Trans-saccadic perception

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A basic question in cognition is how visual information obtained in separate glances can produce a stable, continuous percept. Previous explanations have included theories such as integration in a trans-saccadic buffer or storage in visual memory, or even that perception begins anew with each fixation. Converging evidence from primate neurophysiology, human psychophysics and neuroimaging indicate an additional explanation: the intention to make a saccadic eye movement leads to a fundamental alteration in visual processing itself before and after the saccadic eye movement. We outline five principles of 'trans-saccadic perception' that could help to explain how it is possible – despite discrete sensory input and limited memory – that conscious perception across saccades seems smooth and predictable.

The problem of trans-saccadic perception

Real-world perception is fundamentally trans-saccadic. Most complex activities, such as conversing face-to-face, walking down a busy street or reading the newspaper require a series of eye fixations separated by ballistic eye movements known as saccades. The temporally and spatially discontinuous nature of visual sensory input creates a series of incredible challenges for visual cognition. It is crucial, for example, to keep track of the location of attended objects across saccades to maintain spatial constancy (Box 1). Smooth and continuous perception is also challenged by the relative sluggishness of the process by which information from the retina begins to influence cognition and behavior. If one estimates the time it takes for the first pass of visual processing to go from the retina to object recognition areas to be around 100 ms [1], then multiplying that figure by the approximate 150 000 saccades made daily [2] would yield around four hours each day during which our visual perception does not accurately reflect what is right in front of our eyes. A third question is whether visual information about the same object is combined across separate glances. If not, then the visual system would essentially need to 're-perceive' objects after each saccade and would lose any benefit obtained from integrating information across glances.

Three main theoretical positions have emerged from studies which have investigated the persistence of visual representations across eye movements. First, according to theories of 'trans-saccadic integration', perception across eye movements is akin to superimposing two patterns from the separate fixations [3,4]. It is now widely accepted that patterns are not fused across saccades [5,6], and such

pattern fusion would be ill advised under conditions in which the position or orientation of the object changes with respect to the viewer over time, as illustrated in Figure 1.

A second theory focuses on a general purpose 'visual short-term memory', rather than any special saccade-related mechanism [6]. This working memory capacity is typically measured by our ability to detect changes in two patterns separated by a blank delay of up to a few seconds [6]. Memory capacity is typically estimated at around 3–4 complete objects, although there is currently debate over whether demands to remember highly precise object details might further limit this capacity [7–10].

By contrast, a third group of theories suggests that little or no visual information is maintained across saccades [11,12]. Evidence for this point of view comes from studies of change detection with complex scenes, when such changes occur during eye movements or simulated eye movements. At the least, these studies demonstrate strict limits in our ability to consciously detect changes to stimuli unless those objects are directly attended both before and after the saccade.

Although each of these explanations capture certain features of cognition across saccades, we think that there is an additional, crucial aspect of trans-saccadic perception that is missing from these accounts. Converging evidence from human psychophysics, functional neuroimaging and primate neurophysiology indicates a new theoretical framework for understanding trans-saccadic perception. According to this framework, the visual system combines predictive and useful information across saccades, while also discarding local details which would not, in any case, be consistent across separate views. Here, we describe five principles of trans-saccadic perception that have emerged from recent research and discuss the implications of these recent discoveries for theories of visual cognition.

Principle 1: the dynamic receptive field

In the case of visual processing, it has been assumed that receptive fields are constant, both in terms of stimulus and spatial selectivity, and that any particular neuron can be defined based on the retinal location and visual properties of its preferred stimulus. This supposedly fixed architecture, however, has turned out to be surprisingly flexible. As first described in the lateral intraparietal area LIP of the cortex, most neurons have access to information outside the classical receptive field [13,14]. This spatial flexibility is observed when the animal makes an eye movement.

Two aspects of dynamic receptive fields are relevant for trans-saccadic perception. First is remapping of memory traces of salient stimuli. In brief, the process of remapping is hypothesized to work as follows [15]. When a stimulus

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Box 1. Spatial constancy across shifts in gaze

Visual processing takes place in retinal coordinates, and these coordinates shift dramatically with each saccadic eye movement. This raises an important question: how is it possible to be sure that a particular object that is visible after a saccade is the same object – in the same place – that was visible before the saccade? Matching an object across the saccade is also crucial for guiding motor actions such as grasping. Given the importance of spatial constancy, much of the work in both psychology and neuroscience on trans-saccadic perception has focused on this question (for reviews, see Refs [43,76,77]). Although the debate over the mechanisms involved in spatial constancy is beyond the scope of this review, it is worth noting two interesting phenomena that have emerged from studies of spatial constancy across saccades. First, it has been found that our ability to detect small spatial displacements of a target is 'suppressed' by saccades [78]. However, the presence of a blank gap after the saccade and before the object reappears greatly increases sensitivity to the displacement, indicating that the spatial information was actually available but, at some level, ignored by the brain.

Second, stimuli are often mis-localized when they are briefly flashed immediately before or after the saccade [79–81]. Although mis-localization does occur around the time of saccades, it is a matter of current debate whether this misperception is directly related to remapping [82–86]. The framework for trans-saccadic perception described here does not explicitly favor any of the theories of mis-localization, focusing instead on the potential role of remapping in the perception of object features such as form, color or movement. Yet, it is clear that a complete theory of trans-saccadic perception will need to account for all of these intriguing phenomena.

appears, a set of neurons whose receptive fields cover the stimulus location respond to it. When the eyes move, a copy or corollary discharge of the eye movement command causes the stored representation of the stimulus to be transferred. The neurons that initially encoded the stimulus are thought to transfer their activity to neurons whose receptive fields will encompass the stimulus location after the eye movement. This phenomenon is called 'remapping' to emphasize that visual information is being shifted from the coordinates of the initial eye position to the coordinates of the next eye position. Remapping of memory traces is remarkable because neurons are seen to respond to stimuli that never appeared in the classical receptive field.

Figure 1. Combining separate 'snapshots' of the world. As noted by the Persian scientist Alhazen (965–1039 AD), even the seemingly simple act of visually examining an object involves multiple eye movements, and each of these changes in gaze dramatically alter the projection of the object on the retina. One challenge for theories of trans-saccadic cognition is the fact that objects move and rotate with respect to the viewer, as illustrated in this photo collage by Nathalie Pozzi (Casagrande and Rintala: Installation 1: 2001) – although of course our perception is not like this series of superimposed snapshots. The basic problem of representing a face as it turns towards or away from the viewer is also powerfully illustrated by the photo collages of David Hockney and the multiple-view paintings of faces by Pablo Picasso. Image reproduced with permission of the copyright holder from http://commons.wikimedia.org/wiki/Image:Installation_1_to_2001_collage.jpg.

Although the neural mechanisms that underlie spatial remapping are not yet fully understood (Box 2), progress has been made in delineating the network of brain areas involved. In addition to area LIP, remapping is observed in the frontal eye fields [16,17], extrastriate visual cortex [18] and the superior colliculus [19]. The superior colliculus is one source of the corollary discharge signal that triggers remapping [20]. This copy of the motor command is relayed through the thalamus to the frontal eye fields, where it has an impact on both perception and accuracy of oculomotor behavior (for a review see Ref. [21]). The pathways that transmit corollary discharge signals to parietal and visual cortex are under investigation. Remapping of visual memory traces can occur for saccades of any direction [22] and magnitude [18]. Crucially, remapping indicates that individual neurons have potential access to information located anywhere in the visual field. A challenge for the future is to determine what kind of connectivity and mechanism could produce these dynamic receptive fields.

A second aspect of remapping is shifting the receptive field in anticipation of the saccade (Figure 2). There is an appreciable interval between the time when the decision is made to move the eyes and the moment when the eye muscles are activated (this is called the 'saccadic latency', and averages around 200 ms depending on the subject and experimental conditions). During this interval, a neuron can be described as having both a normal, current receptive field and an additional 'future' receptive field, namely the screen location where the receptive field will be after the intended saccade. If receptive fields were static, neurons could respond to an object placed at the future receptive field only after the saccade had been completed, and then only after a normal visual latency. The surprising discovery, illustrated in Figure 2, was that many parietal neurons respond to a stimulus in the future receptive field at less than a visual latency after a saccade, or even before saccade onset. This is called predictive remapping and it tells us that the visual system anticipates what the world will look like after a saccade. In the example shown, remapping occurs before the onset of the saccade: activity
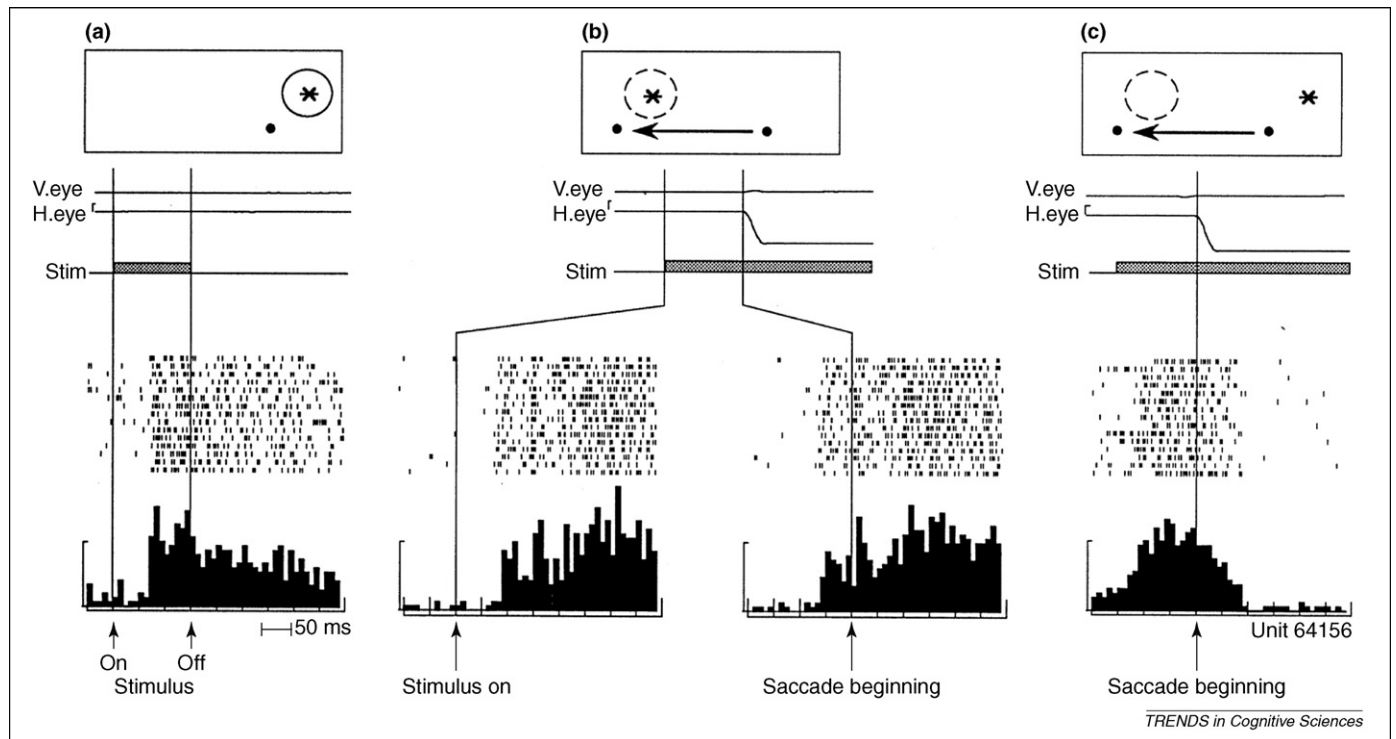

Figure 2. Remapping of visual activity in a single neuron in the lateral intraparietal (LIP) area. Diagrams in each panel show the fixation point (dot), the visual stimulus (star), the location of the receptive field at the end of a single trial (dashed circle) and the saccadic eye movement (arrow). Time lines below show horizontal and vertical eye position and the onset and offset of the visual stimulus. Rasters and histograms are aligned on the event indicated by the long vertical line. **(a)** While the monkey fixates, a stimulus appears in the receptive field. The neuron continues to respond even after the stimulus has been extinguished. **(b)** In a saccade task, the monkey fixates and a stimulus is presented. The visual stimulus and the saccade target appear simultaneously. The stimulus is initially outside of the receptive field. For direct comparison with (a), the data on the left of (b) are aligned on stimulus appearance. The latency of the visual response to this stimulus in the future receptive field is similar to that for a stimulus in the current receptive field. On the right, the same data are aligned on the beginning of the saccade. The neuronal response to a stimulus in the future receptive field begins even before the eyes begin to move. **(c)** Neural activity when a saccade shifts the receptive field away from the stimulated location. This eye movement produces a sharp truncation of activity, in contrast to the slow decay of activity after stimulus offset shown in (a). Adapted, with permission, from Ref. [13].

at the future receptive field increases before the saccade begins. Responsiveness at the original receptive field simultaneously decreases. This truncation of visual responsiveness is essential to maintenance of a spatially constant representation of attended stimuli and locations. Recent work has revealed that visual neurons dynamically change their receptive fields at various times relative to the saccade and exhibit responsiveness to multiple locations (both the current and the future receptive field) at the time of the saccade [18,23].

Remapping might have multiple roles in perception and action. First, remapping provides the 'sensory' signal necessary for making sequences of memory-guided saccades [24–27]. Second, remapping contributes to guiding motor actions such as grasping [28–30]. Third, remapping might be involved in spatial localization (Box 1). Neurophysiological studies to date have focused on the role of remapping in keeping track of object location across saccades. A question for the future is whether and how remapping might contribute to feature analysis. Finally, remapping could be related to visual memory [31,32]. Evidence for the last possibility comes from a recent study by Prime and colleagues [32] who applied trans-cranial magnetic stimulation (TMS) over posterior parietal cortex during a working memory task. They found that performance on the memory task was disrupted by TMS when participants made a saccade between stimulus presentation and test, indicating that trans-saccadic memory is not a general purpose store but instead is influenced by saccades.

Several computational models that simulate human behavior in spatial localization tasks include aspects of remapping [33–36]. It has also been suggested that disordered remapping could have a role in spatial neglect [37–40]. In summary, remapping is considered to be one of the mechanisms that might contribute to stable perception and spatially accurate behavior (see Ref. [41] for a review).

Principle 2: the role of prediction

The second principle is that successful combination of information from separate glances depends upon the ability to anticipate the outcome of a saccade. As stated earlier, remapping can begin before the onset of the saccade. Several studies have shown that perception can also be influenced by the intention to make a saccade (for reviews, see Refs [42,43]). Recent evidence for perceptual consequences of predictive remapping comes from a study of adaptation aftereffects [44]. It was found that the tilt aftereffect was transferred to the future fixation position before the onset of the saccade (Figure 3a). The magnitude and timing of the pre-saccadic transfer of the aftereffect followed the trends predicted by neurophysiological studies of remapping in visual neurons (Figure 3b). Thus, the transfer of the aftereffect provides a perceptual correlate of predictive remapping in neurons. Moreover, a recent study using electroencephalography (EEG) has also found predictive changes in neural activity in the ipsilateral hemisphere consistent with pre-saccadic remapping [45] (Figure 3c). Although these results are consistent with the idea that dynamic receptive fields might have a role in remapping visual feature information, further work is
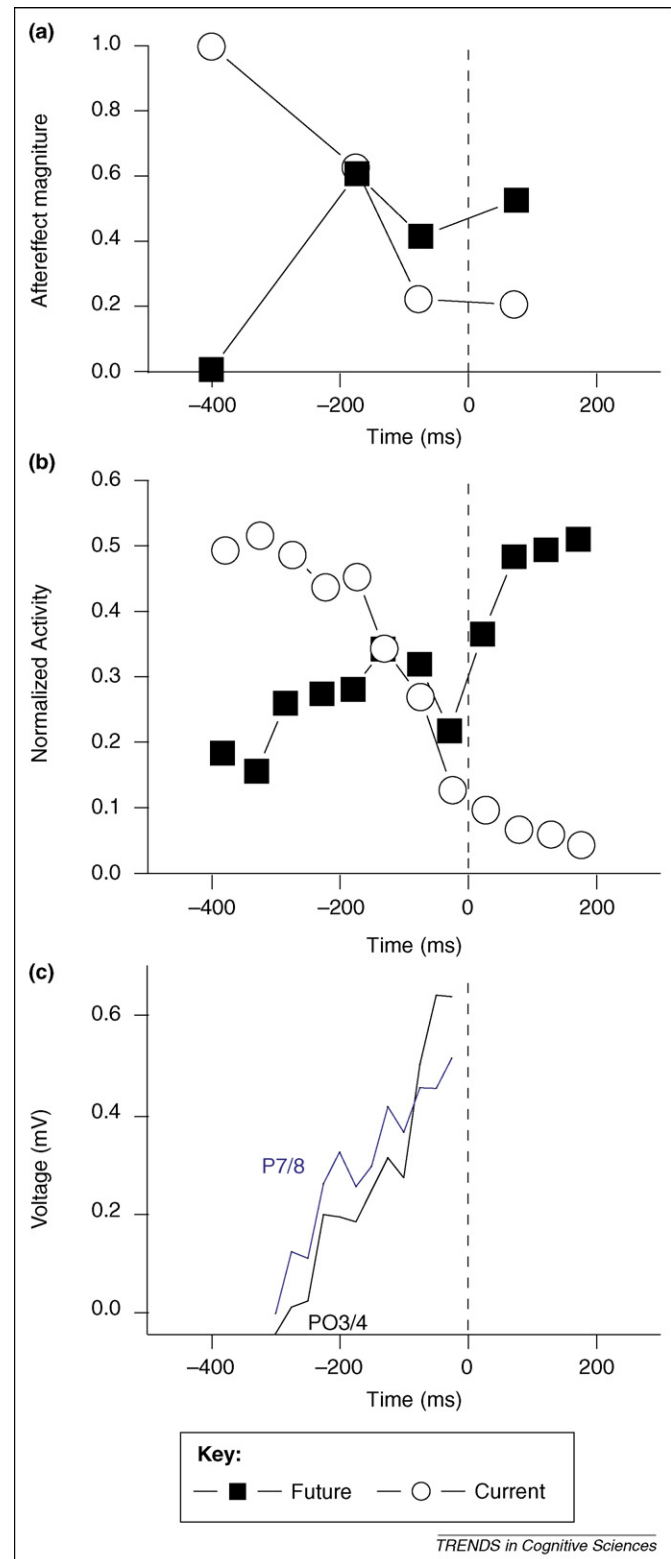

Figure 3. Evidence for predictive remapping. **(a)** Magnitude of the tilt aftereffect found at either the future or current fixation position (data replotted from Ref. [44]). **(b)** Average single neuron firing to stimuli presented in the current and future receptive field as a function of presentation time with respect to saccade onset (data replotted from Ref. [23]). **(c)** Increase in activity in ipsilateral electrodes P7 and P8 (combined) and PO3 and PO4 (combined) on trials in which the stimulus would change hemifields across the saccade, compared to trials in which the stimulus would remain in the same hemifield after the saccade. Here, ipsilateral activity represents activity in the future receptive fields because the location of the stimulus will switch hemifields across saccades (data replotted from Ref. [45]).

necessary to explore this hypothesis at the single neuron level.

Prediction is a mainstay of cognition and motor planning, ranging from the anticipatory opening of a hand for grasping (for a review see Ref. [46]) to music perception [47], spoken language [48,49] or predicting the consequences of our own behavior and that of others [50,51]. Prediction in visual perception can be thought of as connecting two halves of a broken line that is separated by a discontinuity in space and time. The method that would produce the smallest discontinuity would be to extrapolate the line from both ends of the gap. The most commonly used algorithms for video compression (MPEG, motion picture experts group), for example, uses forward and backward prediction to fill in gaps in the sampling process. The phenomenologist Husserl [52] suggested that conscious perception reflects prediction of the immediate future (protention), in addition to current sensorial input and influences from the past. In fact, there is evidence that we tend to think that our eyes have landed at a new location before the actual saccade onset [53,54]. Consistent with the prediction hypothesis, the perceived saccade onset seems to be anticipated mentally by 50–200 ms [55] (Box 2).

Principle 3: intermediate processing stages

The third principle that might help us to understand trans-saccadic perception is that vision involves a series of separate processing stages. In the simple case of recognizing an object, for example, visual information is processed through numerous levels in the hierarchy from primary visual cortex (V1) to object-recognition areas in temporal cortex. These intermediate stages allow the mind to move from a pixel-like, pictorial representation of the world – akin to a photograph in retinal coordinates – to the identification of 3D objects and complex scenes. Although these intermediate stages of processing can still be considered 'visual' – they involve modality specific computations rather than amodal conceptual properties – the representations are no longer tied to local contrast and color information [56,57].

Our emphasis on intermediate stages of processing provides a different way of thinking about how trans-saccadic perception might work. Trans-saccadic buffer theories, for example, required a 'fusion' of pixel-like images, which are now thought to exist only in the earliest stages of visual processing. In contrast, memory-based theories have tended to focus on memory for complete objects, at higher levels of cognition that reflect conscious
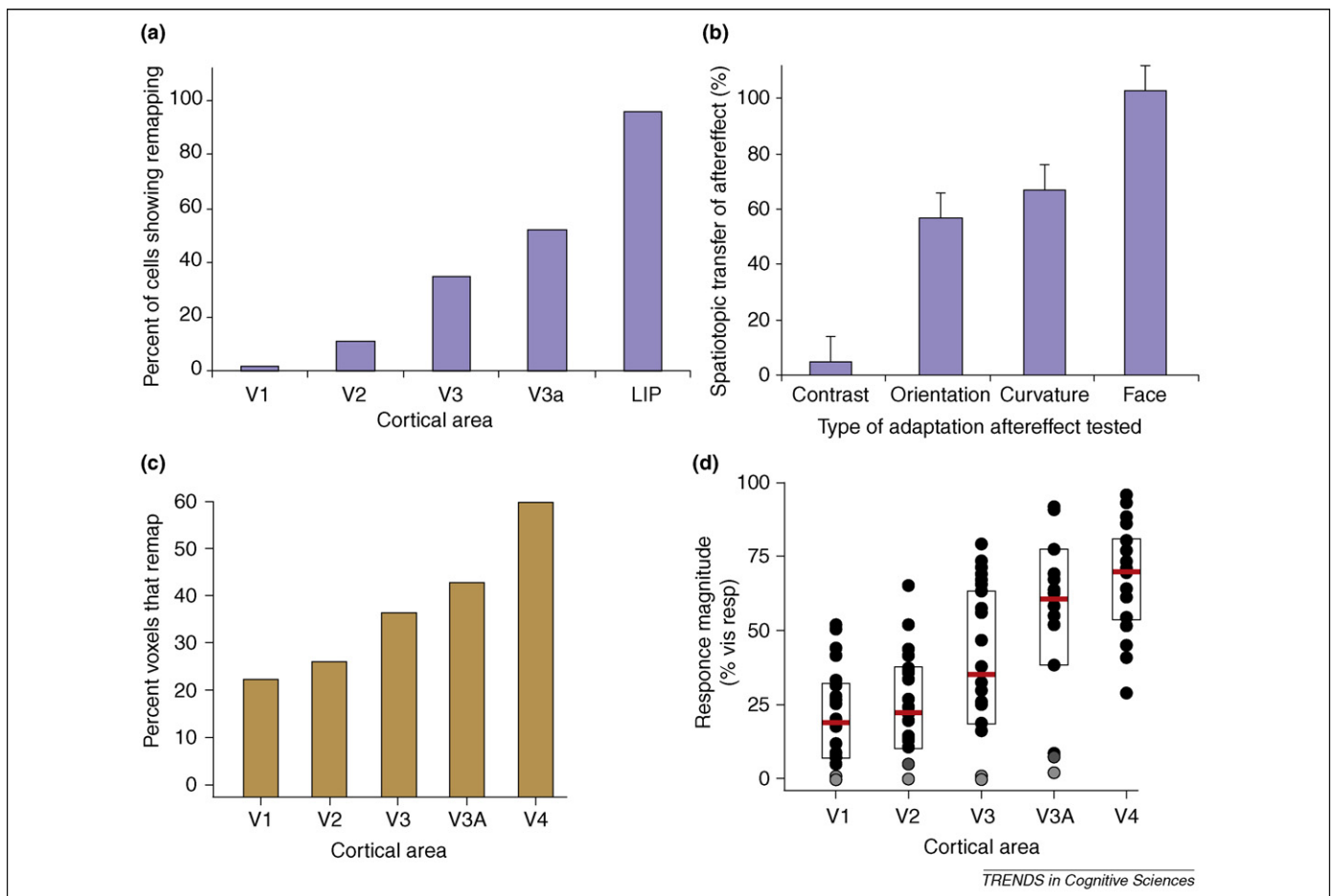

Figure 4. Increasing influence of saccades with increasing stimulus complexity and/or higher visual processing areas. **(a)** Proportion of cells showing saccade-related changes in the receptive field for different visual areas (LIP, Lateral Intraparietal area) (data replotted from Ref. [18].) **(b)** Percent transfer of the adaptation aftereffect based on spatiotopic location for four different visual features (data re-plotted from Ref. [56]). **(c)** Percent of voxels showing a significant change in the hemodynamic response (BOLD, blood oxygen level dependent measure) using functional magnetic resonance imaging (fMRI). Note that no stimulus was actually present in the remapped visual field (data replotted from Ref. [59]). **(d)** Magnitude of the remapped response in the opposite hemifield compared to the BOLD response found for presentation of the actual stimulus to that hemifield.

perception. Although memory for objects is undoubtedly important in many tasks, we suggest that much of the 'action' could be taking place at earlier levels, in which neural firing is not directly linked with what we consciously perceive [58].

Principle 4: graded effects of saccades on intermediate visual representations

The fourth basic principle is that, as one moves further along the hierarchy, visual processing becomes progressively more influenced by remapping. Initial evidence for this graded transformation from more static to more dynamic representations comes from both single cell recordings in the visual cortex of macaque monkeys [18] and from functional imaging studies [59] (Figure 4). Studies in both species reveal substantial remapping at intermediate levels (V3 and V3A) and much less at lower levels (V1 and V2). Indeed, at higher levels of the visual hierarchy the visual system tends to process more enduring properties of the stimulus that are immune to small changes in lighting or viewpoint. Trans-saccadic perception, in other words, requires a balance between learning and forgetting: it is equally crucial to discard information that is no longer relevant.

Principle 5: the etcetera principle

A key observation is that only salient stimuli are updated – stable, unattended stimuli do not activate the remapping process [60]. Likewise, the perceptual correlates of remapping (as measured by adaptation aftereffects) are limited to the most salient objects in a display [61] and trans-saccadic visual memory is thought to contain only 3–4 attended items [31]. What happens to the rest of the scene?

The influential art historian Ernst Gombrich [62] used the 'etcetera principle' to describe our perception – outside of the fovea and center of attention – of the overall pattern and meaning of the scene. According to Gombrich [62], the global pattern in environments such as a forest, beach or street scene enables us to predict more-or-less what we will see, based on the order and redundancy in the scene and on previous experience with that type of environment. In cognitive psychology, this 'etcetera' percept is called 'gist' and denotes the general meaning of a scene which we can grasp in a single glance [63–65]. Recent studies in a variety of fields, including gaze control [66–68], cognitive neuroscience [69] and computer vision [70], have investigated the nature of gist and its role in scene and object recognition. One crucial point is that gist is abstract, rather than retinotopic, and thus it does not need to be 'remapped' in retinal coordinates across saccades.

Studies of 'change blindness' have demonstrated that we are most sensitive to two types of scene alteration: changes to salient objects and changes that violate the general 'gist' and layout of the scene (for reviews, see Refs [11,71]). Non-salient items can change, disappear or appear during saccades without us noticing this change. These findings indicate that there is no need to remap most objects in a cluttered scene because we are fundamentally unaware of the lack of remapping for objects that are not salient. In addition, there is no need to remap the entire scene because most stimuli are not processed in great

enough detail for remapping to be of any use. There would be little or no benefit in integrating information about objects that are not important and are processed only superficially.

At the same time, we can still depend on memory and perception of the overall gist to allow us to detect large violations, which would of course be highly unlikely in nature. The odds that an object would drastically change its nature or disappear during a saccade are sufficiently low that we can depend on our sensitivity to motion transients to notice changes in object location or properties. Thus, the combination of gist and the predictive, dynamic remapping of a limited number of objects could help to resolve the seeming contradiction between the richness of perceptual experience – based mainly on a few salient objects and a visual field full of 'etcetera' – and the strict limits of visual memory.

Conclusions

Here, we have described five principles underlying the perception of objects across saccades. According to our framework, perception across separate glances is mediated by a predictive, saccade-specific mechanism that remaps visual information as part of the updating of spatial location. This updating process begins during the time period between the intention to make a saccade and the onset of the eye movement itself and is instantiated by dynamic receptive fields in parietal, frontal and extrastriate cortex. This remapping is selective, involving only salient objects. We suggest that intermediate visual processing areas are particularly important in remapping object features across saccades.

One possible way to view the entire remapping process is as the updating of a 'pointer' that links the spatial location of an object (in neural maps) to visual information about that object [61,72]. Several studies have indicated that maps in parietal cortex are important for binding features to specific objects in a specific place [73–75]. According to the framework outlined here, the intention to make a saccade sets off a cascade of neural events that cause the 'spatial location' and 'properties' of salient objects to be smoothly and predictively remapped in anticipation of the future saccadic landing position. Although much work is needed to elucidate the mechanisms involved (Box 2), and their relationship to previous theories of spatial constancy and working memory, we think that the five principles outlined here provide a useful framework to guide future investigations.

References

1 Thorpe, S.J. and Fabre-Thorpe, M. (2001) Neuroscience. Seeking categories in the brain. *Science* 291, 260–263
2 Schiller, P.H. (1998) The neural control of visual guided eye movements. In *Cognitive Neuroscience of Attention: A Developmental Perspective* (Richards, J.E., ed.), pp. 3–50, Lawrence Erlbaum Associates
3 Jonides, J. *et al.* (1982) Integrating visual information from successive fixations. *Science* 215, 192–194
4 Pollatsek, A. *et al.* (1990) Role of spatial location in integration of pictorial information across saccades. *J. Exp. Psychol. Hum. Percept. Perform.* 16, 199–210
5 Bridgeman, B. and Mayer, M. (1983) Failure to integrate visual information from successive fixations. *Bull. Psychon. Soc.* 21, 285–286

6 Irwin, D.E. (1991) Information integration across saccadic eye movements. *Cognit. Psychol.* 23, 420–456

7 Rensink, R.A. (2006) Further adventures with the magical number one. *J. Vis.* 6, 1076a

8 Magnussen, S. (2000) Low-level memory processes in vision. *Trends Neurosci.* 23, 247–251

9 Melcher, D. and Morrone, M.C. (2007) Trans-saccadic memory: building a stable world from glance to glance. In *Eye Movement Research: A Window on Mind and Brain* (Van Gompel, R.P.G. *et al.*, eds), pp. 213–236, Elsevier

10 Alvarez, G.A. and Cavanagh, P. (2004) The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychol. Sci.* 15, 106–111

11 O'Regan, J.K. and Noe, A. (2001) A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* 24, 939–973

12 Rensink, R.A. (2000) Seeing, sensing, and scrutinizing. *Vision Res.* 40, 1469–1487

13 Duhamel, J.R. *et al.* (1992) The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255, 90–92

14 Colby, C.L. *et al.* (1995) Oculocentric spatial representation in parietal cortex. *Cereb. Cortex* 5, 470–481

15 Colby, C.L. and Goldberg, M.E. (1999) Space and attention in parietal cortex. *Annu. Rev. Neurosci.* 22, 319–349

16 Goldberg, M.E. and Bruce, C.J. (1990) Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *J. Neurophysiol.* 64, 489–508

17 Umeno, M.M. and Goldberg, M.E. (1997) Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *J. Neurophysiol.* 78, 1373–1383

18 Nakamura, K. and Colby, C.L. (2002) Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proc. Natl. Acad. Sci. U. S. A.* 99, 4026–4031

19 Walker, M.F. *et al.* (1995) Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J. Neurophysiol.* 73, 1988–2003

20 Sommer, M.A. and Wurtz, R.H. (2002) A pathway in primate brain for internal monitoring of movements. *Science* 296, 1480–1482

21 Sommer, M.A. and Wurtz, R.H. (2008) Visual perception and corollary discharge. *Perception* 37, 408–418

22 Heiser, L.M. and Colby, C.L. (2006) Spatial updating in area LIP is independent of saccade direction. *J. Neurophysiol.* 95, 2751–2767

23 Kusunoki, M. and Goldberg, M.E. (2003) The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *J. Neurophysiol.* 89, 1519–1527

24 Goldberg, M.E. *et al.* (1990) The representation of visuomotor space in the parietal lobe of the monkey. *Cold Spring Harb. Symp. Quant. Biol.* 55, 729–739

25 Baker, J.T. *et al.* (2003) Spatial memory following shifts of gaze. I. Saccades to memorized world-fixed and gaze-fixed targets. *J. Neurophysiol.* 89, 2564–2576

26 Sommer, M.A. and Wurtz, R.H. (2006) Influence of the thalamus on spatial visual processing in frontal cortex. *Nature* 444, 374–377

27 Berman, R.A. *et al.* (2007) Dynamic circuitry for updating spatial representations. III. From neurons to behaviour. *J. Neurophysiol.* 98, 105–121

28 Vaziri, S. *et al.* (2006) Why does the brain predict sensory consequences of oculomotor commands? Optimal integration of the predicted and the actual sensory feedback. *J. Neurosci.* 26, 4188–4197

29 Crawford, J.D. *et al.* (2004) Spatial transformations for eye-hand coordination. *J. Neurophysiol.* 92, 10–19

30 Medendorp, W.P. and Crawford, J.D. (2002) Visuospatial updating of reaching targets in near and far space. *Neuroreport* 13, 633–636

31 Prime, S.L. *et al.* (2007) Visual memory capacity in transsaccadic integration. *Exp. Brain Res.* 180, 609–628

32 Prime, S.L. *et al.* (2008) Transcranial magnetic stimulation over posterior parietal cortex disrupts transsaccadic memory of multiple objects. *J. Neurosci.* 28, 6938–6949

33 Dominey, P.F. and Arbib, M.A. (1992) A cortico-subcortical model for generation of spatially accurate sequential saccades. *Cereb. Cortex* 2, 153–175

34 Pouget, A. *et al.* (2002) A computational perspective on the neural basis of multisensory spatial representations. *Nat. Rev. Neurosci.* 3, 741–747

35 Quaia, C. *et al.* (1998) The maintenance of spatial accuracy by the perisaccadic remapping of visual receptive fields. *Neural Netw.* 11, 1229–1240

36 Keith, G.P. *et al.* (2007) Functional organization within a neural network trained to update target representations across 3-D saccades. *J. Comput. Neurosci.* 22, 191–209

37 Heide, W. and Kompf, D. (1998) Combined deficits of saccades and visuo-spatial orientation after cortical lesions. *Exp. Brain Res.* 123, 164–171

38 Pisella, L. and Mattingley, J.B. (2004) The contribution of spatial remapping impairments to unilateral visual neglect. *Neurosci. Biobehav. Rev.* 28, 181–200

39 Husain, M. *et al.* (2001) Impaired spatial working memory across saccades contributes to abnormal search in parietal neglect. *Brain* 124, 941–952

40 Vuilleumier, P. *et al.* (2007) Impaired perceptual memory of locations across gaze-shifts in patients with unilateral spatial neglect. *J. Cogn. Neurosci.* 19, 1388–1406

41 Berman, R.A. and Colby, C.L. (2008) Attention and active vision. *Vision Res.* DOI: 10.1016/j.visres.2008.06.017

42 Wexler, M. (2005) Anticipating the three-dimensional consequences of eye movements. *Proc. Natl. Acad. Sci. U. S. A.* 102, 1246–1251

43 Ross, J. *et al.* (2001) Changes in visual perception at the time of saccades. *Trends Neurosci.* 24, 113–121

44 Melcher, D. (2007) Predictive remapping of visual features precedes saccadic eye movements. *Nat. Neurosci.* 10, 903–907

45 Parks, N.A. and Corballis, P.M. (2008) Electrophysiological correlates of presaccadic remapping in humans. *Psychophysiology* 45, 776–783

46 Flanagan, J.R. *et al.* (2006) Control strategies in object manipulation tasks. *Curr. Opin. Neurobiol.* 16, 650–659

47 Krumhansl, C.L. (1991) Music psychology:tonal structures in perception and memory. *Annu. Rev. Psychol.* 42, 277–303

48 DeLong, K.A. *et al.* (2005) Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nat. Neurosci.* 8, 1117–1121

49 Federmeier, K.D. (2007) Thinking ahead: the role and roots of prediction in language comprehension. *Psychophysiology* 44, 491–505

50 Griffiths, T.L. and Tenenbaum, J.B. (2006) Optimal predictions in everyday cognition. *Psychol. Sci.* 17, 767–773

51 Schutz-Bosbach, S. and Prinz, W. (2007) Perceptual resonance: action-induced modulation of perception. *Trends Cogn. Sci.* 11, 349–355

52 Husserl, E. (1964) *The Phenomenology of Internal Time Consciousness,* Indiana University Press (Original work published 1905 in German)

53 Deubel, H. *et al.* (1999) The subjective direction of gaze shifts long before the saccade. In *Current Oculomotor Research: Physiological and Psychological Aspects* (Becker, M.W. *et al.*, eds), pp. 65–70, Plenum

54 Yarrow, K. *et al.* (2001) Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. *Nature* 414, 302–305

55 Yarrow, K. *et al.* (2008) Saccadic chronostasis and the continuity of subjective temporal experience across eye movements. In *Space and Time in Perception and Action*, (Nijhawan, R. and Khurana, B. eds), Cambridge University Press (in press)

56 Melcher, D. (2005) Spatiotopic transfer of visual-form adaptation across saccadic eye movements. *Curr. Biol.* 15, 1745–1748

57 Melcher, D. and Morrone, M.C. (2003) Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nat. Neurosci.* 6, 877–881

58 Logothetis, N.K. (1998) Single units and conscious vision. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 353, 1801–1818

59 Merriam, E.P. *et al.* (2007) Remapping in human visual cortex. *J. Neurophysiol.* 97, 1738–1755

60 Gottlieb, J.P. *et al.* (1998) The representation of visual salience in monkey parietal cortex. *Nature* 391, 481–484

61 Melcher, D. (2008) Selective attention and the active remapping of object features in trans-saccadic perception. *Vision Res.* DOI: 10.1016/j.visres.2008.03.014

62 Gombrich, E.H. (1979) *The Sense of Order: A Study in the Psychology of Decorative Art,* The Phaidon Press

63 Potter, M.C. (1976) Short-term conceptual memory for pictures. *J. Exp. Psychol.* 2, 509–522

64 Intraub, H. (1980) Presentation rate and the representation of briefly glimpsed pictures in memory. *J. Exp. Psychol.* 6, 1–12

65 Oliva, A. and Torralba, A. (2006) Building the gist of a scene: the role of global image features in recognition. *Prog. Brain Res.* 155, 23–36

66 Melcher, D. (2001) Persistence of visual memory for scenes. *Nature* 412, 401

67 Melcher, D. and Kowler, E. (2001) Visual scene memory and the guidance of saccadic eye movements. *Vision Res.* 41, 3597–3611

68 Tatler, B.W. *et al.* (2003) The time course of abstract visual representation. *Perception* 32, 579–592

69 Bar, M. (2004) Visual objects in context. *Nat. Rev. Neurosci.* 5, 617–629

70 Oliva, A. and Torralba, A. (2007) The role of context in object recognition. *Trends Cogn. Sci.* 11, 520–527

71 Simons, D.J. and Rensink, R.A. (2005) Change blindness: past, present, and future. *Trends Cogn. Sci.* 9, 16–20

72 Melcher, D. Dynamic object-based remapping of visual features in trans-saccadic perception. *J. Vis.* (in press)

73 Serences, J.T. and Yantis, S. (2006) Selective visual attention and perceptual coherence. *Trends Cogn. Sci.* 10, 38–45

74 Treisman, A. (1996) The binding problem. *Curr. Opin. Neurobiol.* 6, 171–178

75 Walther, D. and Koch, C. (2006) Modeling attention to salient proto-objects. *Neural Netw.* 19, 1395–1407

76 Schlag, J. and Schlag-Rey, M. (2002) Through the eye, slowly: delays and localization errors in the visual system. *Nat. Rev. Neurosci.* 3, 191–215

77 Deubel, H. (2003) Localization of targets across saccades: role of landmark objects. *Vis. Cogn.* 11, 173–202

78 Deubel, H. *et al.* (1996) Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Res.* 36, 985–996

79 Matin, L. and Pearce, D.G. (1965) Visual perception of direction for stimuli flashed during voluntary saccadic eye movmements. *Science* 148, 1485–1487

80 Honda, H. (1991) The time courses of visual mislocalization and of extra-retinal eye position signals at the time of vertical saccades. *Vision Res.* 31, 1915–1921

81 Kaiser, M. and Lappe, M. (2004) Perisaccadic mislocalization orthogonal to saccade direction. *Neuron* 41, 293–300

82 Lappe, M. *et al.* (2000) Postsaccadic visual references generate presaccadic compression of space. *Nature* 403, 892–895

83 Niemeier, M. *et al.* (2003) Optimal transsaccadic integration explains distorted spatial perception. *Nature* 422, 76–80

84 Pola, J. (2004) Models of the mechanism underlying perceived location of a perisaccadic flash. *Vision Res.* 44, 2799–2813

85 Hamker, F.H. *et al.* (2008) The peri-saccadic perception of objects and space. *PLOS Comput. Biol.* 4, e31

86 Bays, P.M. and Husain, M. (2007) Spatial remapping of the visual world across saccades. *Neuroreport* 18, 1207–1213