

Introduction

Visual stability

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Our vision remains stable even though the movements of our eyes, head and bodies create a motion pattern on the retina. One of the most important, yet basic, feats of the visual system is to correctly determine whether this retinal motion is owing to real movement in the world or rather our own self-movement. This problem has occupied many great thinkers, such as Descartes and Helmholtz, at least since the time of Alhazen. This theme issue brings together leading researchers from animal neurophysiology, clinical neurology, psychophysics and cognitive neuroscience to summarize the state of the art in the study of visual stability. Recently, there has been significant progress in understanding the limits of visual stability in humans and in identifying many of the brain circuits involved in maintaining a stable percept of the world. Clinical studies and new experimental methods, such as transcranial magnetic stimulation, now make it possible to test the causal role of different brain regions in creating visual stability and also allow us to measure the consequences when the mechanisms of visual stability break down.

Keywords: visual stability; spatiotopic; remapping; corollary discharge; saliency map; trans-saccadic memory

1. INTRODUCTION

The goal of perception is to yield accurate information about the objects and events in the world in order to guide our thoughts and actions. Yet each single act of sensation is limited by the extent to which our sensors and objects in the world can interact. While holding a pen, for example, the sensory input is limited to the receptors of a few fingers, leaving the majority of the surface of the pen outside of our direct sensory range. Nonetheless, we perceive a complete object, not a pen with holes where our fingers do not touch [1,2]. Similarly, our visual system actively perceives the world by pointing the fovea, the area of the retina where resolution is best, towards a single part of the scene at a time. Using fixations and saccadic eye movements to sample the environment is an old strategy, in evolutionary terms [3], but this strategy requires an elaborate system of visual processing in order to create our rich perceptual experience. One of the most basic, yet impressive feats of the visual system is to correctly tell us whether movement on the retina is owing to real motion in the world or rather to self-movement (displacement of our eyes, head or body in space).

The articles in this theme issue investigate the mechanisms by which our brains achieve visual stability: the ability to tell whether we, or rather the world is moving. This problem has occupied great thinkers, such as Descartes and Helmholtz, at least since the time of the Persian scholar Alhazen. At the

heart of this ancient riddle is a fundamental disconnection between our subjective experience (visual stability) and the discrete and discontinuous nature of the retinal input. This qualitative difference between our naive impression and our knowledge of how the retina works is, in the words of O'Regan [2], one of the 'real mysteries' of visual perception.

2. THE CHALLENGE OF VISUAL STABILITY

It may be useful here to divide the problem of visual stability into a series of smaller questions. The most basic question, of course, is how the brain takes into account the fact that the retinal image is never particularly stable. This instability is owing to the frequent occurrence of tremors, drifts, microsaccades, blinks and small movements of the head. The fact that a stabilized retinal image actually disappears from consciousness [4] suggests that the visual system has not only developed mechanisms to take small perturbations into account but may actually use retinal drift strategically. For example, small eye movements may help us to discriminate fine spatial details [5] and the optic flow from head movements may give information about depth and form-from-depth [6]. A second, related issue is how the brain deals with the retinal smear created by large movements, such as saccades and smooth pursuit eye movements, which create streaks of movement across the retina for tens of milliseconds. We do not perceive this retinal smear, and are unable to see our own saccadic eye movements in the mirror. Is the retinal motion during rapid movements actively suppressed, and if so, what are the underlying mechanisms [7,8]?

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One contribution of 11 to a Theme Issue 'Visual stability'.

Many of the articles in this theme issue focus on one specific and puzzling issue in visual stability: the problem of creating spatial and temporal continuity across movements of the eye and head. These ubiquitous movements (around three saccadic eye movements per second) create large discontinuities in the flow of information from our eyes to our brain. One challenge created by these large retinal shifts is to spatially match the same object across separate fixations. Spatial continuity across saccades is important both for guiding *action* and for ensuring that subjective experience of the world is stable and continuous (transsaccadic perception). One basic question is whether perception and action have access to the same spatial representations, or, to put it differently, whether they access spatial representation at the same level. The motor system requires accurate, online analysis of the position of objects with respect to the motor effector in real time [9]. In contrast, visual updating in perception can be described as the ability to match an object across separate glances at a more coarse level (e.g. ‘this is the same object’). Conscious perception of complex events is likely to occur at a higher level of the hierarchy of time-scales in the brain, compared with early sensory processing and motor control (for review, see [10]). A number of studies, using different paradigms, suggest that action and perception access different levels of spatial representation (for review, see [11]). For example, people tend to perceptually mis-localize the location of a briefly flashed stimulus around the time of a saccade (a phenomenon known as perisaccadic mis-localization [12,13]). In contrast, pointing to the target remains veridical [13]. While this finding is consistent with the claim that spatial stability is predominantly a feature of the motor system [9], such perception–action dissociations are always problematic to interpret (for reviews, see [11,14]).

Visual constancy can also be viewed as a *temporal* phenomenon: objects appear to be continuously present over time. Yet the duration of external events are typically longer than that of a single sensory ‘sample’ such as a fixation. Although movements of the eyes, head and body disrupt our steady access to these objects and events, the stream of consciousness continues smoothly across these sensory disruptions. This is an amazing feat, given that each saccadic eye movement creates a temporal disruption in the flow of information from the retina to higher perceptual areas. The motor smear on the retina during the saccade is suppressed, making us largely unaware of the retinal stimulation during this time period [7,8]. In addition, each saccade requires the visual system to ‘re-perceive’ the information from a new fixation. In laboratory conditions, it takes around 150 ms for neurons in the visual system to begin to recognize and categorize a newly appearing visual input [15]. If real-world perception were to follow this same pattern, then for a considerable time after each saccade we would still be perceiving the old retinal input, rather than the information currently on the retina. In fact, we should have to wait around 150 ms to ‘see’ what is in front of our eyes after each saccade, by which time the oculomotor system has already begun to

choose the next saccadic target [3]. One possibility is that this delay is relatively unimportant, which would be the case if high level areas involved in perception operate with a constant delay (ie. if we always perceive the past). However, there is growing evidence for a second hypothesis by which temporal continuity is *actively* created. At the neurophysiological level, there is evidence that brain predicts what will be on the retina after the saccade (see §2). One possible function of this prediction could be to minimize the delay period during which the brain is caught in the retinal past. Support for this idea comes from a number of studies which have reported that temporal perception is distorted around the time of saccades [8,16–19]. Specifically, perceived time seems to shift forward, towards the beginning of the new fixation, essentially compressing the time immediately before and during the saccadic eye movement [8]. One possible interpretation is that space and time are inextricably linked in the brain, with the pattern of strange perceptual effects reported for stimuli flashed around the time of saccades reflecting a *spatio-temporal transformation* between fixations [8].

3. NEURAL MECHANISMS OF VISUAL STABILITY: REMAPPING AND SPATIOTOPY

The study of visual stability presents us with the challenge of linking neurophysiological, behavioural and clinical results. In many ways, neurophysiology has led the way in re-framing the issue of visual stability in terms of dynamic changes in the receptive fields of neurons (see [20,21]). The change in the spatial profile of the receptive fields of neurons around the time of saccades is called ‘remapping’ [20–22], since the spatial map of the receptive field is temporarily altered. The neurophysiological evidence for remapping is discussed in detail in several of the reviews in this theme issue [20,21,23]. A number of studies which explore the pattern of remapping neurons in the brain, including the proportion of neurons that show remapping in different brain regions and the potential pathways that underlie remapping, are beginning to shed light on this process. However, there is much that is not known about remapping. Previous research has been limited by technical issues (such as the difficulty of recording from multiple neurons simultaneously) as well as methodological constraints (a small number of stimulus and task parameters which have been used). As Hamker *et al.* point out [24], more work is needed to constrain the set of possible models which can account for the pattern of receptive field changes reported in the literature.

It is also important to note the heterogeneous nature of remapping, which includes at least three different patterns of receptive field changes. *Predictive remapping* describes a neuron which responds to a stimulus in its ‘future receptive field’ (where the receptive field will be after the saccade) faster than its normal latency or, in some cases, even before the saccadic eye movement occurs. *Memory remapping* occurs when neural responses after the saccade reflect the stimuli that had been present in their pre-saccadic receptive field. Finally, there are neurons the receptive

fields of which seem to spatially expand or contract, or even split into multiple zones. An important question for future work is to understand whether the heterogeneous pattern of remapping reflects a single spatial–temporal transformation or, rather, multiple independent mechanisms that serve different aspects of visual stability (as suggested, for example, in this issue in the Discussion section of [25]). As reviewed by Hamker *et al.*, different computational models of visual stability incorporate varying types of dynamic receptive fields. Remapping in the frontal eye fields (FEF), for example, has been linked to the development of a predictive map of the expected consequences of the saccade [21,26] while remapping in the posterior parietal cortex has been linked to post-saccadic updating of visual working memory [27]. Two of the articles in this special issue [20,21] review the recent attempts to directly link remapping circuits to behaviour by disrupting the flow of information within the primate brain. These pioneering studies are a first step in understanding the how and why of remapping.

At a more fundamental level, the interpretation of remapping activity ties into a larger question about the nature of oculocentric/retinotopic coordinate frames in the visual system. Retinotopy has been fundamental to the development of vision science and is widely accepted to form the native coordinate frame of at least the early visual processing areas. When it comes to spatial maps in frontal and parietal cortex, however, there is a debate over whether remapping describes a transient change in an otherwise stably retinotopic map or, rather, that receptive fields in these areas are fundamentally dynamic. Multiple coordinate frames coexist simultaneously in sensory and motor areas (for reviews, see [28,29]). Examples include head-centred, hand-centred or even face-centred coordinates. In order to respond to an audio-visual stimulus, for example, it must be initially encoded in both head-centred auditory space and in oculocentric visual coordinates. Then, to guide behaviour to that stimulus, such as a reaching movement, the spatial location of the stimulus would need to be translated into hand-centred coordinates. This continuous transformation between multiple coordinate systems is thought to involve ‘gain fields’ [30,31]. These gain fields might play a role in visual stability by updating and predicting movement plans with respect to sensory stimulation, and the interplay between these different coordinate frames would tend to lead to dynamic receptive fields.

In addition, many neurons in visual processing areas are influenced by the position of the eye (gaze modulation [32,33]). From these two sources of information (gaze + retinal coordinates), it is straightforward to transform the visually evoked response into head-centred coordinates [34]. Such non-oculocentric visual representations (typically grouped under the term ‘spatiotopic’) are interesting for at least two reasons. First, these representations could help to integrate information across separate fixations. Several of the articles in this theme issue explore the potential role of allocentric and spatiotopic reference frames in supporting visual integration and visual memory updating [8,35,36]. Second, non-oculocentric

representations might be important for sensorimotor and multisensory interactions that underlie *multimodal* properties such as visuo-haptic shape [37,38] and audio-visual movement [39,40]. Indeed, there is a suggestive parallel between the increase in the proportion of neurons that show multisensory interactions for higher levels of sensory processing (for review, see [41]) and the similar increase in neurons showing dynamic receptive field changes at higher stages of visual processing [42,43]. If areas at the higher levels of the hierarchy need to incorporate information from multiple modalities with motor signals, and if these areas are active over longer time-scales that span multiple fixations [10], then it would not be surprising that the activity in these areas would reflect information from other senses and from the motor system.

At present, ‘spatiotopy’ remains useful as an umbrella term to describe a large group of non-retinotopic effects. As a case in point, consider the finding that inhibition of return—slower reaction times to stimuli presented at a previously cued position—occurs in spatiotopic coordinates across saccades [44–46]. This spatiotopic effect is eliminated in patients with parietal lobe lesions [45] and is disrupted by transcranial magnetic stimulation (TMS) over right posterior parietal cortex [46]. Thus, the discovery of a spatiotopic behavioural effect was the first step in investigating neural mechanisms underlying potential neural correlates of visual stability. At the same time, these and other analogous effects are not really ‘spatiotopic’ in the strongest sense. True space-defined neurons which code for a single, specific location in the world would continue to do so even after the subject stands up and walks to the other side of the room (analogous to ‘place cells’ in the rat hippocampus). However, it is clear that such a fixed spatiotopy, in which a neuron’s receptive field is tied to a particular location in the world, is not computationally tractable. Instead, what is meant, in practice, is either a non-retinotopic, egocentric frame (head-centred, body-centred) or an allocentric reference frame based on the location of a small set of salient reference objects. Evidence for the importance of allocentric reference frames comes from studies showing failures to detect spatial displacements of stimuli that are surreptitiously moved during the saccadic eye movement [47]. Spatial landmarks, including the saccadic target but also bystander objects, influence the detection of these displacements [47], showing that the perception of motion (versus stability) depends also on external coordinates. A third possibility is that a spatiotopic effect is temporary and spans a short time after saccadic remapping. It will be important to distinguish between these three types of spatiotopy in future studies to see which, if any, of these mechanisms underlie visual stability.

In real-world situations, visual stability is important for keeping track of objects, not just spatial localizations. Grasping or identifying an object, for example, depends on the shape of the object. Might what we call spatiotopy actually be a case of ‘object-otopy’ or, more generally, of event perception [43,48]? For example, consider a simple event such

as a two-frame motion stimulus, in which a stimulus changes its location or shape in the second frame. This apparent motion event is perceived, across the saccade, in external spatiotopic coordinates rather than in retinal coordinates [49–51]. In this motion task, as in real life, the challenge for the brain is not to remap all of space but simply to keep track of a single object which is undergoing a transformation as part of a temporal event. This capacity to perceive events across saccades has received much less attention than studies of single stimuli which appear or disappear around the time of saccades. In recent years, however, a number of studies have begun to consider the perception of multi-stimulus events across a saccade, and have shown that perception of the post-saccadic stimulus can be influenced by the pre-saccadic view of the item [52–57].

In addition, a number of interesting effects have been reported which are neither spatiotopic nor retinotopic in nature [8,58,59]. For example, we recently tested shape discrimination for a brief target that was followed by a mask. We varied the time of target presentation with respect to the saccade in order to test whether predictive remapping might influence the processing of the target stimulus. We found that the discrimination of the target stimulus increased dramatically when it was presented shortly before a saccade [59]. In other words, the intention to make a saccadic eye movement ‘unmasked’ the target, even when both target and mask were shown in the same retinal position. Interestingly, the target stimulus was often (but not always) spatially displaced as well, such that it was perceived at a location where it was never shown on either the retina or on the screen. In contrast, the mask, which was shown second and for a longer duration, appeared to remain perfectly stable on the screen across the saccade. These and other similar results illustrate how the brain actively creates an interpretation of stimuli on the retina, in order to construct visual stability, and does so in a way which is not strictly tied to either retinal or spatial coordinates.

4. THE ROLE OF SELECTIVE ATTENTION IN VISUAL STABILITY

Selective attention can dramatically alter the way in which a visual stimulus is processed. The potential role of attention in creating visual stability is a common thread across many of the articles in this theme issue, and it is the focus of the review by Mathot & Theeuwes [60]. The most basic way that attention influences visual stability is by limiting the number of items that are fully processed and remembered [43,60]. After all, visual instability is perceived only when our expectation to see a particular object in a particular place is violated. Thus, failure to remember an object removes the need to spatially update that object. Does that suggest that the best strategy is simply to forget everything each time we move our eyes [61]? As Tatler & Land [35] point out, this scheme would not actually lead to visual stability, nor would it allow us to be so efficient in realworld environments. For example, visual stability

when making a cup of tea seems to depend on a representation of the scene that allows us to quickly locate and grasp the teacup that we had seen several seconds earlier. In fact, we are remarkably efficient in the use of eye and body movements in natural tasks. This ability to keep track of the task-relevant items in the scene, which requires updating of transsaccadic memory, would seem to be an important component of our subjective experience of visual stability. Moreover, the ‘gist’ of a scene, both in terms of its semantic meaning and the global statistics of the environment [62] may play a role in visual stability, since the gist is highly robust to eye and body movements. Thus, both the details (object identities and location) and the ‘non-details’ (the gist) of the scene provide reassurance that our environment is stable across self-movement [35,43,63].

A second potential link between attention and visual stability comes from the proposal that there is a ‘saliency map’ (also called an attention priority map [64]) which is updated across saccades. The saliency map model, originally coming from computational models of attention and from neurophysiological studies of attention, provides a common spatial framework for perception, attention and action [65]. Perhaps the best-studied saliency map is in the lateral intraparietal area (LIP), where the response of neurons to a stimulus in the receptive field depends on the bottom-up saliency of the stimulus and its task relevance (for review, see [65]). Critically, remapping in LIP occurs only when there is a salient item in the receptive field [66]. Thus, saliency maps in LIP might play a vital role in the spatial updating of task-relevant items across saccades. If so, then the updating of saliency maps would need to be synchronized, both within the different parietal regions (encoding space in different reference frames and providing output to different effectors) and with saliency maps in other sensory and motor areas. In this way, visual stability can be viewed as the ability to maintain a limited number of object pointers, which link spatial and visual information, across saccades [43,48,53].

In a certain sense, attention itself is remapped across saccades, as illustrated by the studies cited above showing inhibition of return in spatiotopic coordinates. But why bother to remap attention to a blank area of the screen? One reason may be that attention reflects our expectations about future events. Many of the studies which claim to measure the influence of attentional cueing are confounded with predictions about the future location or features of task-relevant objects. In addition to showing spatiotopic effects, attention (as measured by cued priming) predictively remaps prior to the saccade [60]. Thus, attention experiments could be a potentially useful method for studying remapping and spatiotopy. At present, however, most of these studies have looked at relatively small reaction time differences. Given the availability of more sophisticated tools in the vision science repertoire to measure spatial attention [67], future studies using other measures may be able to shed more light on the underlying mechanisms of transsaccadic attention.

It has recently been suggested by Cavanagh *et al.* that the remapping of attention is, by itself, sufficient to explain all aspects of visual stability [50]. Certainly, spatial updating of object location is an important aspect of perceived stability, and this likely occurs only for attended items. But what is new in Cavanagh *et al.*'s proposal is to challenge the entire idea of dynamic receptive fields by suggesting that attention moves but receptive fields stay fixed. It does seem difficult, initially, to reconcile their proposal with all of the research showing receptive field shifts (see reviews in [20,21,23]). Another departure in their proposal is the claim that attentional pointers represent only a spatial location (in retinal coordinates), not objects or their features. Objects—spatiotemporally coherent collections of features such as shape, colour and texture—are central to cognition and action. Is it true that only spatial pointers, without any features, are remapped? Well, the existence of remapping in visual areas (for review, see [43]), as well as the encoding of object features in areas like FEF and LIP [68–70], suggests that the brain should be able to remap object features and not just a spatial pointer. Thus, there are plausible neural mechanisms for feature-remapping at the level of medium-level (colour, shape) and high-level (object identity) properties (but probably not low-level ‘snapshots’ or pixel-like representations such as would be found in areas like V1 [8,43]). This raises the question of why the brain would expend so much energy altering neural activity in feature processing areas if these neurons play no role in visual stability. One last concern with their proposal is that it replaces concepts like ‘saliency map’ or ‘dynamic receptive fields’, which have specific operational definitions, with ‘attention’—a term which is more poorly (and more broadly) defined. This would seem to reduce explanatory power, not increase it.

In sum, given the close link between attention and the oculomotor system, and between parietal saliency maps (and analogous maps in FEF and superior colliculus) and remapping, it is clear that attention does play a role in visual stability. In addition to the factors mentioned above, it has been suggested that the gain fields that modulate neural firing based on gaze direction, in order to combine retinotopic and head-centred information, might be modulated by attention [8]. But more generally attention is likely to be important for maintaining active representations of objects and events across eye and body movements [48]. The visual system is able to integrate information about complex events and complex scenes over a period of seconds, during which time people typically make multiple saccades. Attention probably influences the ability of the brain to keep track of these events and integrate information over time [71,72]. Transsaccadic integration and transsaccadic memory may only be possible if the stimulus is attended and actively maintained across the saccade.

5. A VISUAL STABILITY NETWORK

Given the number of different potential mechanisms for visual stability described in this theme issue, it

might be useful to postulate the existence of a visual stability *network*. Such a network would involve overlapping mechanisms that, either working in parallel or redundantly, accurately guide our behaviour and create our impression of a stable world. At the core of any visual stability network would be the oculomotor control areas, which of course also play a critical role in selective attention. Regions in posterior parietal cortex (LIP, in monkey), the frontal eye fields and the superior colliculus work together in guiding eye movements and, not surprisingly, these areas show remapping of oculocentric receptive fields [20,21]. In humans, evidence from TMS and clinical studies (reviewed in [25,27]) suggests that the right posterior parietal cortex may play a special role in maintaining spatial constancy (see also [73]). Lesions to the thalamus can also lead to failures of visual stability, in which self-movement and external, object movement are confounded [74]. Moreover, as Prime *et al.* point out [53], other areas involved in spatial memory (such as dorsolateral prefrontal cortex) may play an as-yet unexplored role in maintaining visual stability across self-movement.

There is also evidence, both from single-cell recording in primates and functional MRI (fMRI) in humans, for dynamic receptive fields in the visual system itself (see [20,23]). One possibility is that the well-established connection from the FEF to visual areas such as V4 [75,76] plays a role in predictive remapping of visual neurons. Likewise, as Prime *et al.* [27] point out, the link between visuo-spatial working memory areas would need to be maintained across saccades. There is growing evidence that visual processing areas play an important role in maintaining details in visual memory [77]. The finding that saccades typically have little or no effect on visual-spatial memory (for review, see [27]) suggests that these visual-spatial links are maintained across saccades—perhaps through predictive or post-saccadic memory remapping. A major challenge for the brain is to link ‘what’ and ‘where’ in visual-spatial memory, and so it would seem that one goal of spatial updating is to maintain the link between the so-called ‘ventral stream’ areas (object recognition areas in temporal cortex) and the more dorsal regions (space/action maps in parietal regions). Prime *et al.* [27] argue that feed-forward or parallel connections between regions may not be sufficient to explain this complex visual-spatial updating process. Instead, they suggest that re-entrant pathways from frontal areas to visual areas may be necessary to continuously maintain the link between ‘what’ and ‘where’ information (see also [20] for a discussion of candidate remapping circuits).

In humans, the visual stability network has been examined mainly through fMRI, TMS and clinical studies. Any attempt to systematize these studies into a coherent picture, however, raises the basic question of how to define the neural correlates of visual stability in the brain. Consider, for example, studies showing the wholesale remapping of activity across hemispheres after a large horizontal saccade [20,23,78]. These results are certainly evocative, but they suggest a ‘cut-and-paste’ version of predictive remapping that

may not be the only (or indeed the most important) part of the visual stability network. Other potential mechanisms of visual stability (including changes in gain fields, shifts in object pointers, spatiotopic maps and post-saccadic memory remapping) would probably involve changes in neural activity *within* the same hemisphere, making them invisible in most previous studies of remapping in humans.

In addition to areas of the oculomotor and visual system, Tatler & Land [35] argue for the importance of spatial memory systems in hippocampus and medial temporal cortex in updating across self-movement. At present, however, there have been few studies that have examined the influence of eye and body movements on neural activity in these regions [79–81]. It will be important, in future work, to examine how scene representations are updated, and how updating in scene maps might interact with retinotopic processing in early visual areas. In the case of self-movement, there is evidence that updating visual–spatial memory for objects in the scene involves parietal regions such as the precuneus [82]. This question of how to update spatial maps for navigation (in hippocampus, for example) returns us again to the basic question raised earlier about how ‘what’ and ‘where’ are linked in the brain, and how those links are updated across saccades.

6. CONCLUSIONS AND FUTURE DIRECTIONS

The aim of this theme issue has been to review the current state of the art in neurophysiology, psychophysics, cognitive neuroscience and clinical neuropsychology. Bringing together this interdisciplinary knowledge helps us to provide a snapshot of research at this time, but also points out future directions for research. The articles in this theme issue provide a myriad of suggestions for future work, of which a few will be mentioned here.

As many of the articles show, progress is being made in investigating the causal role of different brain regions in creating visual stability. Reviews of studies with clinical patients [25] and with TMS [27] show how the use of well-designed behavioural tests can give insight into the mechanisms of visual stability. At the same time, the presence of redundant circuits [20] might mask the functional role of individual brain regions. Thus, it is important to use carefully designed methods that get at the heart of visual stability, beyond the usual clinical measures. For example, the fact that a patient with focal damage to parietal cortex shows a deficit in visual search could be based on a number of different underlying mechanisms, such as a failure of spatial updating, disordered spatial integration, difficulty at predicting the consequences of self-movement, or even because of damage to the spatial maps themselves.

As described above, some mechanisms that may be part of a visual stability network are beginning to be identified. Several of the authors in this special issue offer hypotheses about the specific role of different cortical and subcortical regions in visual stability based on connectivity, lesion studies, or neuroimaging. At the same time, computational models of visual

stability will play an important role in designing future neuroimaging and neurophysiology studies (see [24]). To better constrain theories and models of remapping, more complex stimuli and events will need to be tested, as well as multiple simultaneous recording sites. In studying humans, future work would benefit by using more complex stimuli/events and by using methods that map out both the spatial and temporal pattern of neural activity.

One basic challenge will be to build on our understanding of ‘passive vision’ during laboratory conditions (stimuli briefly presented on a flat screen during maintained fixation) by including more complex spatio-temporal events as stimuli and by allowing self-movement in laboratory studies. As several authors in this issue argue, visual perception takes into account both sensory input and planned actions. There is a growing list of studies that examine how perception can integrate information across separate fixations [52–57]. There is certainly more work to be done in creating a list of ‘retinotopic’ versus ‘non-retinotopic’ perceptual effects. But it is also important to consider what conditions and context tend to increase our sensitivity to finding such effects.

To date, almost all of our knowledge about visual stability comes from studies in which *visual stability is violated*: i.e. briefly flashing stimuli appearing without warning on a flat computer screen. In contrast, visual stability in the real world is found in a context of three-dimensional, multisensory objects in dynamic environments. The stability of objects in the real world is based on the laws of physics, which order the environment in which the visual system evolved and which make it highly unlikely for items to appear or disappear during a saccadic eye movement. The mechanisms of visual stability have evolved to deal with real-world, stable objects. It is certainly plausible that the brain would react differently to stimuli that are actually stable (such as a coffee cup on a table) than to the sudden appearance of a flashed grating. This is one of many issues that will need to be addressed in future work.

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