the distribution, it is less certain that the system can adapt to higher-order moments. Later processing stages may also be governed by different constraints, such that the severe information bottleneck at early stages gives way to different strategies at later stages. For example, the CRFs of cortical neurons may be set for a lower operating range so that the cell only transmits larger stimulus levels rather than optimally conveying its inputs (Ringach & Malone, 2007). However, this operating range is again continuously adjusted by adaptation to the prevailing inputs.

Just as response levels should be equated within a channel, efficient coding also predicts that responses should be equated across channels. In some cases this may reflect evolutionary adaptations. For example, in natural scenes image contrast or amplitude varies inversely with spatial frequency, leading to the characteristic 1/f amplitude spectrum. However, because the bandwidth of spatial channels increases roughly in proportion to the preferred frequency there are relatively constant responses across spatial scale for 1/f spectra (Field & Brady, 1997). At much shorter timescales adaptation can adjust for changes in the channel distribution. Optical imperfections blur the retinal image, increasing the slope of the amplitude spectrum, but observers are adapted to the magnitude and to some extent the pattern of blur in their eyes and rapidly adapt to changes in blur (Webster & Marcos, 2017). Similarly, populations of visual cortical neurons show a rebalancing of responses that can counteract biases in stimulus distributions (Benucci et al., 2013; Westrick et al., 2016). Notably the changes in the response distribution could in principle reflect independent gain changes within each mechanism. That is, balanced responses could occur simply because each individual channel is adapting its operating range. However, as described below the dynamics and consequences of these adjustments depend on the neural networks in which they are embedded (Solomon & Kohn, 2014).

A second critical component of coding efficiency is removing redundancies in the channel responses. This principle again predicts many aspects of visual coding, including center-surround receptive fields which remove correlations in the responses to nearby spatial locations, or color-opponent receptive fields which remove correlations between the cone signals (Srinivasan et al., 1982). Barlow and Foldiak (1989)

suggested that some short-term adaptation could similarly involve inhibitory synaptic interactions between channels designed to decorrelate their responses. This interaction was described as "anti-Hebbian" learning since it contrasts with the Hebbian learning central to developmental plasticity and learning, in which coactivation increases the excitatory connections between units. Models of decorrelation have been proposed for a number of visual aftereffects (Atick et al., 1993; Barlow & Földiák, 1989; Westrick et al., 2016).

3.3. Norms and predictive coding

A related computational principle for understanding sensory processing is predictive coding, which is based on the idea that the system generates a prediction for the stimulus that is compared to the current sensory signals. This allows information to be encoded with higher fidelity in terms of the deviation from the prediction, or the error (Srinivasan et al., 1982). These ideas have seen wide application in sensory neuroscience (Friston, 2010; Rao & Ballard, 1999; Spratling, 2013). The theory of predictive coding accounts for complementary perceptual phenomena related to adaptation, namely the suppression of sensory responses to repeated or expected stimuli, and the enhancement of responses to unexpected stimuli (Atick & Redlich, 1990; Keller & Mrsic-Flogel, 2018). These effects are also central to models of perceptual salience, in the spatial domain, or surprise, in the temporal domain (Itti & Baldi, 2009). From this perspective some forms of calibration like adaptation can be conceptualized as adjustments of the prediction, and notably, adaptation has been shown to enhance the salience of stimuli that differ from the adapting stimulus (McDermott et al., 2010; Wissig et al., 2013). However the evidence for neural encoding of prediction errors is controversial (Latimer et al., 2019; Solomon et al., 2021). In typical visual cortex adaptation paradigms, the response suppression to repeated stimuli and enhancement to rare stimuli is consistent with genuine encoding of prediction errors, but could also reflect neuronal or synaptic fatigue (Solomon & Kohn, 2014). Conversely, a recent pattern adaptation study showed strong repetition suppression of the expected pattern but minimal modulation of the unexpected pattern, in contrast with direct encoding of prediction errors (Solomon et al., 2021).

Predictions are also closely related to the concepts of norms in visual coding. Many perceptual dimensions appear to be encoded as deviations from an expected value or norm. Examples of these norms include gray for color, static for motion, or prototypes for faces. An important function of adaptation and other homeostatic processes may be to calibrate or update these norms, by renormalizing responses for the ambient stimulus. That is, what looks gray or like an average face is set by the average spectra or faces you have been exposed to. In this regard norms and many aspects of prediction cannot be divorced from plasticity, because these norms are defined by the observer's state of adaptation (Webster, 2015).

3.4. Neural labeling

Models of visual coding typically assume that information is represented by the distribution of activity across populations of mechanisms tuned to different levels of a stimulus dimension (e.g. to different orientations in classic "multiple-channel" models; Atkinson et al., 1978). The way in which plasticity, particularly visual adaptation, modifies the gains of these mechanisms has been relatively well studied, but more contentious is the question of the extent to which the channel *labels* (i.e. the information carried by the population responses) as well as weights are malleable. Indications that they might be come from a variety of sources. For example, phantom-limb patients experience sensations from their amputated limbs, presumably because of activity in cortical neurons still labeled to convey information carried by the lost afferents. However, for some patients even brief exposure to a visual impression of their missing limb may effect reinterpretation of the somatosensory signals (Ramachandran & Rogers-Ramachandran, 2000). Some studies

have also reported rapid reorganization within primary visual cortex following a real or simulated visual scotoma, but the interpretation of these effects and the neural changes they implicate are complex and unresolved, so that the evidence for relabeling is in question (Wandell & Smirnakis, 2009).

Researchers have explored cross-modal plasticity in sensory cortices, where sensory information from a new modality can be represented when the usual input is lost (Fine & Park, 2018; Voss, 2019). For example, auditory processes have been found to activate visual cortex in blind individuals, including sound discrimination (Kujala et al., 1995), sound localization (Gougoux et al., 2005) and sounds from complex objects and scenes (van den Hurk et al., 2017; Vetter et al., 2020). When visual information is encoded in sound via sensory substitution, activity in specialist visual areas have been found to occur in response to higher level representations including those of body shape (Striem-Amit & Amedi, 2014), objects (Merabet et al., 2009) and words (Striem-Amit et al., 2012). On the other hand, as well as recruiting visual cortex for the representation of auditory and somatosensory information (which could be considered to generate representations analogous to visual ones), visual cortex has also been shown to be recruited in blind individuals for representations that are not so obviously spatial, with fMRI activity patterns implying that visual cortex can be involved in processing language (Bedny et al., 2011; Röder et al., 2002) and mathematics (Crollen et al., 2019; Kanjlia et al., 2019). Such findings have led to the suggestion that the cortex, including the visual cortex, consists of canonical modules that are 'pluripotent' (Bedny, 2017) and may at least initially be plastic enough to assume a variety of functions depending on the inputs (though this is disputed, e.g. Fine & Park, 2018).

But can the visual cortex be recruited in the same way in sighted individuals for the representation of information encoded in sound? It has been found that representations of auditory information can be decoded from activity patterns in early visual cortical areas V1-V3 (Vetter et al., 2014), though it is unclear whether or not the visual cortical activity was associated with visual mental images triggered in response to the sound stimuli. A recent finding (Vetter et al., 2020) that sound information can be similarly decoded from the early visual areas of congenitally blind individuals (who were assumed to lack visual mental images), also showed the same foveal to peripheral gradient of decoding performance as found in the sighted individuals, implying that visual cortex may be involved in representing auditory information even in sighted individuals. (Alternatively though, another recent study found that early visual areas in sighted vs blind observers responded differently to visual concepts of color; Wang et al., 2020). There is also some evidence that cross-modal plasticity can be induced in normally-sighted individuals following sensory deprivation. For example, Merabet et al. (2008) deprived sighted individuals of visual input for five days while immersing them in an intensive Braille training program. Following the training, there was a transient (<1 day) increase in BOLD signal in the occipital cortex in response to tactile stimulation. Similarly, Weisser et al. (2005) found an effect of only two hours of blindfolding on functional connectivity between V3A and ventral intraparietal sulcus, and Lazzouni et al. (2012) found an effect of 6 h of sensory deprivation on visual cortical responses to amplitude-modulated tones.

Thus there is reasonable evidence for cross-modal plasticity in blind people, and emerging evidence for similar plasticity in sighted individuals, especially when deprived of visual input, but is there any evidence for within-modality plastic changes in channel labels, such that the stimulus feature signaled by a channel can change? Though visual adaptation often changes the appearance of a subsequently presented stimulus, this has not generally been thought to result from a plastic change in channel label, but from a change in a population code (as in the tilt after effect) or an opponent code (as in color or motion after effects), following differential adaptation across the set of channels that contribute to the encoding of the visual attribute (Mollon, 1977). A plastic change in channel labels would lead to a neural mechanism encoding a stimulus dimension it previously did not, such as, for

example, leftward preferring motion selective neurons changing their preference to rightward motion. More recently there has been some evidence that following adaptation that results in perceptual after-effects, there are both gain changes in individual neurons, and changes in stimulus preference, the latter of which could constitute a change in channel label. For example, Dragoi et al. (2001, 2002) found that following adaptation to an oriented grating, single neurons in cat and primate V1 reduce their gain (as in the traditional model), but also shift their orientation preference repulsively from the adapting orientation. Including the latter in models improves their ability to predict the size of the tilt after effect (Jin et al., 2005). Similar changes in the stimulus preferences of single neurons have since been reported for other stimulus dimensions, including spatial frequency (Ren et al., 2016), motion (Zavitz et al., 2016) and stereoscopic depth (Duong et al., 2011).

One class of plastic relabeling of channels that has been intensively investigated is the retinotopic re-mapping that follows prism displacement or larger disruptions such as left–right or up-down visual field inversion. There has long been a debate about the processes underlying behavioral adaptation to visual field inversion, over the extent to which adaptation is *perceptual* (i.e. objects, following adaptation, appear at their correct physical locations), or in the *response* (i.e. objects still appear to be mis-located, but plasticity compensates motor or other responses) (Degenaar, 2014; Linden et al., 1999). Though it is difficult or impossible to distinguish these possibilities behaviorally, retinotopic encoding of visual information can be assessed at a mechanistic level. In favor of perceptual plasticity, Sugita et al. (1996) found, in adult macaques, that V1 cells begin to respond to ipsilateral visual stimuli following several months of visual field inversion. In humans, Miyauchi et al. (2004) found that ipsilateral visual activity in BOLD signals could be observed in V1 and area MT after 1–2 weeks, but Linden et al. (1999) observed no change in the retinotopy of early visual areas after a shorter period of 6–10 days.

In color vision the onset of red-green color discrimination in adult dichromatic squirrel monkeys following transfection with a viral vector containing a new class of photopigment (Mancuso et al., 2009) indicates that the cortex may be plastic enough to produce a new color 'channel' following the addition of a new sensor (however, note the argument by Makous (2007) that the signal underlying red-green 'color' discrimination following similar work in mice (Jacobs et al., 2007) could actually be spatial luminance inhomogeneity). There has been one attempt to remap color channel labels in adult humans by applying an altered-reality "gamut rotation" over approximately 1 week: although there were some significant effects on color constancy, memory color and aesthetic judgements, there was no "remapping" observed of subjective color appearance (Grush et al., 2015). In sum, the current evidence suggests that there may be some plastic relabeling of channels as well as the more well-studied weight changes during visual re-calibration. However, there seem to be limits on the extent of plastic changes – relabeling may usually be limited to channels that are already selective for nearby levels of a given stimulus dimension, and alternative bases for the observed effects that do not require an actual relabeling may often be difficult to exclude. Finally, evidence for recalibrations of channel labels should be interpreted in light of the marked stability that these labels often exhibit despite pronounced changes in the visual inputs (Wandell & Smirnakis, 2009).

3.5. Bayesian inference

In this section, we review explanations of visual calibrations based on the theory that visual processing relies on probabilistic Bayesian computations. The Bayesian framework has been used to formulate normative explanations of plasticity in the visual system, to answer questions like "Why is there plasticity?" and "Why does plasticity take the form it does?" Even when not cast specifically in a Bayesian framework, many accounts of coding and plasticity—including

sensitivity regulation, efficient coding, and predictive coding, as described above—have ties to, or can be formulated in terms of, probabilistic inference (Aitchison & Lengyel, 2017; Itti & Baldi, 2009; Lochmann et al., 2012; Młynarski & Hermundstad, 2018).

There are a few components to Bayesian explanations. Some of them have to do with the *inference*, that is, the interpretation of sensory signals, and the *learning* processes required to achieve correct inferences. Other components relate to how *decisions* are formulated and actions selected, combining those interpretations of the sensory input with the goals of the organism and the expectations about the consequences of different courses of action. Here we focus on the perceptual inference and learning angle, which has been fruitful for much foundational work on Bayesian explanations in vision research, and we highlight examples that suggest a relation between different forms of plasticity and the calibration of different components of Bayesian models.

At the core of Bayesian inference for visual perception are two elements: the *prior distribution* of the possible interpretations of visual inputs (e.g. how often we expect to see edges with cardinal orientations rather than tilted diagonally; Girshick et al., 2011); and the *likelihood function* (e.g. a specific change in the activation pattern of retinal photoreceptors, could be more likely due to an object moving from left to right than from top to bottom in the visual field; Weiss et al., 2002). Together, the prior and likelihood are combined via Bayes rule to obtain the *posterior distribution*, i.e. the attribution of probability values to all the possible interpretations of the actual sensory input (Knill & Richards, 1996).

How does the Bayesian inference framework afford normative explanations of perceptual phenomena in general, and visual calibration in particular? The first part of the answer relates to the prior distribution. When evidence is scarce or unreliable (e.g. it's dark and foggy, or part of an object of interest is occluded by another, closer object) prior knowledge helps to fill in the missing information in the input. Classical examples include the perception of 3-dimensional object shape (Kersten et al., 2004) and the perception of surface slant (Knill, 1998; Malik & Rosenholtz, 1997; Saunders & Knill, 2001): in both cases, the information is missing because 3-dimensional objects are projected on the 2-dimensional retina, and many 3-dimensional configurations could have produced the same 2-dimensional visual input. In other words, the likelihood of those 3-dimensional configurations is the same, and prior knowledge, e.g. of object shapes and sizes, helps disambiguate between those possibilities.

In the Bayesian framework, some forms of calibration of the visual system can be explained, normatively, as strategies to establish a prior distribution that matches the statistics of the environment or to adjust the prior when the environment changes. Establishing an ecological prior is usually thought to occur on long timescales of evolution and development (Berkes et al., 2011), and priors matched to the natural visual environment have been invoked often to explain perceptual biases and illusions: when the sensory evidence is unreliable, perceptual inferences tend to be biased towards the prior (Mamassian & Landy, 1998; Stocker & Simoncelli, 2005; Weiss et al., 2002). Shifts towards a prior established over long timescales, can also explain why adaptation produces perceptual repulsion away from the short-term adaptor but attraction towards stimulus distributions presented farther in the past (Chopin & Mamassian, 2012; though there are alternative accounts of these effects, Maus et al., 2013). The framework can also explain calibration phenomena on shorter timescales (Dayan et al., 2002; Orbán, 2017; Snow et al., 2017). For instance, neural adaptation in primary visual cortex following prolonged exposure to a biased stimulus ensemble (Benucci et al., 2013) might reflect refinements of the pre-existing ecological prior (Snow et al., 2016). Similarly, recent empirical observations on the structure of response variability in cortical populations (Rumyantsev et al., 2020) can be explained by changes in the prior after training on a specific visual task (Haefner et al., 2016; Lange & Haefner, 2020).

The second component of Bayesian explanations of perceptual

plasticity is the likelihood function. This is sometimes referred to as the *noise model*: different retinal inputs can be produced by the same physical object both because of stochasticity in sensory neurons (e.g. noise in the photoreceptors) and because of other uncontrolled *nuisance* variables (e.g. object pose, viewing angle, light conditions). Performing correct inferences requires that the likelihood, just like the prior, be well calibrated, and re-calibrated when needed. This in turn requires knowledge of both environmental statistics (because they determine the effects of nuisance variables) and of the structure of variability of the sensory signals (because it can affect the shape of the likelihood function). Different from Bayesian priors, which have often been invoked to explain perceptual biases and illusions, the likelihood function notably helps explain the different weights placed by an observer on different parts or aspects of the sensory input. Multisensory integration is a well-known example: e.g. when cues from different sensory modalities have different reliabilities (i.e. different width of the likelihood), more weight is placed on the more reliable (narrower likelihood) cue (Angelaki et al., 2009; Knill & Saunders, 2003). Similar reasoning can explain why different weights are placed on different visual features (Jogan & Stocker, 2015) or spatial regions of the visual input (Najemnik & Geisler, 2005). Similar to the prior, the likelihood function too needs to be learned from experience and adjusted to changes in the environment, such as following adaptation to experimental manipulations of the relative reliability of different features (Burge et al., 2010), perceptual learning (Bejjanki et al., 2011), and changes in the sensory apparatus for instance throughout development or aging—thus potentially addressing plasticity over multiple timescales. It should also be emphasized that, although these first two components of Bayesian explanations (prior and likelihood) could in principle be calibrated independent of each other, considerations about the efficiency of neural representations suggest that calibration of the prior and likelihood function to the input distribution may not be independent (Wei & Stocker, 2015).

What potential roles do the prior and likelihood function play in short term sensory adaptation? While exposure to an adapting stimulus might intuitively predict a shift in the prior so that the prevailing stimulus is more expected, visual aftereffects instead suggest that is the likelihood function that is changing. This is because changes in the prior should make stimuli appear more like the adaptor, whereas many aftereffects are instead characterized by a repulsion away from the adaptor. A model which assumes that the likelihood function is sharpened around the adaptor predicts both these repulsion aftereffects and increased discrimination for stimulus changes around the adapting level (Stocker & Simoncelli, 2006). Many adaptation aftereffects also involve a renormalization of the adapting level, so that the adaptor appears more neutral. This normalization is again inconsistent with changes in the prior (e.g. as we adapt to red the world does not appear more red), but can again be accounted for by a change in the likelihood function so that it is closer to the prior distribution (i.e. as we adapt to a red it appears more like the gray we expected). Recently Emery (2021) modeled adaptation in this way – as an error correction of the likelihood, at the level of response changes within a channel. By this account, gain changes "correct" the sensitivity of the channel so that the outputs match the expectations. This predicts both repulsion and renormalization depending on the properties of the population code, and also provides a principled account of when and how much the system should adapt.

Although Bayesian models of perception often address one-shot inference, that is, a single application of Bayes rule to combine the prior and the sources of evidence, perceptual systems in the real world face the more complex problem of dynamic inference. For instance, visual stimuli during natural vision are dynamic, due both to self motion and to motion of objects in the environment. Even with static stimuli, information is communicated over time between neurons and across visual areas, effectively producing temporal sequences of inputs. The framework of dynamic Bayesian inference prescribes how this information ought to be combined over time, leading to continuous updates of the posterior distribution (Särkkä, 2013). Phenomena related to the perception and neural processing of visual motion have been explained from this perspective (though traditionally evidence accumulation has been studied more extensively in decision-making neural circuits; Beck et al., 2008). Because dynamic inference implies dynamic changes of the posterior distribution, similar ideas could also capture aspects of neural plasticity (Kappel et al., 2015; Legenstein & Maass, 2014). However, an additional difficulty in relating dynamic inference to visual plasticity within the Bayesian framework, is that, if probabilities are represented by collecting samples (known as the neural sampling hypothesis; Fiser et al., 2010; Orbán et al., 2016), the temporal dynamics of neural and perceptual phenomena might reflect the progressive refinement of the representation of a fixed probability distribution, in addition to the changes in the distribution itself due to evidence integration (Lengyel et al., 2015). In summary, dynamical features of visual plasticity might reflect both dynamic inference and the dynamics of the algorithms adopted by the visual system for static inference. Untangling those two aspects remains an exciting open area of research.

Summary and open questions: As this discussion illustrates, calibrations are intrinsic to many of the general theoretical accounts of how information is encoded, represented, and interpreted in the visual system. In turn, these principles provide fundamental insights into the nature and function of many forms of calibration. This is because common to all of these principles is the idea that vision is matched and optimized for processing information about the observer's environment, and thus this optimization depends on the properties of the environment. The prevalence of these adjustments indicates that the visual world (as well as the optical and neural characteristics of the observer) varies enough so that the codes must be calibrated for the specific context. It remains uncertain how closely the actual calibrations that the visual system can implement allow for the precise adjustments predicted by computational principles versus rough approximations (Gardner, 2019), as well as which aspects of the contextual statistics can be adjusted for. A further issue is whether different computational goals require different and potentially conflicting patterns of adjustment, and how calibrations associated with any given goal (e.g. sensitivity regulation or coding efficiency) depend on constraints imposed by differences in the properties of different stages of the visual system or in the types of information that is being coded. A further important question is to understand the principles or mechanisms determining why some aspects of the codes are more readily adjustable than others. For example, why are neural gains more plastic than neural labels, under what conditions should the system adjust its priors rather than the likelihood, and over what timescales can and should the appropriate adjustments occur? Answering these questions will help shed light on both the consequences and constraints of visual calibrations and advance computational accounts of visual coding.

4. Calibrating visual networks

In this section we re-examine the nature of visual calibrations from the perspective of the structure and dynamics of the network architecture of the visual system. Recordings from neurons in all parts of the visual system reveal a strong effect of recent visual experience on visual response. Substantial work has now provided a good understanding of how the activities of individual neurons depend on short-term (e.g. adaptation effects) and longer-term (e.g. learning, or development) experience. But vision is based on the concerted activity of many neurons, across many brain areas, and what experience's effects on individual neurons might tell us about its effects on vision remains unclear.

The impact of experience on the responses of individual neurons can be highly variable, even among neighboring neurons within a particular area. The diversity of experience's effect is likely to be explained by the three general principles that govern the organization of visual pathways. The first principle is that visual processing is *serial*, with each stage of processing performing computations over its inputs, and feeding the

output of these computations to other areas. The effects of experience at one stage will therefore be cascaded onto other stages. The second principle is that the visual pathway consists of multiple *parallel* pathways. Each of these parallel pathways comprise neurons with distinct biochemical properties, which may make them more or less sensitive to experience. The third principle is that there are *lateral* interactions between neurons within each stage of visual processing. The activity of these lateral connections, which are often inhibitory or suppressive, will themselves be shaped by experience. The idea that there are parallel visual pathways that perform serial computations, in which lateral interactions are important, is beyond doubt. It follows that the functional impact of experience must be diverse among visual neurons. Additional potential for diverse influence of experience is provided by the *feedback* pathways that convey signals from higher visual areas (and areas with putative role in higher cognitive functions) to lower visual areas. The functional role(s) of these feedback projections remain unclear, but they are thought to provide supervising signals that can inform lower areas with predictions about the state of the visual environment (Bastos et al., 2012; Gilbert & Li, 2013; Rao & Ballard, 1999), the context of the current task, or behavioral outcomes (e.g. Jing et al., 2021). These top-down signals are likely to be important in mediating the effects of visual experience in lower areas, and may themselves be influenced by experience.

The functional impact of visual experience on different stages of visual processing is likely to be shaped by specific features and roles of the circuits involved. For example, a relatively small number of retinal ganglion cells provide representations of the retinal image that are important for all subsequent behavior. It therefore seems likely that mechanisms for plasticity in the retina should act over short time scales to increase the amount of information transmitted along the optic nerve without imposing large or long-term burdens on subsequent processing, or substantially constrain the range of analyses that can be undertaken. By contrast, there are several hundred visual cortical cells for every retinal ganglion cell – the cortex may prioritize mechanisms that allow visual experience to improve representational efficiency, or allow memory and cognition to provide expectations. In addition, visual cortex comprises multiple subnetworks which project to different targets and are likely to contribute to different functions – the cortex may be able to implement larger and longer impacts of visual experience in some or all of these networks, while retaining the information contained in the sensory input.

A great deal of work has examined the effect of short-term visual experience on visual networks. We note that it is hard to establish an impact of very brief visual experience (10 s-100 s of milliseconds), because the propagation of activity through a network takes time, and what appear to be adaptive changes in activity may simply reflect the time it takes for the network to settle (e.g. Quiroga et al., 2016). Over slightly longer timescales, on the order of several seconds or minutes, visual experience can have different effects on different pathways. For example, in the primate visual system, prolonged exposure to a high contrast grating ('contrast adaptation') reduces the response of neurons in the magnocellular part of the thalamocortical pathway, but has little effect on the response of neurons in the parvocellular part (Solomon et al., 2004; Tailby et al., 2008). The lack of contrast adaptation in the parvocellular pathway is consistent with the idea that it provides a relatively linear representation of the retinal image to visual cortex for further analysis. The lack of adaptation effects in parvocellular neurons may therefore be functionally beneficial, because if parvocellular neurons showed substantial adaptation effects, then accurate reconstruction of the retinal image would require cortex to have access to information about their adaptation state. In other species, adaptation effects are more ubiquitous in the retina. In these animals, the response of some retinal neurons is suppressed by visual experience while the response of other neurons is enhanced (Di Marco et al., 2013; Kastner & Baccus, 2013). The relative contributions of serial and lateral interactions is harder to dissect, but it is clear that experience can change the activities

of bipolar cell-mediated excitatory inputs and amacrine cell-mediated inhibitory inputs to retinal ganglion cells (e.g. Baccus & Meister, 2002; Kastner et al., 2019; Nikolaev et al., 2013; Wark et al., 2009). Experience also alters the activities of both excitatory and inhibitory neurons in the visual cortex (e.g. Heintz et al., 2022). Optical techniques now allow for monitoring of the inputs and outputs of identified neurons, and these will be important in providing a better understanding of how short-term experience affects the flow of signals into and through neural networks.

Long-term experience may also have different effects on different pathways. While the functional properties of parallel pathways to visual cortex, and those of early cortical neurons, appear to be well established early in postnatal development (Movshon et al., 2005), subsequent cortical pathways show longer functional developmental trajectories (Kiorpes & Movshon, 2013). These functional changes are likely to be accompanied by refinement of serial feedforward (and subsequently feedback) projections between visual areas (e.g. ferret: Khalil et al., 2018). Further, there is some evidence that 'dorsal' cortical pathways, that cascade through area V5/MT, develop earlier than other cortical areas (e.g. Bourne & Rosa, 2006). Lateral inhibition is important in the influence of postnatal visual experience (e.g. Hensch & Fagiolini, 2005), and experience helps cortex form appropriately balanced excitation and inhibition (at least in auditory cortex, Dorrn et al., 2010). Thus, developmental visual experience may have specific impacts on visual function because, while early visual pathways mature rapidly, the parallel pathways through later stages in the visual pathway can develop at different rates. Whether inhibition develops at different rates at different stages of visual processing, or differently among parallel pathways, remains to be discovered.

Some of the potential effects of experience on neural networks, and of neural networks on experience's effects, can be revealed by examining computational models of visual processing (e.g. Roelfsema & Holtmaat, 2018). Many of the effects of short-term visual experience can be reproduced in a multi-layered convolutional neural network simply by supposing that each unit is suppressed following activation (akin to 'spike rate adaptation'; Vinken et al., 2021). More complex phenomena may need only simple additions. For example, the widely used normalization framework proposes that excitatory visual responses from a neuron's receptive field are suppressed by the accumulated signals of nearby neurons, which provide a 'normalization pool'. The normalization pool usually has different visual tuning than the neuron that it suppresses, so the impact of experience on cortical visual response depends on how previous visual experience has driven the neuron, and how it has driven the normalization pool. Some formulations of the normalization framework provide predictions for how populations of neurons will respond to various visual stimuli, before and after experience (e.g. Solomon & Kohn, 2014; Westrick et al., 2016). Notably, these predict that because the response of a visual neuron depends both on the strength of excitatory input from the receptive field, and suppressive input from the normalization pool, the expression of experience in the visual responses of individual neurons can be very dependent on the spatio-temporal structure of the visual stimulus, and the particular organization of an individual receptive field. The upshot is that even if visual experience has specific effects on a specific element of a neural circuit, it can have diverse effects on the visual responses of individual neurons, and neural populations.

The overall levels of excitation and inhibition in visual cortex appear tightly linked, with increases or decreases in excitation accompanied by yoked changes in inhibition (e.g. Ahmadian & Miller, 2021). This balancing of excitation and inhibition is thought to be important in allowing recurrent cortical networks to operate around a critical point (Whitmire & Stanley, 2016), avoiding regimes where signaling is suppressed (too much inhibition) and regimes of epileptiform activity (too much excitation). Visual experience is likely to perturb this balanced excitatory-inhibitory network, at least briefly. Similarly, other manipulations – such as those provided by arousal, or attention – are also likely

to perturb the balance of excitation and inhibition. The question that arises is whether these effects on excitation-inhibition balance may be important in understanding the impact of visual experience. For example, if arousal changes the excitation-inhibition balance, and in turn the dynamics of that circuit (e.g. Huang et al., 2019), it may enhance or diminish short-term effects of visual experience such as adaptation. Similarly, if visual experience changes the excitation-inhibition balance, it may enhance or diminish the capacity for longer-term plasticity, where inhibitory pathways are particularly important (Froemke, 2015; Mongillo et al., 2018; Wilmes & Clopath, 2019). Understanding the relationship between visual experience and balanced networks is likely to be important for understanding the effect of mid-term visual experience (days or weeks) on neural circuits. These effects remain poorly established, because the necessary experimental tools (allowing monitoring of activity in specific neurons over many days) have only recently become available.

Summary and open questions: Experience has diverse effects on neural circuits, making it challenging to explain the neural basis of calibration. The origin and meaning of this diversity are not clear. In retina, where it has been possible to target specific visual pathways, diversity is primarily expressed between rather than within cell classes; this is also the case in thalamus. In cortex, however, we are only starting to know how experience has different impact on different cell classes. In imaging experiments, gene expression can help specify subpopulations of cortical neurons, and early results suggest substantial within-class as well as between-class diversity in primary visual cortex of mouse (Heintz et al., 2022). It seems likely that some diversity will be explained by the pathway(s) that the particular neurons contribute to – for example, whether their signals contribute to processing in the 'ventral' or 'dorsal' streams. However, it is also possible that diverse expressions of visual experience are beneficial. For example, if responses to particular images are increased in some neurons, decreased in others, and unchanged in others, this may help preserve overall activity levels against changes in the visual diet ('homeostasis', e.g. Benucci et al., 2013) or ensure that the recalibration induced by visual experience does not inadvertently make us blind to important visual events.

The diverse expressions of visual experience may, however, also suggest that the fundamental purpose of this plasticity is not well captured by asking how experience changes the mean activity of neurons, or neural populations. The fundamental computations of neural circuits are likely to be latent (Gallego et al., 2020; Jazayeri & Ostojic, 2021) and the impact of visual experience on these latent computations may be much more stereotyped than its impact on overall activity. Indeed, perceptual learning is more likely to be associated with changes in the patterns of activity across neurons than with changes in their mean activity (e.g. Gu et al., 2011; Ni et al., 2018). If adaptation and other shorter-timescale processes of calibration alter the pattern of neural activity that may also help understand longer term changes, because the pattern of activity over neural populations is likely to be important in guiding Hebbian-like plasticity.

If calibration relies on changes in the pattern of activity across specific, multiple stages of a serial and parallel visual pathway, full experimental measurement of the neural activity that supports calibration will be difficult or impossible in most species. Computational models of calibration that link behavior and theory to operation in neural circuits, and that can support better hypothesis testing in practical experimental regimes, are therefore increasingly important.

5. Visual calibrations during development

5.1. Critical periods, sensitive periods and sleeper effects

We next focus on the special importance of calibrations in visual development. These have been intensely studied, because it is well established that the extent of visual plasticity is greatest early in development, and that there are particular time windows during development when the visual system is most malleable and shaped by experience. The concept of a 'critical period' in vision, where experience has a heightened effect on the visual system and is essential for normal visual development, gained momentum from Hubel and Wiesel's pioneering investigation of monocular deprivation in kittens (Hubel & Wiesel, 1970; Wiesel & Hubel, 1963). These studies showed that when one eye of a kitten was deprived of light stimulation by eyelid suture during a period in early development, then recordings from V1 revealed a long term shift in which eye was best able to excite visual cortex neurons. Monocular deprivation had caused a reorganization of V1 ocular dominance columns in favor of the open eye, causing a long term loss of responsiveness and visual acuity in the deprived eye when re-opened. This effect, termed 'ocular dominance plasticity' was strongest during a particular postnatal 'critical' period in the kitten's development and had little or no effect at older ages (Hubel & Wiesel, 1970).

The classic finding of ocular dominance plasticity being heightened during a critical period in development has spawned many decades of research and a wealth of physiological, anatomical and behavioral evidence from a range of different species to support the concept of a critical period in many aspects of vision. There has been a massive effort in the field of neuroscience to identify the cellular and molecular mechanisms responsible (e.g. Hensch, 2004). For example, research has identified that excitatory NMDA and AMPA receptors and inhibitory GABA receptor expression function together to enable plasticity during the critical period, providing triggers and breaks to determine the onset and offset of critical periods (see Table 1 in Hensch, 2004). There is also evidence that the expression of these receptors changes in the human visual cortex postnatally (Murphy et al., 2005). Importantly, cellular and molecular studies identify that the brain's potential for plasticity is not 'lost' with age, but that the molecular breaks constrain visual plasticity beyond critical periods and, quite amazingly, pharmacological interventions have been shown to lift these breaks and enhance plasticity in adult visual cortex (e.g. Hensch & Quinlan, 2018).

Since the work of Hubel and Wiesel, there has been a large body of research which has aimed to understand the role of visual plasticity in human visual development and to identify the implications for the treatment of visual conditions which alter visual experience or cause visual deprivation early in development. There has been much investigation of the condition of amblyopia which is the most common cause of permanent vision loss in childhood affecting between 1 and 4 % of the population (e.g. Levi et al., 2015; Sachsenweger, 1968). Amblyopia (or 'lazy eye') is where asymmetrical vision in childhood due to "unequal alignment (strabismus), unequal refractive error (anisometropia) or form deprivation (e.g., due to cataracts)" (p.2, Hensch & Quinlan, 2018), leads to profound deficits in processing signals from the abnormal eye. Based on Hubel and Wiesel's concept of ocular dominance plasticity, there is evidence that the early deprivation or poor visual experience of one eye during the critical period leads to a reorganization of ocular dominance and alterations in early cortical areas V1 and V2 as well as LGN (e.g. Kiorpes, 2006; Levi, 2013). This ocular dominance imbalance then leads to a range of deficits in the 'lazy eye' including loss of visual acuity, stereopsis and contrast sensitivity (Levi, 2013) as well as deficits in higher level aspects of vision, attention and visual cognition such as audio-visual processing (e.g. Richards et al., 2019). The common treatment for amblyopia, called 'occlusion therapy', involves patching the dominant eye for extended periods of time in childhood in an attempt to re-dress the ocular dominance imbalance.

The traditional view is that amblyopia can be treated up until 7–8 years old during the critical period when ocular dominance plasticity is still active, but that the condition is resistant to reversal beyond this (e.g. Webber & Wood, 2005). However, a growing, converging body of evidence also points to significant capability for plasticity in the adult brain and visual system beyond the so called 'critical period' (e.g. Castaldi et al., 2020). The potential for visual plasticity beyond early development explains the success of occlusion therapy in some children older than 7–8 years (Scheiman et al., 2008). Adult visual plasticity has also

motivated the development of new treatments for amblyopia in adults, for example that aim to enhance vision in the affected eye by using perceptual learning (Levi & Li, 2009), and video game play (Li et al., 2011). The finding that molecular breaks on critical periods can be lifted with pharmacological intervention (e.g. Hensch & Quinlan, 2018), has also motivated pharmacological treatment for amblyopia (Vagge et al., 2020). Given adult visual plasticity and some success in the treatment of amblyopia in adults, some prefer to consider the time window from birth to 7–8 years as a 'sensitive' rather than 'critical period'. During a 'sensitive period' experience still has a profound effect on the brain yet visual plasticity is still retained beyond it (Hooks & Chen, 2007). It is clear that further understanding the nature of visual plasticity at different stages throughout development, as well as individual differences in visual plasticity, will provide further insight into the treatment of amblyopia and why treatment is successful in some individuals and not others (e.g. Tao et al., 2020).

Another condition which has provided insight into critical and sensitive periods in visual development is the condition of dense cataracts where the lens of one or both eyes is opaque and prevents patterned light from reaching the retina. Cataractous lenses which can be congenital or acquired can be removed and replaced with artificial lenses to enable visual input. Given the evidence that postnatal visual experience has a profound impact on visual development, clinical opinion is generally that congenital cataracts are better removed as early as possible in infancy, yet in countries where access to healthcare is limited cataracts may not be removed until later in childhood, adulthood or never at all (Project Prakash: Sinha, 2013). Even when the period of postnatal deprivation is short and when perceptual abilities are assessed in adulthood following a lifetime of potential learning, profound deficits in visual perception persist. For example, individuals treated for congenital cataracts have been found to have poorer aspects of low-level vision such as visual acuity (Lewis & Maurer, 2009), spatial contrast sensitivity at medium and high spatial frequencies (Ellemberg, Lewis, Maurer, et al., 1999) and stereopsis (e.g. Tytla et al., 1993). Long term deficits following treatment of congenital cataracts are also evident for discrimination of faces on the basis of the location of internal features (e. g. Le Grand et al., 2001), memory for faces (de Heering & Maurer, 2014), visual feature binding (Putzar, Hötting, et al., 2007), and ability to identify the odd shape out on the basis of illusory contours, shading or occlusion (McKyton et al., 2015). Related deficits have also been found in a case of visual recovery of blindness from corneal scarring (Fine et al., 2003). Deficits in individuals treated for congenital cataracts have also been documented for multisensory and cross-modal processing, for example, reduced multisensory facilitation in speech perception (Putzar, Goerendt, et al., 2007); impaired audio-visual simultaneity perception (Chen et al., 2017); reduced audiovisual and audiohaptic sound-shape associations (Sourav et al., 2019), and atypical visual and auditory temporal biases (Badde et al., 2019).

This catalogue of pervasive visual and multisensory perceptual deficits in individuals who experienced even a brief postnatal period of visual deprivation due to congenital cataracts attests to the importance of postnatal visual experience for normal visual development. Investigating the impact of the timing of visual deprivation has also given insight into the timing of the heightened visual plasticity during critical and sensitive periods for different aspects of vision and perception (e.g., see Maurer's 2017 review). Maurer (2017) contrasts the timing of the critical period for visual acuity and global motion based on the impact of congenital and acquired cataracts. For the case of visual acuity, the presence of dense cataracts at any time during the first ten years of life, whether congenital or acquired, leads to long term deficits in acuity (Lewis & Maurer, 2009), suggesting a critical period of 10 years. However, for the case of global motion, congenital cataracts lead to poorer acuity but acquired cataracts do not – even if they are acquired before the first birthday, suggesting a short critical period for global motion in the first few months of life (Ellemberg et al., 2002; Hadad et al., 2012; Rajendran et al., 2020). Although the timing of the critical periods for

visual acuity and global motion differ, they both mature in normal visual development mid childhood: at 7 years for visual acuity (Ellemberg, Lewis, Hong Liu, et al., 1999) and 12 years for global motion (Hadad et al., 2012), potentially suggesting that the timing of critical periods is not determined by the timing of normal visual maturation (Maurer, 2017).

The progression of visual ability following treatment of congenital cataracts also gives insight into the role of experience in visual development. For individuals treated for congenital cataracts before 9-months, visual acuity was equivalent to that of a newborn after ten minutes of visual experience with fitted contact lenses, yet during the first hour there was more improvement than during normal visual development (Maurer et al., 1999), and by 1 year acuity was normal (Lewis & Maurer, 2005). This rapid improvement suggests that the visual system is 'experience expectant' – the visual system becomes ready to respond to visual input once it is received (Maurer, 2017). However, for these individuals, the initial improvement in visual acuity later slowed around 2 years resulting in poorer visual acuity than for normal visual development in the long term (Lewis et al., 1995; Maurer & Lewis, 2001). Therefore, although a few months of postnatal visual deprivation appeared to spare visual acuity at 1 year of age, permanent visual deficits appeared later in life. This effect, whereby deprivation causes deficits to appear later in development has been termed a 'sleeper effect' and has been attributed to postnatal visual experience setting up a neural substrate for visual abilities that emerge later in life (Maurer et al., 2007).

Despite the mounting evidence for pervasive deficits in visual perception following a brief postnatal period of visual deprivation, some aspects of visual perception appear behaviorally normal. For example, those treated for congenital cataracts perform typically for some aspects of face perception such as discriminating faces using the shape of internal features or contours of the face (Mondloch et al., 2010), or detecting facial expressions (Gao et al., 2013; Geldart et al., 2002). Performance on biological motion tasks (Hadad et al., 2012), and those requiring the identification of human actions (Rajendran et al., 2020) also appears typical. Congenital cataract patients can identify the odd one out element from an array based on color, size or shape, even when cataracts are treated relatively late in childhood (McKyton et al., 2015), and performance on other basic tests of color discrimination also appears normal (Pitchaimuthu et al., 2019). In addition, studies of individuals who have been treated for congenital cataracts in adulthood (Sinha, 2013) have identified that even with very late treatment, certain visual abilities such as a transfer of tactile shape knowledge to the visual domain and visual parsing of scenes can develop rapidly (Held et al., 2011; Ostrovsky et al., 2009). As for the case of amblyopia, studies of visual deficits in adults treated for congenital cataracts reveal that adults retain some visual plasticity to enable improvement with rehabilitation. For example, playing a video game for 10 h for 4 weeks led to improvements in visual acuity, spatial contrast sensitivity, global motion and face processing in adults previously treated for congenital cataracts (Jeon et al., 2012).

Although several aspects of visual perception appear unaffected by congenital cataracts, typical performance on behavioral tasks does not necessarily indicate that visual deprivation has had no effect on the visual modality tapped by the task. Alternative visual strategies could be employed to return the same behavioral result as those with no history of cataracts, and the neural systems typically involved in that aspect of perception could still have been affected or even reorganized as a result of the deprivation. The recent advance of employing neuroimaging (e.g. EEG) methods to reveal the impact of dense cataracts on neural circuits and neural processes is therefore an important one, and more broadly improves understanding of visual plasticity in human neural systems. The few studies completed so far generally suggest that visual plasticity during critical or sensitive periods does not determine the establishment of basic visual neural circuits, but could determine the tuning and specialization of these for particular categories. For example, the N170

event-related potential component which is normally enhanced for faces did not distinguish faces from other stimuli and was therefore less specialized in individuals who had congenital cataracts treated between 2 months and 14 years old (Röder et al., 2013). Furthermore, the retinotopically mapped C1 component appears normal for those treated for congenital cataracts, yet the extrastriate *P*1 component related to object processing is reduced (Sourav et al., 2018). This suggests that the basic retinotopic organization of early visual cortex is spared by early visual deprivation and not determined by experience, which is supported by research which finds retinotopic organization of visual cortex in non-human primates at birth (Arcaro & Livingstone, 2017). One explanation for reduced functional specialization of neural circuits in congenital cataract patients is that a period of postnatal visual deprivation affects the development of inhibitory neural circuits which decrease the responsiveness of neural systems to non-preferred categories (e.g., which inhibit the N170 response to non-faces, Röder et al., 2013). Reduced EEG posterior alpha oscillatory activity in individuals treated for congenital cataracts is potentially aligned with this explanation since posterior alpha has been related to the inhibition of task irrelevant neural circuits (Bottari et al., 2016).

Congenital cataracts can also shed light on the time period for cross-modal reorganization. Whilst studies of the blind have revealed that the occipital cortex responds to non-visual stimuli following long term visual deprivation (Bavelier & Neville, 2002), an fMRI study of congenital cataract patients treated before 1 year of age suggests that even a very brief period of visual deprivation is sufficient for this kind of cross-modal re-organization (Collignon et al., 2015). This again emphasizes the heightened plasticity of neural systems during the postnatal period.

5.2. Perceptual narrowing and expertise

Conditions that cause postnatal visual deprivation such as amblyopia and congenital cataracts shed light on the developmental time course of visual plasticity. Another approach to understanding the role of visual plasticity during development is to investigate the impact of the type of visual experience and the kinds of stimuli infants are exposed to on their perceptual abilities and expertise. An example of this is the case of perceptual narrowing (e.g. Maurer & Werker, 2014). Here, infants' initial 'broadly tuned' perceptual ability becomes more narrowly tuned to the specific input from their environment in the first year of life (e.g. Scott et al., 2007). The original example of this is that 6–8 month old infants raised in an English speaking environment can discriminate non-native dental / retroflex contrasts such as Hindi /Ta/ vs /ta/, but by 10–12 months they appear to fail at this discrimination (Werker & Tees, 1999). Examples of perceptual narrowing have been provided for other types of speech perception (e.g., vowels: Cheour et al., 1998), music perception (e.g., Hannon & Trehub, 2005), face perception (e.g., Pascalis et al., 2002) and alternative forms of social communication such as visual sign language (Palmer et al., 2012) and cross modal voice-face matching (Lewkowicz & Ghazanfar, 2006).

For the case of perceptual narrowing of face perception, whether or not infants retain an early ability to discriminate faces of a certain type is determined by whether infants experience those faces during a particular period in the first year of life, typically around 6–9 months old (Pascalis et al., 2014). Perceptual narrowing of face perception has provided a developmental account of the Other Race Effect whereby adults find it difficult to discriminate individual faces of another race relative to their own race faces (e.g. Meissner & Brigham, 2001). For example, developmental studies have shown that three month old infants can discriminate faces of other races, yet this ability declines around 9 months if other race faces are not experienced (Kelly et al., 2007; Sangrigoli & de Schonen, 2004). This tuning of perceptual face space by experience also occurs for infants' discrimination of faces of other species: at 6 months infants can discriminate both human and monkey faces, but by 9–10 months their discrimination of monkey faces appears diminished (Pascalis et al., 2005; Pascalis et al., 2002).

Perceptual narrowing provides insight into the role of experience in perceptual development and the timing and nature of visual plasticity. Studies have shown that if infants are exposed to a broader range of stimuli early in infancy, then infants retain the ability to discriminate stimuli from the exposed category. For example, when Caucasian infants were read a book containing Chinese named faces for a total of 70 min between 6 and 9 months, they retained the ability to discriminate novel Chinese faces at 9-months (Heron-Delaney et al., 2011; see also Pascalis et al., 2005). Other research has identified that perceptual narrowing can actually be reversed if there is childhood exposure to the category of stimuli not experienced in infancy, but that this flexibility diminishes at around 12 years old (Pascalis et al., 2020). For example, the strength of the other race effect correlates with other race contact in primary / elementary school but not thereafter (McKone et al., 2019). This suggests that there is a sensitive rather than critical period for the effect of experience in the first year of life as perceptual systems retain the ability to be flexible to experience later in childhood (Pascalis et al., 2020). Even after childhood, perceptual learning in adults and possible examples of face specialization (e.g., teachers of young children are better at discriminating child faces, Harrison & Hole, 2009), suggest that some residual plasticity remains (Maurer & Werker, 2014). Other research agrees with the interpretation that the perceptual narrowing effect is due to a sensitive period rather than a critical one. For example, infant macaques reared with no exposure to macaque or human faces for the first 6–24 months of life have no specific preference for macaque or human faces following deprivation (they prefer both types of face to objects), but after one month exposure to either macaque or human faces their preference is dependent on what type of face they experienced during that month (Sugita, 2009). In other words, the macaque's perceptual face system is not hampered by early deprivation, it just waits for experience to determine what kind of perceptual system to become.

The benefit of perceptual narrowing is clear: it enables the immature perceptual system of infants to calibrate to experience, and to efficiently tune in and specialize to the types of stimuli that are relevant for social communication in an infant's environment (e.g. Lewkowicz, 2014). However, there is debate over the nature and mechanisms of the effect. Whilst perceptual narrowing has traditionally been framed in terms of a loss of discrimination of stimuli not experienced, it has more recently been characterized in terms of a reorganization of perceptual sensitivity and a 'decline in responsiveness' rather than a loss of discriminability (Lewkowicz, 2014). In addition, Maurer and Werker (2014) emphasize that the nature of experienced representations changes too (see also Kuhl et al., 2006), and suggest that the effect should be reframed in terms of a shift in attention and the level of processing of experienced and non-experienced stimuli rather than maintenance or loss of discrimination. The role of attention has been emphasized by others too. For example, perceptual narrowing has been attributed to a change from mostly bottom-up processing in early infancy to a combination of bottom-up and top-down processing at the time of perceptual narrowing (Hadley et al., 2014). In addition, the i-MAP model of perceptual narrowing suggests that bottom-up attention fosters perceptual learning for commonly experienced stimuli and top-down attentional biases to familiar stimuli which leads to refined perceptual representations in the first year of life (Markant & Scott, 2018). In support of the role of attention, if selective attention is biased during learning then this affects 9 month old's discrimination of own versus other race faces (Markant et al., 2016). Other accounts have suggested that non-experienced stimuli shift to being processed at a categorical rather than individual level around the time of perceptual narrowing (Hadley et al., 2014; Maurer & Werker, 2014). In support of the categorical argument, the other species bias in face processing is eliminated at 9-months if infants are trained to associate individual names with monkey faces but not if monkey faces were associated with category labels or no label at all (Scott & Monesson, 2009). This categorical interpretation suggests that language acquisition helps tune perceptual systems to what is relevant in

a particular culture (e.g. Timeo et al., 2017).

There is potential for perceptual narrowing to provide greater insight into the neurobiological basis of visual plasticity during development. However, there is currently little evidence which identifies the neurobiological underpinnings of the effect. It has been hypothesized that perceptual narrowing is due to pruning of exuberant neural connections in early infancy (Low & Cheng, 2006; Maxwell et al., 1984; Scott et al., 2007). In support of the pruning hypothesis, individuals with synesthesia, a condition which has also been framed in terms of a weaker neural pruning during development, also demonstrate weaker perceptual narrowing (Maurer et al., 2020). However, others have rejected this interpretation, arguing that the dominant process in brain development in early life is in fact neural growth and proliferation and the formation of new synaptic connections (Lewkowicz, 2014). In support of the argument that perceptual narrowing is associated with synaptic connectivity, one ERP study has found greater frontal and occipital connectivity to a cross-modal face and voice match for human stimuli than monkey stimuli at 8 months (Grossmann et al., 2012). Other research suggests that the time course of perceptual narrowing, at least for the case of speech, is driven by maturational factors rather than amount of experience since perceptual narrowing of non-native contrasts occurs at the same gestational age for preterm and full term infants (Peña et al., 2012).

5.3. General role of experience in visual development

Studies of amblyopia and congenital cataracts highlight that a lack of visual experience during even a brief postnatal period disrupts the development of many aspects of vision and visual perception, and the phenomenon of perceptual narrowing indicates that the type of visual input in infancy shapes later visual perceptual abilities. Beyond this, there is a question about the more general role of experience in visual development and the extent to which the time course of normal visual development is determined by general experience rather than preprogrammed neural maturation. This question has been addressed in studies which contrast the visual abilities of pre-term and full term infants. If experience matters then pre-term infants should have equivalent visual ability to full-term infants matched on postnatal age (equivalent experience), but an enhanced ability relative to infants matched on gestational age due to their additional experience. In other words, does the additional visual experience of infants born early give them an advantage over infants conceived at the same time but born full term?

Taking this approach, studies have shown that experience clearly matters for the time course of normal visual development. For example, 2 months of additional experience due to prematurity leads to an advanced developmental timing of binocular vision relative to infants matched on conceptual age (Jandó et al., 2012). Pre- and full-term infants perform equivalently on a gaze following task when matched on postnatal age but pre-terms excel when matched to full-terms on conceptual age, again suggesting the importance of experience over general maturational factors (Peña et al., 2014). Experience also matters for the development of chromatic and luminance contrast sensitivity: in a study that assessed infants born 0, 2, 6 or 8 weeks premature, an additional 4–10 weeks of experience enhanced chromatic sensitivity, and an additional 6–10 weeks of experience enhanced luminance contrast sensitivity. Importantly though, both chromatic and luminance contrast sensitivity lagged behind that of full-term infants of the same postnatal age, highlighting the importance of biological factors as well (Bosworth & Dobkins, 2013, see also Bosworth & Dobkins, 2009). An additional study on contrast sensitivity found a greater influence of factors unrelated to visual experience such as infants' gestational length on infant luminance contrast sensitivity, and a greater influence of factors related to visual experience such as postnatal age on infant chromatic sensitivity (Dobkins et al., 2009). On the basis of this, it has been proposed that the parvocellular pathway may be more driven by experience than the magnocellular pathway (Dobkins et al., 2009). Other aspects of visual development, such as visual acuity, have also been identified as experience-independent based on the pre-term approach (e.g., Brown & Yamamoto, 1986). In addition, comparison of VEP components in pre- and full-term infants, such as the *P*1 peak latency which indicates the general maturation of the visual system, reveal experience-independent processes are at play postnatally as well (Mikó-Baráth et al., 2014).

Summary and open questions: The reviewed body of work on amblyopia, congenital cataracts, perceptual narrowing and prematurity converge in clearly showing that early experience shapes visual development, and in some instances has long lasting effects on mature vision and visual perception. The influence of early experience on visual development can be seen as a form of calibration which enables vision and visual perception to be tuned to optimally represent the experienced environment. That there is calibration during some aspects of visual development is no longer contentious. However, there are key issues that need to be better understood. First, the field lacks a clear understanding of why some aspects of visual development are shaped by early experience more than others, and why some aspects appear to be more malleable by experience later in life. This does not appear to be determined by developmental trajectory: for example, the effect of visual deprivation during development on visual acuity and global motion discrimination differ, yet both mature at the same time during childhood (Maurer, 2017). There are also aspects of visual development where the effect of early experience remains unknown. For example, it is currently unclear whether perceptual narrowing is restricted to stimuli relevant for social communication (e.g., faces, speech, music). Second, further research is needed which more directly relates neural mechanisms and the neurobiological processes of plasticity to the effect of early experience on visual development in humans. For example, Siu and Murphy (2018) identify parallels between early visual development and developmental changes in neurobiological mechanisms in V1 such as the trigger proteins that promote neuroplasticity and the brakes that limit it. Further research that strives to relate such neurobiological mechanisms in V1 and other relevant brain regions to phenomena such as perceptual narrowing would provide leverage in understanding the likely distinct set of processes that make up calibrative effects in visual development. Such research also has potential for further development of pharmacological interventions for those who experience a period of early visual deprivation such as in the case of amblyopia (e.g. Vagge et al., 2020).

6. Individual differences in calibration and plasticity

We have learned that plasticity in the visual system is strongly dependent on age, with strong plasticity initially in early visual development that decreases through the lifespan into old age (e.g. Abuleil et al., 2019; Siu et al., 2017). However, beyond the relatively well-investigated dependence on lifespan, are there reliable individual differences in the extent to which the visual system can calibrate, and if so, can they be used, as for other visual processes (Mollon et al., 2017; Peterzell, 2016; Samuel, 1981; Wilmer, 2008), to isolate and investigate the processes underlying the calibrations?

Individual differences in visual plasticity might be observed ad-hoc in the results of studies targeting other questions, but they have relatively rarely been the subject of research themselves. Exceptions include investigations into individual differences in dark adaptation (McGuinness, 1976; Philips, 1939), prism adaptation (Melamed et al., 1979; Warren & Platt, 1975), motion and tilt aftereffects (McGovern et al., 2017), face adaptation (Dennett et al., 2012; Engfors et al., 2017; Palermo et al., 2018), blur adaptation (Vera-Diaz et al., 2010), and chromatic contrast adaptation (Elliott et al., 2012). In a few studies, individual differences in visual plasticity have been associated with other variables, such as blur adaptation with refractive error (Cufflin et al., 2007; Ghosh et al., 2017; Khan et al., 2013; Sawides et al., 2011) and adaptation in L and M cone pathways with the menstrual cycle (Eisner et al., 2004). In some cases, individual differences are used to investigate the *purpose* of adaptation. For instance, Mattar et al. (2018)

found that individual differences in the level of repulsive perceptual 'bias' induced by adaptation (which was correlated across face stimuli and colors) correlates negatively with the mean precision of stimulus matches, implying that sensory precision may contribute to variation in the magnitude of adaptation. Webster and Leonard (2008) found that individual differences in perceived white are reduced when observers are adapted to a common white, implying that differences in color appearance may be at least partly accounted by differences in how receptor responses are normalized via long-term adaptation. Individual differences have also been used to study the *mechanisms* of adaptation. For example, Heuer and Hegele (2015) used individual differences to isolate an explicit component and two different implicit components of visuomotor adaptation.

Latent variable analysis has been applied to individual differences measured in visual functions to understand their inter-relationships and underlying mechanisms (reviewed by Mollon et al., 2017; Tulver, 2019). Such studies have typically not included measures of plasticity (perhaps owing to the relatively time-consuming natures of the tasks involved), but factor analysis applied to individual differences in the results of a battery of psychophysical measures involving adaptation, perceptual learning and other plasticity could shed light on whether individual differences reveal a general trait of visual plasticity, or whether they are specific to different types of plasticity or even more specific to the task contexts. In this vein there are two recent studies that used individual differences to investigate the influence of priors on visual perception. Tulver et al. (2019) tested 44 participants on a battery of 4 perceptual tasks thought to rely on perceptual priors. The intercorrelations between individual differences on the expected effects of the four priors were generally low, and a factor analysis revealed two factors rather than a single factor underlying the correlation matrix. Andermane et al. (2020) tested 75 participants on a battery of 7 tasks involving perceptual priors. In agreement with Tulver et al. they did not find evidence for a common factor, with generally low inter-task correlations and a three factor solution to their factor analysis.

Whether individual differences in visual plasticity are general or specific to particular calibration processes or even tasks (as seems to be favored by the rather scant evidence so far), they can still be used to explore the underlying mechanisms. Specifically, individual differences may be used to unify explanations for traits at different levels, e.g. behavioral and anatomical (Kanai & Rees, 2011) or behavioral and genetic (Gu & Kanai, 2014). The behavioral genetics of neuroplasticity is a particularly provocative subject, because it challenges the still pervasive (false) dichotomy between nature (genetics) and nurture (environment). A genetic basis of neuroplasticity would provide a pathway for gene-environment interactions in behavioral and perceptual traits broadly: innate specification of the degree to which a neural system is able to adapt to environmental contexts. This is so far a little studied area, but one candidate gene study (Barton et al., 2014) has targeted the brain-derived neurotropic factor (BDNF) gene, which is thought to be involved in neuroplasticity in other domains (e.g. Barton et al., 2014), finding that Val[66]/Met heterozygotes were able to compensate for a left–right reversal in visual input better than Val/Val homozygotes. However, one *meta*-analysis (McPhee et al., 2020) and one review (Toh et al., 2018) on the relationship between the Vall[66]Met polymorphism in BDNF and cognitive traits have not found clear directional effects.

Summary and open questions: Individual differences in visual calibration and plasticity are under-studied, but offer a potential method for unifying accounts of visual plasticity at different levels (e.g., genetic, neural and computational). Though the few recent studies on individual differences in visual plasticity have not revealed common mechanisms across tasks, it remains a promising avenue for future research, which could target other manifestations of plasticity, such as perceptual learning, adaptation and long-term recalibration. Further work that could include candidate gene or genome wide association studies is needed to shed light on the genetic and neural differences that may contribute to individual variation in visual plasticity.

7. Limits to calibrating the visual system

What constrains what can be adjusted to? Ultimately, constraints on neuroplasticity are biological, and place limits on the range of environmental inputs that the system can adapt to. However, biological constraints are not simply imposed at the limits of biological plausibility, but may be adaptive in that they are evolved to limit neuroplasticity at different stages of life and in different environmental contexts, as evolutionary adaptations to niches that require particular plasticities. For example, as described in Section 5, recent research has revealed biological constraints on the sequence and timing of a series of sequential critical periods, that regulate plasticity in response to environmental inputs in a particular order necessary for efficiently installing the capacities underlying complex visual representations (Reh et al., 2020). There are also *functional* constraints: in many cases though plasticity can have a large effect on visual appearance, only a subset of plastic changes impact visual performance. Finally, there may be important functional advantages to stability in neural representations (Wandell & Smirnakis, 2009), which may constrain how much the system can and should recalibrate in the face of change.

As well as constraints on which visual processes are plastic, there are constraints on the speed, strength and endurance of calibrative changes. As discussed in Section 2.2, plasticity of a particular visual function may be achieved via several different neurobiological mechanisms operating over different timescales (e.g. Inoue et al., 2015), the mechanisms themselves presumably placing limits on the speed of calibrative change. The strength of visual plasticity also shows great variety: some changes amount to a complete recalibration, others a small shift in the direction of the required compensation for an environmental or observer perturbation. Lastly the endurance of plastic changes in the visual system is also variable in a way that may or may not be adaptive. Sometimes only short-term recalibrations are required: it would be maladaptive for example to have a long-term change in color vision in response to a short-term change in illumination. Longer term calibrative changes, for example in response to long term changes in the peripheral visual system, may typically be more enduring, but the training of a particular visual skill via medium to long term perceptual learning may dwindle once the training is discontinued. Both the short-term strength and time course of the adjustments could reflect mechanisms that track and calibrate for different rates of change in the stimulus or the observer (Kording et al., 2007; Shadmehr et al., 2010).

7.1. Neurobiological constraints

What places limits on the speed, endurance and size of calibrative changes in the visual system is also the ability of the underlying neural systems to modify their structure and function. What exactly these neurobiological constraints are depends on the type of plasticity involved, and there may be a complex interaction of neurobiological mechanisms (and constraints) behind every calibration of the visual system. The neural mechanisms of light and dark adaptation occurring in photoreceptors are perhaps the best understood of any calibrative process in vision, but still involve a complex interplay of processes including the switch from rods to cones with increasing light intensity, a number of distinct intracellular processes in photoreceptors (Fain et al., 2001; Pugh et al., 1999; Rieke & Rudd, 2009), and changes to post-receptoral circuits to reduce spatial integration or gain with increasing light (Chen et al., 1987). The precise constraints on the rate of adaptation depend on the time point as well as the illumination level. Contrast adaptation, occurring postreceptorally (Smirnakis et al., 1997), involves plasticity at multiple levels of the visual system, including in the retina, where the distinct contributing mechanisms have separate time courses (Baccus & Meister, 2002; Kim & Rieke, 2001). The precise synaptic and cellular mechanisms are not fully understood, but involve depression of bipolar cell output, synaptic inhibition of bipolar and ganglion cells by amacrine cells and changes in the intrinsic properties of ganglion cells

(Demb, 2008). Adaptation to other visual features such as motion and spatial frequency also involves processes at multiple stages of the visual system, in the retina Gollisch & Meister, 2010), LGN and visual cortex (Kohn, 2007). Longer term adaptation may require changes in gene expression (Maya-Vetencourt & Origlia, 2012) which means that the associated plastic changes may be both slower and more enduring (e.g. following monocular deprivation: Tropea et al., 2006). The neurobiological constraints on short term adaptation will again depend on the precise neural circuits involved (Whitmire & Stanley, 2016).

The following considers a number of general factors that may be important in limiting the form and magnitude of visual calibrations:

7.2. Age-related constraints

As reviewed in section 5, specific neurobiological constraints on plasticity are dependent on age, meaning that some forms of plasticity may be confined to or enhanced during certain 'sensitive periods' early in life. At the other end of the age spectrum, there is evidence that light and prism adaptation can be slower (Baker, 1992; Fernández-Ruiz et al., 2000; Jackson et al., 1999) though the overall strength of pattern contrast adaptation may be maintained (Elliott et al., 2007) or even increased (Elliott et al., 2012; Karas & McKendrick, 2015) in old age. Some adaptation effects (e.g. for face viewpoint) have also been found to become less selective in older adults and have been attributed to changes in the tuning of the mechanisms due to age-related declines in GABA-mediated inhibition (Wilson et al., 2011). Though more research is needed to understand the effect of ageing on the rate and strength of adaptation, considering the neurobiological constraints on calibrative changes early and late in the lifespan may lead to an improved understanding of neurobiological constraints in general.

7.3. Evolutionary constraints

Constraints on the size and speed of adaptive visual changes could contribute to their efficiency and effectiveness for achieving accurate visual representation in changing visual environments. Specifically, either during evolution or early development, the constraints on adaptation may be set to coincide with the range of changes expected in visual environments. Though this is an attractive hypothesis, research targeting it has produced mixed results. For example, studies of color constancy have investigated whether adaptation to plausible natural illuminants (blue or yellow daylight illuminants) is stronger than adaptation to artificial illuminants (green and red). Such studies have produced mixed results, with some finding in favor (Pearce et al., 2014; Weiss et al., 2017), and others against (Brainard, 1998; Delahunt & Brainard, 2004), but a recent study suggests that the time course of adaptation to achieve color constancy does not differ between natural or artificial colors of illumination (Gupta et al., 2020). Alternatively, studies of adaptation to faces suggest that the size of aftereffects is tied to the dimensions of natural variation in facial configurations (Robbins et al., 2007).

7.4. Functional constraints

The forms of plasticity are also limited by the functions it is trying to achieve. For example, maximizing information imposes specific forms of adjustments and is also a zero-sum game, for as in perceptual narrowing (Section 3.2), tuning sensitivity for some levels or attributes must come at the cost of reducing discriminative capacity for other levels. Moreover, because plasticity plays multiple roles, there are limits to which these can be collectively realized. For example, enhancing sensitivity or redundancy reduction is not always consistent with maintaining stability or constancy (Abrams et al., 2007; Webster & Mollon, 1995). Studies of how the visual system adjusts when different goals are in conflict could provide insights into the relative efficacy and importance of different functional adjustments. The pattern of adjustments could

also depend on task-demands. For example, Vergeer and Engel (2020) found that the effects of adaptation waned more quickly when it increased the difficulty of a subsequent task, implying that participants' visual systems modulated the speed of recovery from adaptation depending on task demands.

7.5. Constraints on the speed and strength of calibrative changes

The speed of calibrative change is ultimately constrained by the speed and scope of the underlying neural processes. These themselves may be constrained by the energy required to stabilize adaptive states: in basic chemosensory adaptation in *E. Coli,* there is an energy-speed-accuracy trade off (Lan et al., 2012), which may also limit adaptation in more complex neural systems (Tu & Rappel, 2018). At a systems level, the efficient coding framework has been extended to the process of adaptation itself, where optimal adaptive mechanisms must allocate resources to detection of changes in the environmental context (Fairhall et al., 2001; Młynarski & Hermundstad, 2021). Here limits on the dynamics of *adaptation itself* depend on a balance of metabolic resources and sensory performance.

Temporal contingency may also work to optimally drive visual plasticity. For example, in prism adaptation a fast temporal contingency is typically needed between motor activity and its perception: The insertion of an experimentally induced delay between the two renders adaptation both weaker and slower (Held & Durlach, 1989; Kitazawa et al., 1995). Recent evidence indicates the effect of delay may be specific to the particular processes underlying plasticity: implicit learning is attenuated by delay but explicit learning may be unaffected (Brudner et al., 2016) or even facilitated (Schween & Hegele, 2017), showing that this manipulation can isolate particular contributing mechanisms.

Via any of the constraints discussed above, it seems reasonable to suppose that the strength of adaptive visual change may be influenced by the magnitude of recalibration required. Specifically, the visual system may find it easier to recalibrate in response to small perturbations than large ones. In concordance with this idea, the magnitude of visual aftereffects often seem to be compressively related to the magnitude of the inducer (Keck et al., 1976; Klein et al., 1974; Nishida et al., 1997; Robinson & MacLeod, 2011). In contrast, the magnitude of adaptation in response to prism rotation of the visual field is linearly related to the rotation angle (Ebenholtz, 1966). However, the magnitude of change also depends on properties of the representation. For example, in population codes, the size of aftereffects and the range of stimulus levels affected by adaptation depends on the selectivity of the mechanisms, with narrower tuning predicting narrower effects. Other representations such as opponent coding predict increasing aftereffect strength with the increasing of the adaptor from the null point for the opponency, and this is one of the criteria that have been proposed for distinguishing between opponent vs multiple-channel models in face aftereffects (Rhodes et al., 2005; Webster & MacLeod, 2011).

7.6. Constraints on transformation of visual information

What constraints are there on the types of plastic transformations of visual information that the visual system can make? For positional adaptation, lateral, vertical or angular displacements are adapted to efficiently and quickly, while adaptation to a left–right or up-down reversal (reflection) of the visual field takes many days or may never occur (Harris, 1965). In color vision, adaptation to colored illumination may be almost complete (Witzel & Gegenfurtner, 2018), while adaptation to a rotated color gamut confers only subtle effects on visual judgements (Grush et al., 2015). As well as evolved or developed constraints on plasticity that depend on the plausibility of the recalibration required, and constraints ultimately depending on metabolic resources, there may be limits to the type of transformations of visual information that the cortex can perform. Gain changes such as those that underlie lateral prism adaptation (in positional space) or adaptation to colored

lenses (in color space) may be relatively easy, while reflections and nonlinear transformations may be more difficult or impossible. Adaptation to rotational transformations of position seem to be easy (Ebenholtz, 1966), but not to a rotational transformation of color through color space (Grush et al., 2015) or to a brightness reversal (Anstis, 1992).

A related issue is that there may be many stimulus properties that the visual system cannot adjust to, either because they are lost in the representation (e.g. metamers) or because the mechanisms of plasticity do not have the requisite ability to calibrate for them (so that they are metamers for states of adaptation). For example, light and contrast adaptation adjust to the mean and variance of a luminance or color distribution, but there is less evidence that they can selectively adapt to higher-order moments of the distribution (Webster, 1996). Moreover, information about different attributes is often multiplexed in the representation. For example, color-opponent cells in the retina and LGN respond to spatiotemporal variations in both luminance and color (Atick & Redlich, 1992), so that at this level color and luminance could not be calibrated independently. Similarly, if the representation of an attribute is over complete (e.g. by densely tiling a dimension, like orientation), then it may not be possible to separately calibrate even for orthogonal axes. The connection between what information different levels represent and what they can adapt to is probably very deep, and it may be more appropriate to frame it as what they "want to" adapt to. For example, in many cases plasticity corrects for changes in the mean (and in some cases the variance), and this is in order to provide a better representation of the relative variations or differences within the stimulus distribution. However this adjustment removes information about the property that is being calibrated for, while preserving the information for which the system is not adjusting.

Summary and open questions: Constraints on visual plasticity are ultimately metabolic, but there are many factors that may limit the type and range of achievable calibrations, such as age, precise neural mechanisms, evolutionary or within-lifetime tuning of plasticity to the plausible range of encountered stimulus variations, and functional trade-offs between an increase in accuracy following adaptation for one task or stimulus representation but a decrease for another. Relatively little work exists that sheds light on whether adaptation is possible to features of visual information more complex than the mean and variance along a stimulus level (e.g. higher-order moments of stimulus distributions, rotations of stimulus dimensions or conjunctions of several visual features). This is partly because studies of adaptation generally involve exposure to simple stimuli with only one or two attributes manipulated. Recent work using augmented reality has the potential to allow us to explore a greater variety of transformations of visual information (Bao & Engel, 2012; Haak et al., 2014; Schweinhart et al., 2017; Zhang et al., 2010), where stimulus attributes can be transformed across the visual scene, and longer-term adaptation studied using naturalistic visual stimuli (Bao & Engel, 2019) while allowing natural interaction with the visual world. Identifying the negative cases in which the system fails to adapt might turn out to be as important as positive cases for understanding the constraints on visual calibration.

8. Conclusions

In this review we have focused on a small sample of the remarkably diverse ways that vision adjusts to changes in the environment or observer and their experience and goals. These adjustments affect most if not all aspects of perception, and emphasize the importance of calibrations not only in shaping vision, but as a fundamental process that is closely intertwined with many of design principles that have shaped our understanding of vision. While the impacts of these calibrations are profound and manifest in many ways, they nevertheless remain poorly understood, because we do not have a clear account of the number and nature of different types of visual plasticity, or a clear roadmap for how to delineate them. An important direction for future research will therefore be to move beyond assessing different forms of calibration and

plasticity - to understand how they are related, how they interact at different stages and levels of processing and across different stimulus and developmental timescales, when and whether they serve compatible or conflicting goals, and how they are constrained and therefore limit the ways in which vision can be molded.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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