Functions of Memory Across Saccadic Eye Movements

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Contents

Abstract Several times per second, humans make rapid eye movements called saccades which redirect their gaze to sample new regions of external space. Saccades present unique challenges to both perceptual and motor systems. During the movement, the visual input is smeared across the retina and severely degraded. Once completed, the projection of the world onto the retina has undergone a large-scale spatial transformation. The vector of this transformation, and the new orientation of

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the eye in the external world, is uncertain. Memory for the pre-saccadic visual input is thought to play a central role in compensating for the disruption caused by saccades. Here, we review evidence that memory contributes to (1) detecting and identifying changes in the world that occur during a saccade, (2) bridging the gap in input so that visual processing does not have to start anew, and (3) correcting saccade errors and recalibrating the oculomotor system to ensure accuracy of future saccades. We argue that visual working memory (VWM) is the most likely candidate system to underlie these behaviours and assess the consequences of VWM's strict resource limitations for transsaccadic processing. We conclude that a full understanding of these processes will require progress on broader unsolved problems in psychology and neuroscience, in particular how the brain solves the object correspondence problem, to what extent prior beliefs influence visual perception, and how disparate signals arriving with different delays are integrated.

Keywords Saccadic eye-movements · Transsaccadic processing · Visual working memory

1 Introduction

Light entering the human eye is focused by the crystalline lens onto the retina, a light-sensitive layer at the back of the eye. Within the retina, photoreceptor density falls off with distance from the fovea, the region corresponding to the centre of the visual image. This preferential distribution of neural resources to the centre of the visual field is reiterated in the subcortical and cortical visual areas that process and refine the retinal input. As a result, identification and discrimination of visual details is substantially better at the fovea than in the periphery. To bring different portions of the visual scene to project onto the fovea, six strong ocular muscles generate brief bursts of movement, termed saccades, that change the orientation of the eye in its socket. Natural viewing behaviour therefore consists primarily of a sequence of stable fixations directed to different locations in the environment, each lasting a few hundred milliseconds, separated by saccades.

Due to inherent limitations in the rate at which photoreceptors can respond to visual stimuli, integrating information over tens of milliseconds, any substantial movement of the eye smears the retinal image (Wurtz 2008) (Fig. 1a). To account for this, the saccadic system has evolved to move the eye at velocities of up to 500°/s, minimizing the period for which the nervous system does not receive a reliable visual input (Westheimer 1954; Wurtz 2008). Nonetheless, uptake of visual information from the external world is compromised for 30–50 ms with every saccade. Additionally, the rapid movement of the image across the retina would generate salient and distracting motion signals if not for a combination of passive and active suppression mechanisms (Wurtz 2008). The pre- and post-saccadic visual images may act as forward and backward masks, respectively, effectively hiding the intrasaccadic blur from perception (Castet et al. 2002). Active down-weighting of the magnocellular pathway has been reported to suppress visual information

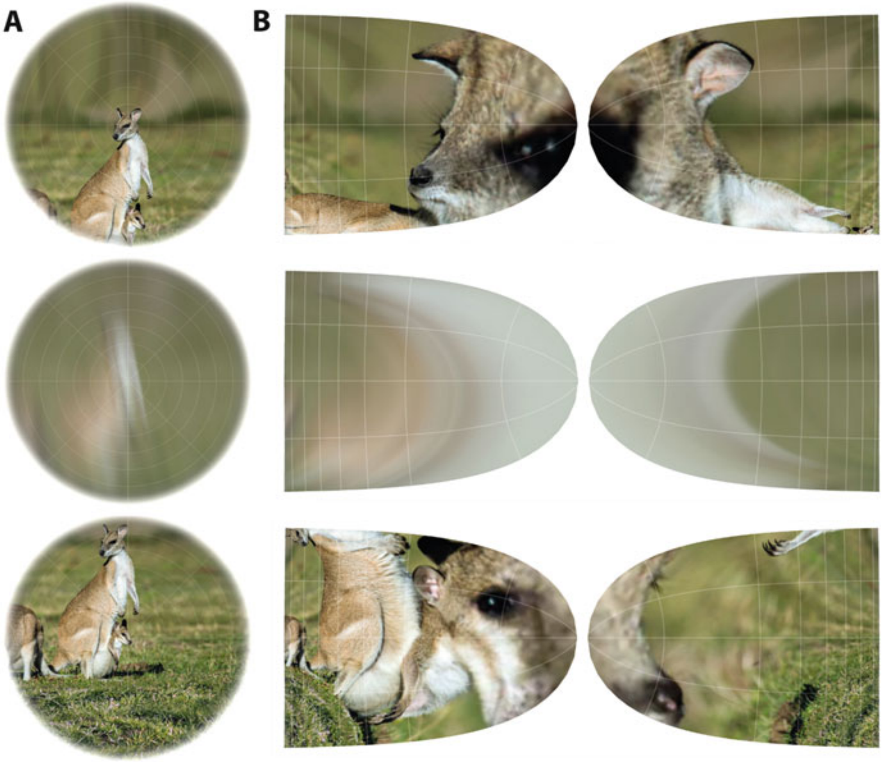

Fig. 1 Saccadic eye movements cause global changes to the retinal image and its cortical representation. (**a**) As gaze shifts from its pre-saccadic location (here centred on the face of the kangaroo; top panel), the rapid movement smears the retinal image (middle panel), before steady fixation is re-established at the new location (the joey in its mother's pouch; bottom panel). (**b**) Projection of the retinal image onto the cortical map (e.g. of V1). Note the substantial over-representation of the fovea. Comparison of visual information between fixations must take into account the large-scale reorganization of visual cortical representation due to the saccade

processing, particularly for motion (Burr et al. 1994). This suppression seems to begin even before saccade onset (Diamond et al. 2000; Bremmer et al. 2009), indicating that it is not merely a passive response arising from changes in input during an eye movement (see Ross et al. 2001 for a review). In combination, these suppression mechanisms ensure that disruptive visual signals associated with the eye movement are annulled, at the cost of slightly increasing the duration for which reliable visual information is unavailable.

With each saccade, representations of objects located in the periphery are suddenly shifted to the fovea and vice versa. This means that, at least in early visual areas where receptive fields are small, after the saccade the same object is represented by an entirely distinct neuronal population coding for a different location in the visual field (Fig. 1b). As such, decisions about the continuity of an object – or detecting whether the properties of an object have changed – cannot be determined by simple changes in firing rate of individual neurons, as might be possible during fixation. Furthermore, because resolution varies with eccentricity, the pre- and post-saccadic representations of an object will rarely correspond in spatial resolution. The challenge of understanding how such spatially distinct sources of information can be compared across a saccade has eluded researchers for decades (see Cavanagh et al. 2010; Burr and Morrone 2011; Tatler and Land 2011; Melcher and Morrone 2015; Higgins and Rayner 2015). In brief, explanations have varied from the problem being so difficult that nothing is stored across saccades, with stability simply assumed (O'Regan and Noë 2001), to dedicated world-based (spatiotopic) representations which remain unchanged across gaze shifts (Burr and Morrone 2011; Melcher and Morrone 2015), to the active remapping of pre-saccadic visual information to the correct post-saccadic location (Wurtz 2008; Cavanagh et al. 2010; Burr and Morrone 2011; Higgins and Rayner 2015). Rather than the neurophysiological implementation, here we will address the computations involved in comparing and integrating information across saccades. Our focus will be on transsaccadic memory – the internal representation of the pre-saccadic scene available after the eye movement – and the functions it serves in perceptual and motor systems.

2 Transsaccadic Memory

In the last three decades, substantial evidence about the properties of transsaccadic memory has accumulated from studies that ask observers to compare or directly report information from the pre-saccadic scene that is absent or changed in the post-saccadic input (Irwin et al. 1990; Irwin 1992, 1996; Irwin and Andrews 1996; Deubel and Schneider 1996; Hollingworth et al. 2008). While these results suggest an image-like snapshot of the whole visual scene is not stored across the saccade (Tatler and Land 2011; Higgins and Rayner 2015), detailed information about the colour, size, shape, and identity of select objects can be maintained (Henderson 1994; Henderson and Siefert 1999; Henderson and Hollingworth 1999, 2003; Melcher and Kowler 2001; Irwin and Zelinsky 2002; Tatler et al. 2003). In this respect, transsaccadic memory strongly resembles visual working memory (VWM), a limited store of visual information that survives masking inputs and decays over seconds (Baddeley and Hitch 1974; Luck and Vogel 1997).

Early research into transsaccadic memory, like VWM, assumed that the limits of representation could be captured by a single number, defining an upper limit on items stored (Miller 1956; Pashler 1988; Luck and Vogel 1997; Cowan 2001). Capacity estimates calculated on this basis have typically been similar whether recall was tested after an intervening saccade or at fixation with an intervening delay (Irwin 1992; Irwin and Andrews 1996; Gordon and Irwin 1998; Prime et al. 2007). Additionally, these results suggested that multiple features of the same object could be maintained across a saccade with little or no additional cost, mirroring results from VWM that suggested different feature dimensions are held in independent stores (Wheeler and Treisman 2002; Bays et al. 2011).

More recent conceptions of VWM recognize that the precision or resolution with which visual information is maintained can vary substantially as a function of memory load and the distribution of attention (Ma et al. 2014). Increasing the number of items in memory (Zhang and Luck 2008; Bays and Husain 2008; van den Berg et al. 2012), or enhancing the storage resolution of a specific item (Bays et al. 2011; Gorgoraptis et al. 2011; Melcher and Piazza 2011), conveys a cost to the precision of other remembered items. While the average precision of recall for a stimulus array changes little when a saccade is made to one of its elements, this finding hides a strong redistribution of memory resources towards the saccade target, with precision for that object increased at a cost to other items in the display (Bays and Husain 2008). When the information required for memorization is dissociated from the location of the saccade target, memory performance is considerably worse (Shao et al. 2010; Hanning et al. 2015; Tas et al. 2016; Ohl and Rolfs 2017; Jeyachandra et al. 2018), with task-irrelevant information unavoidably encoded. Demonstrating that this is not due to the saccade itself, no deficit was observed when subjects made eye movements to empty locations (Tas et al. 2016), indicating the effects originate from the cost of additionally encoding the saccade target. An exception is if the saccade is to an empty location matching the location of an item in memory, in which case changes in memory performance occur consistent with a redistribution of resources between the items in memory (Ohl and Rolfs 2017, 2018).

Memorization of the saccade target may be an unavoidable consequence of the obligatory shift of attention to the target location that precedes a saccade (Deubel and Schneider 1996; Peterson et al. 2004; Rolfs and Carrasco 2012) or may be an adaptive behaviour that ensures a reliable representation of the saccade target is available for post-saccadic comparison. In any case, this compulsory encoding occurs at the expense of some of the usual flexibility in distributing VWM resources (Gorgoraptis et al. 2011).

2.1 Other Memory Representations

In addition to VWM, researchers have explored whether other types of visual representation contribute to recall of a pre-saccadic scene. Visible persistence refers to the fact that a visual stimulus can appear to still be present very briefly after it is removed. During fixation, visible persistence means that rapidly interleaved sequential inputs can be perceived as a single image (perceptual fusion). However, for such a mechanism to operate across an eye movement would require persistence to be tied to spatial rather than retinal location. The possibility of fusion in spatial coordinates was investigated and discounted by Irwin and others (Irwin 1996), and while participants in one recent study reported spatiotopic fusion (Paeye et al. 2018), the very specific conditions required suggest its relevance to natural viewing is minimal (see Sect. 3.1 for further discussion).

Beyond the point at which an extinguished stimulus remains visible, there appears to be a further short-lived “informational persistence” (or iconic memory) – a very high capacity, pre-attentive memory of the visual image that is easily disrupted by masking (Sperling 1960; Gegenfurtner and Sperling 1993). Although iconic memory has commonly been assumed to be eliminated by eye movements, one study (Germeys et al. 2010) presented evidence that such a representation could survive and be spatially updated with the saccade. However, this transsaccadic informational persistence was masked by the presence of stimuli after the saccade. A role in typical vision, in which there are almost always post-saccadic stimuli to overwrite such representations, has not been established. However, we will return to this topic in the final section of our review.

In summary, while visible and non-visible high-capacity representations of a scene may survive long enough to contribute to transsaccadic memory, evidence for a role in natural viewing is sparse, and VWM-only accounts have generally proved sufficient to explain post-saccadic memory performance.

2.2 Role of VWM Across Eye Movements

In the following sections, we will consider evidence for three key functions that VWM has been proposed to fulfil with respect to saccadic eye movements. First, it could enable the detection of changes in the external world that occur during the saccade. Second, it could enable pre-saccadic information to supplement and enhance post-saccadic vision, so processing does not have to start anew with each new fixation. Third, it could support the correction of saccade errors and calibration of saccadic motor commands. Each of these roles will prove heavily interrelated, and common themes arising from their evaluation will be discussed in the final section.

3 Identifying Changes in the Environment

The world we live in is filled with dynamic stimuli capable of changing their appearance or position, often without warning. During fixation, such changes produce transient responses in the activity of visual neurons, supporting rapid detection and reorienting of attention to the changed stimulus (Boehnke and Munoz 2008). However, when a change occurs during a saccade, this transient response is unavailable, and the perceptual system must instead infer the occurrence of a change by comparing pre-saccadic visual information in memory to the current percept. Due to the substantial spatial reorganization caused by a saccade, this task is particularly challenging when attempting to detect spatial changes. In this section we will investigate our ability to infer the occurrence of changes in the external world across saccadic eye movements. As will become clear, this requires not only that we have a pre-saccadic memory representation of objects for comparison but also that we have an accurate estimate of the saccade vector and that we can determine how objects present after the saccade correspond to those seen before it.

3.1 Detection of Displacements

One of the most impressive demonstrations of the difficulty of inferring changes during an eye movement is saccadic suppression of displacement (SSD; Bridgeman et al. 1975) (Fig. 2a). Here, during execution of an eye movement to a target object, the location of the target can be shifted considerably backward or forward along the saccade path without observers' awareness (Bridgeman et al. 1975; Deubel et al. 1996; Niemeier et al. 2003). While the magnitude of displacement required for reliable detection varies across studies (Higgins and Rayner 2015) – from 10% (Li and Matin 1990) up to 30% (Bridgeman et al. 1975) or even 50% of the saccade amplitude (McConkie and Currie 1996) – within a single experiment the range of displacements tolerated scales linearly with saccade amplitude (Bridgeman et al. 1975; Li and Matin 1990; Deubel et al. 1996).

Early theories of visual stability had proposed a global subtraction or cancellation of the retinal shift based on the outgoing saccadic motor signal (efference copy)

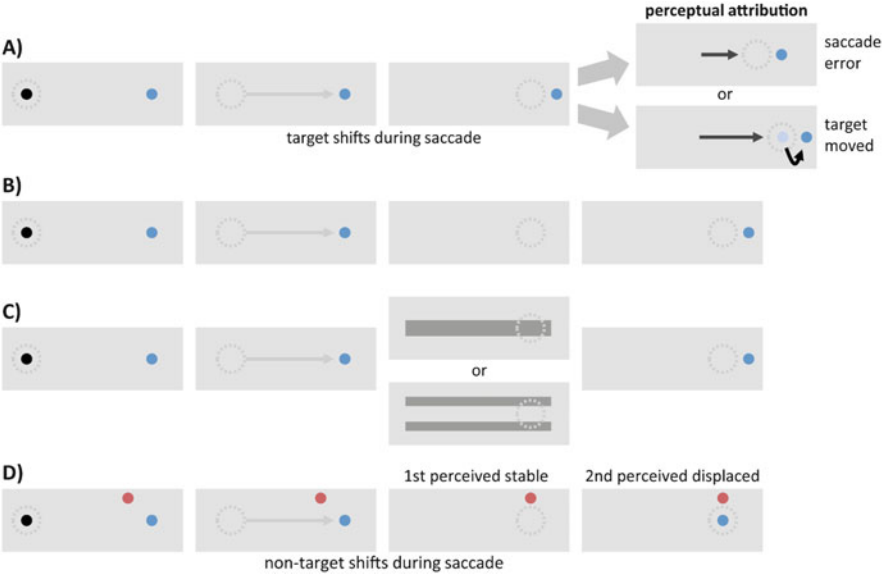

Fig. 2 Experimental methods for investigating saccadic suppression of displacement (SSD). (**a**) When the target of a saccade is displaced while the eyes are moving, the visual system can attribute the failure of gaze to land on the target to either error in the saccade (visual stability preserved) or movement of the stimulus (visual stability violated). Typical observers tolerate surprisingly large displacements without perceiving the target to have moved. (**b**) A brief delay or blank on saccade landing before reappearance of the target is sufficient to substantially reduce SSD, making the target movement readily detectible. (**c**) When the blank is replaced with an occluding object (top panel), the target movement again becomes hard to detect, but a similar object that would not have occluded the target (bottom panel) does not have this effect. (**d**) When multiple stimuli are present before the eye movement, the first post-saccadic stimulus to appear is assumed stable, regardless of whether it is the target or (as depicted) a different stimulus

(Bridgeman 2007; Higgins and Rayner 2015). In other words, the shift in the visual image across the retina would be exactly cancelled out by a contrary internal transformation based only on the intended saccade vector. Observations of SSD and related phenomena led researchers to instead suggest that a stable external world is the "null hypothesis" of the visual system (Mackay 1972; Bridgeman et al. 1994) and that post-saccadic visual input is critical in evaluating when this assumption is violated (Deubel et al. 1996; McConkie and Currie 1996; Currie et al. 2000). According to one version of this theory, there is a brief spatiotemporal "constancy window" in which the visual system searches for the saccade target within a few degrees of the post-saccadic landing position (Deubel et al. 1998; Deubel et al. 1998; Bridgeman 2007). If found, the post-saccadic input is deemed compatible with the assumption of a stable world, and previous spatial information is discarded or ignored. However, if the target is not found, then the assumption is violated, and eye proprioception, efference copy, and other "extraretinal" sources of information are consulted. This idea was conceptually similar to that of McConkie and Currie (1996), who emphasized the role of post-saccadic visual input and suggested a two-step search in which, after locating the saccade target, the relative distances between other salient objects in the surroundings are also examined (Currie et al. 2000). If the spatial discrepancies at either stage are too great, visual stability is broken, and the scene is perceived as changed.

Functionally, these ideas were based on the reasoning that preventing small spatial displacements from reaching awareness would be critical in enabling continuous perception of the world despite noise in sensory and motor signals (Bridgeman et al. 1994; Deubel et al. 1996; Currie et al. 2000). There is some evidence that an immediate, automatic attempt to locate the saccade target indeed takes place after each eye movement. The speed and accuracy of eye movements to matching singletons (Hollingworth et al. 2013) and the targeting of corrective saccades (Hollingworth et al. 2008; Hollingworth and Luck 2009) suggest that VWM representations are used as search templates post-saccade (see Sect. 4.1 below).

Deubel et al. introduced a brief blank period after the eye movement – delaying the post-saccadic appearance of the saccade target – and found a substantial improvement in the ability to identify displacements of the target (Deubel et al. 1996, 1998, see Fig. 2b). At first glance this result (known as the "blanking" effect) seems paradoxical, as the elimination of a source of information (post-saccadic vision) allows observers to judge target displacements much more precisely. Indeed, it was interpreted as a demonstration that the perceptual system *always* has access to high-quality information about the extent of the movement but routinely elects to ignore this information in favour of post-saccadic visual information (Deubel et al. 1996; Higgins and Rayner 2015). Only when forced, by the absence of the saccade target or other violations of the stability assumption, are saccade estimates consulted. Within this view, the perceptual system rigidly switches between two distinct states, either relying solely on post-saccadic visual input (assuming visual stability is maintained) or solely on the intended saccade vector (assuming visual stability is violated) to determine the location of post-saccadic gaze.

Niemeier et al. (2003) proposed an alternative to this heuristic account, suggesting that the inability to detect displacements across a saccade could actually represent the perceptual system making the best decision possible with noisy information. They used a Bayesian framework (Kersten et al. 2004) in which sensory inputs are used as evidence to update prior beliefs about the state of the world. Specifically, in their model, visual input and efference copy are optimally integrated with a prior belief that the visual scene is stable. When the saccade target is blanked, this discontinuity in the scene causes the prior to be weakened, making a displacement easier to detect. This model not only reproduced the patterns of spatial distortions and SSD typically observed in human observers but also made new predictions about the link between eye movement variability and magnitude of SSD that were experimentally verified (Niemeier et al. 2003, 2007; Wexler and Collins 2014). The Bayesian model captured both the increase in SSD with saccade magnitude (Li and Matin 1990) and the observation of greater sensitivity for detecting changes orthogonal than parallel to the saccade vector (van Opstal and van Gisbergen 1989). In both cases, the degree to which judgements are based on the prior assumption of stability is determined by the magnitude of uncertainty in saccadic landing position.

Subsequent findings have demonstrated that displacements of the saccade target which are orthogonal to the eye movement relieve SSD even when these shifts are irrelevant to the task (Wexler and Collins 2014). This further suggests that estimates of the spatial change induced by a saccade vector are critical in inferring the source of spatial inconsistencies across eye movements.

Atsma et al. (2016) recently expanded on this idea by incorporating causal inference into the integration process. They noted that the Niemeier model always integrates pre- and post-saccadic estimates of location – even for very large displacements – and argued that a causal judgement of whether the input is consistent with viewing a single stable object is critical to determine whether to integrate the two estimates. Rather than a heuristic decision to integrate or segregate inputs, they found the data were best described by a statistically optimal mixture of the two strategies. Finally, noting considerable variation in the strength of the “stable world” prior between participants, they suggested that experimental context and instructions might be idiosyncratically incorporated into individuals’ beliefs that objects could change during a saccade, making some participants more sensitive to location changes than they would have been outside the laboratory.

3.2 *Object Continuity*

Spatiotemporal correspondence between objects represents one cue as to whether pre- and post-saccadic information relate to the same object or whether the post-saccadic stimulus represents an entirely new object (Cox et al. 2005; Li and DiCarlo 2008; Schneider 2013). Recent results indicate that changes to surface properties of objects also influence the magnitude of SSD, suggesting these properties are also used as cues to correspondence (Demeyer et al. 2010b; Tas et al. 2012; Poth et al. 2015; Poth and Schneider 2016). In one study (Tas et al. 2012) changes in surface features across a saccade decreased the spatial range of SSD – although not to the maximum detectability – suggesting they decreased the strength of the stability assumption but did not eradicate it. This indicates that, in addition to spatial information, information about surface features is automatically stored and maintained during an eye movement for comparison with post-saccadic input (Prime et al. 2007, 2011; Melcher and Colby 2008).

Relatedly, SSD has been found to be reduced for stimuli that are in motion before saccade onset (Gysen et al. 2002a). This could be interpreted as evidence that the prior for stability is down-weighted for these objects, suggesting that the "stable world" prior is in fact a "stable object" prior determined on an item-by-item basis.

Briefly replacing the saccade target with an elongated bar immediately after the saccade produces less reduction in SSD than a blank of the same duration (Deubel et al. 2002) (Fig. 2c; top panel). One hypothesis is that the bar presents less evidence for a break in object stability, because the stimulus could still be present but hidden by the bar. Supporting this interpretation, when the bar was split in two, so the saccade target should have been visible in the gap, the discrepancy from the blanking condition was eliminated (Deubel et al. 2002) (Fig. 2c; bottom panel).

Interruptions in object continuity benefit not only the detection of changes in spatial location but also detection of non-location changes such as spatial frequency (Weiß et al. 2015). This suggests that breaking continuity alters the way that new visual information is processed by our perceptual system. It has been suggested that a break in continuity causes post-saccadic object information to be represented separately to pre-saccadic information (Deubel et al. 1996; Tas et al. 2012; Schneider 2013), as opposed to the new information simply updating existing representations. This has important implications for VWM, given its very limited capacity: allocating memory resources separately to both pre- and post-saccadic objects will greatly diminish the fidelity of these representations, as set size has effectively doubled (Bays et al. 2009) – in a sequence of saccades the number of independent representations would quickly become unmanageable. Alternatively, if pre-saccadic representations are simply updated or overwritten with post-saccadic information, then subsequent comparison between pre- and post-saccadic information would no longer be possible, as only the combined representations persist (Schneider 2013). More research is needed to understand the circumstances under which visual information obtained in different fixations is segregated versus integrated.

3.3 Visual Landmarks

Although most studies focus on the role of the saccade target in determining the accuracy of saccadic eye movements, other objects in the pre-saccadic visual scene may also be remembered and influence our judgements (Deubel 2004). In contrast to the sparse visual displays used in most experiments, natural scenes typically contain an abundance of other objects. Remembered information about these objects – in particular their distance from the saccade target – may provide an additional, important source of information to aid localization and determine the magnitude of a saccade.

The ability to detect displacements in the location of saccade target and nontarget stimuli was investigated by Deubel et al. (1998), who independently blanked and/or displaced either the saccade target or the nontarget stimulus during the eye movement (Fig. 2d). They found that while the identity of the blanked stimulus (target or nontarget) had no effect, temporal order was critical. When the stimulus that remained visible after the saccade was displaced from its original location, and the blanked stimulus returned in its original location, observers typically incorrectly reported that the blanked stimulus had moved. This held true for displacements of the first stimulus of up to 50% of the saccade vector and for temporal asynchronies as short as 50 ms. When both stimuli were blanked, despite a temporal discontinuity occurring for both stimuli, the first stimulus to reappear was always perceived as stable. This suggests that the visual system prioritizes the first available visual feedback after a saccade. In general, post-saccadic objects which match the remembered pre-saccadic stimuli appear to be able to function as “anchor points” for aligning expectations about where other objects – even the saccade target – should be located after the saccade.

Ostendorf and Dolan (2015) examined how the proximity of nontarget objects to the target stimulus influenced the magnitude of SSD. They found that, as the distance to the landmark object increased, the precision of judgements of displacement decreased, suggesting that the reliability of visual distance estimates scaled inversely with eccentricity. Importantly, the presence of the landmark did not cause subjects to ignore the planned saccade vector but rather altered the weighting between visual and non-visual information, with the influence of nontargets depending on the reliability of the spatial evidence they provided. Particularly in more ecological settings, where visual landmarks are abundant, memory for the relative distances between objects is likely to have a dominant influence on discriminating transsaccadic displacements.

3.4 Conclusion

Saccades momentarily compromise our access to reliable visual information while also creating a dramatic spatial transformation of the retinal image. As a result, the signals that normally allow us to detect changes in the environment are largely eliminated. Inferring such changes therefore requires that information about the pre-saccadic scene be actively maintained and compared to post-saccadic vision. Our review of studies testing detection of transsaccadic changes – both spatial and nonspatial – leads us to conclude that the visual system, around the time of a saccade, engages in a dynamic process of integrating multiple sources of information to determine if and how visual objects have changed. Because the post-saccadic visual input provides the most reliable and precise evidence about object locations and features, it frequently outweighs other signals, such as a discrepancy between the retinal shift and planned saccade vector, that could indicate a change has taken place. This weighting of multiple sources of evidence is captured by Bayesian models of perception and stands in contrast to heuristic accounts that propose a stepwise decision process based primarily on the visual input.

4 Integrating Information Across Saccades

Visual exploration often involves a repeated process of identifying an object of interest in peripheral vision, followed by a saccade that brings it into foveal vision for detailed examination. While peripheral vision is relatively imprecise and often impaired by crowding (Pelli and Tillman 2008; Strasburger et al. 2011), it would be inefficient to discard information obtained from it entirely (Harrison and Bex 2014). In this section we investigate the ability to incorporate information from before the saccade into post-saccadic perception.

4.1 Transsaccadic Fusion

Early accounts of transsaccadic memory suggested that the visual system adds post-saccadic input to a high-resolution, image-like representation of the scene accumulated from previous fixations (see Higgins and Rayner 2015). This hypothesis, commonly termed the "integrative visual buffer" (McConkie and Rayner 1976) or "spatiotopic fusion" (Irwin 1992), would predict that observers could effortlessly combine partial pre- and post-saccadic images into a single percept, as if they had been presented simultaneously (Fig. 3a). While initial findings seemed to support this prediction (Wolf et al. 1980; Jonides et al. 1982), these results were subsequently found to be artifactual, due to the persistence of the CRT displays (Jonides et al. 1983; O'Regan and Lévy-Schoen 1983; Irwin et al. 1983; Rayner and Pollatsek 1983; Bridgeman and Mayer 1983), and the hypothesis of an integrative buffer was largely abandoned.

However, a recent study by Paeye et al. (2018) found surprising evidence for a form of transsaccadic fusion. Unlike the stimuli used in previous fusion experiments (e.g. the dot matrix stimuli of Irwin et al. 1983), they chose pre- and post-saccadic stimuli whose integration would not require precise spatial alignment. Specifically, they presented a single vertical bar before and a set of three horizontal bars after the saccade. They asked participants to report whether they saw neither stimuli, one stimulus, both in succession or both simultaneously. The stimuli were frequently reported as simultaneously occurring when the post-saccadic contrast was made very low. The authors suggested that, under normal circumstances, post-saccadic input acts as a backward mask of the pre-saccadic scene, preventing transsaccadic fusion.

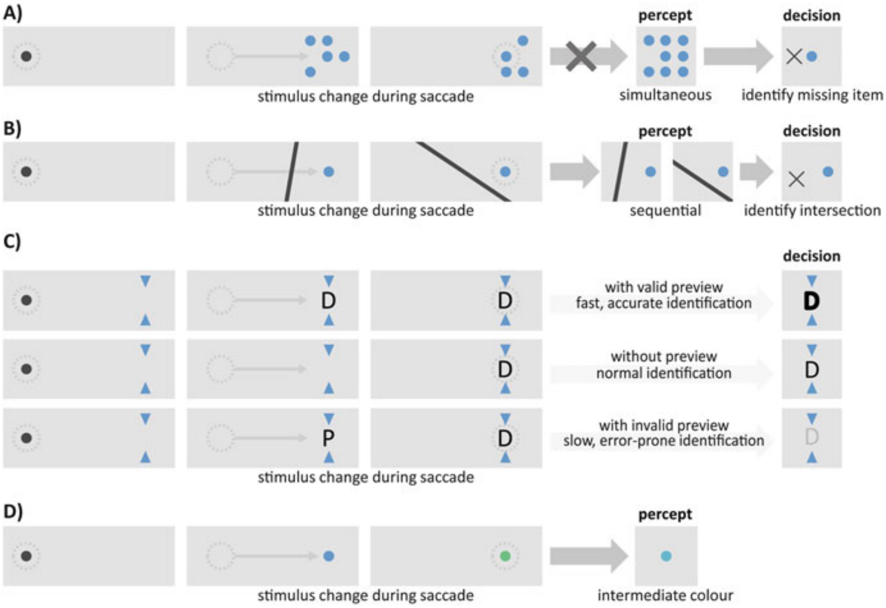

Fig. 3 Experimental methods for investigating the integration of information across saccades. (**a**) Partial images presented immediately before and after a saccade are in general not “fused” into a single perception of the full image. (**b**) While not experienced as a single image, different objects presented before and after saccade can be compared to make decisions which require both sources of information. (**c**) A valid peripheral “preview” of an object improves the speed and accuracy of its subsequent identification at the fovea, compared to a situation with no preview or a misleading, invalid preview. (**d**) When a small change is made to a surface feature (here, colour) of an object during a saccade, observers may report having seen a feature intermediate between the pre- and post-saccadic values

This implies that fusion would have little impact on everyday perception, where objects rarely change drastically in form or reduce substantially in contrast during a saccade.

4.2 Transsaccadic Comparison and Preview Effects

Despite the lack of support for explicit fusion, there is ample evidence that pre-saccadic information can be stored and processed alongside post-saccadic information. Such transsaccadic comparison has been shown for shapes and lines (Hayhoe et al. 1991; Prime et al. 2006), in studies where observers report information that is only accessible by comparison of the pre- and post-saccadic displays (Fig. 3b). It is important to note that stimuli are not merged into a single perception in these studies but rather that observers perceive and remember two presentations in sequence that they can relate together to make their decision.

Numerous studies have demonstrated an influence of pre-saccadic peripheral visual input on the speed with which perceptual decisions can be made after the saccade. For a wide variety of different stimulus types, exposure to a valid peripheral "preview" before an eye movement results in an approximately 100 ms reduction in the time it takes to discriminate details about the stimulus (Pollatsek et al. 1984, 1990; Henderson et al. 1987; Henderson 1992). This improvement, known as the transsaccadic preview effect (TPE), appears to reflect the memory of coarse peripheral information giving a "head-start" to object identification and perceptual decision-making (Fig. 3c).

Pollatsek et al. (1984) had subjects make eye movements to line drawings located in the periphery and name them as rapidly as possible. They examined the effects of a variety of different changes to the stimulus made during the saccade and compared them to a control condition with no peripheral preview. While they observed the greatest benefit for valid (i.e. unchanged) previews, they found that naming was also faster when previews shared visual features with the post-saccadic display (e.g. ball – tomato), compared to those that did not (ball – carrot). Additionally, the benefit was substantially weakened by spatial manipulations (such as mirror reflection or perspective changes), even when the object identity remained the same, but the benefit was unchanged when the object's spatial scale was manipulated. These results suggested that the TPE reflects a specifically visual representation that is nonetheless, based on the tolerance for changes in scale, to some degree abstracted from the retinal image.

Subsequent work in which subjects made eye movements to a location in-between two objects – one of which disappeared during the saccade – indicated that a precise spatial correspondence was not critical (Pollatsek et al. 1990). Naming latency was largely unaffected when the remaining object switched locations, provided it matched one of the previewed stimuli. These researchers concluded that the TPE originates from priming of perceptual processes – such as the preactivation of long-term memories that can contribute to object identification, rather than a precise spatial integration of pre- and post-saccadic inputs. However, subsequent studies suggested that spatiotemporal alignment was important to observing the full preview benefit (Kahneman et al. 1992; Germeys et al. 2002). Indeed, Kahneman et al. (1992), using letter stimuli inside moving frames during fixation, found preview benefits only when the same letter appeared in the same frame that it had previously been shown in. Henderson et al. reported independent – and additive – spatially invariant and spatially dependent saccadic preview benefits. They observed that, compared to when new letters (Henderson and Anes 1994; Henderson 1994) or line drawings (Henderson and Siefert 2001) were used, repeating any stimulus from the pre-saccadic display sped up response times while repeating it at the same location boosted performance even more.

These results were based on tasks in which observers directed saccades to land equidistant between objects. Germeys et al. (2002) found that when observers directed gaze instead to one of the previewed objects, only a valid preview of the saccade target benefited performance, with no TPE when neighbouring objects were switched to the saccade target. Re-examining the findings of Henderson and

Anes (1994), they found that when saccade landing position was carefully controlled – eliminating trials where the eyes strayed to either object – the spatially independent benefit was eliminated, revealing that the object observers selected as the saccade target was critical. Finally, explicitly comparing saccade targets to surrounding flankers revealed a TPE for the saccade target regardless of its post-saccadic location, whereas flanker items required spatiotemporal continuity for any benefit to occur.

In summary, the TPE demonstrates that memory for visual attributes of pre-saccadic stimuli can facilitate post-saccadic visual processing, particularly when the stimulus is the saccade target. However, the extent to which the TPE represents a true integration of visual inputs, as distinct from priming of object and feature identification, has proven difficult to establish.

4.3 Transsaccadic Integration

While the hypothesis of transsaccadic fusion implies an image-like overlay of pre- and post-saccadic inputs, transsaccadic integration refers to an averaging of feature information extracted before and after the saccade (Fig. 3d). Because visual inputs are noisy, averaging could reduce error and uncertainty in perceptual estimates. In the lab, when pre- and post-saccadic features of an object are made to differ, transsaccadic integration is demonstrated by observers reporting an intermediate perception, falling between the two feature values.

Several lines of research have been suggestive of such a process. A number of studies have demonstrated that two static images seen before and after an eye movement may be perceived as a continuous motion or object transformation (Gysen et al. 2002b; Fracasso et al. 2010; Szinte and Cavanagh 2011). These results indicate that pre- and post-saccadic input can be combined to generate a continuous percept, and further that the representation maintained across the saccade includes shape as well as location information (Fracasso et al. 2010). The apparent motion results indicate that this process takes into account the shift in retinal location of objects caused by the saccade, although this compensation appears to be imperfect (Szinte and Cavanagh 2011).

Demeyer et al. (2010a) asked observers to make a judgement about the aspect ratio of an ellipse after making a saccade to it. When a small change was made to the aspect ratio during the eye movement, they observed that judgements were distributed around a point roughly mid-way between the two stimulus values. While the strongest evidence for integration was found in the condition where participants were reportedly not aware of the change, some integration occurred even when the two views were separated by a blank display, disrupting spatiotemporal continuity, and it took the presence of an interstimulus mask to fully eliminate the influence of the pre-saccadic stimulus. This finding was consistent with results of Wittenberg et al. (2008) who showed a small influence of stimuli presented during a previous fixation on judgements of briefly flashed colours, even though the pre- and post-saccadic colours were uncorrelated and separated by a blank, and observers were explicitly instructed to judge the colour of the flashed stimulus.

Oostwoud Wijdenes et al. (2015) demonstrated that the extent to which an integrated percept resembles either the pre- or the post-saccadic input depends on the relative reliability of each input. Examining integration of multiple coloured patches that shifted hue imperceptibly during a saccade, they found that manipulating the eccentricity of stimuli, or explicitly adding colour noise to one display, biased the integrated percept towards either the pre- or post-saccadic colour. They concluded that transsaccadic perception reflects a statistically optimal integration of visual inputs. A corollary of this result is that the information retained in transsaccadic memory does not consist only of point estimates of pre-saccadic feature values but also includes the reliability of those estimates.

Two subsequent studies confirmed using single-orientation stimuli that transsaccadic integration closely approximates the predictions of a maximum likelihood estimation model (Ganmor et al. 2015; Wolf and Schütz 2015). A similar result was obtained for numerosity judgements, using clouds of coloured dots (Hübner and Schütz 2017). Here it was observed that detectable changes in features of the stimuli (dot colour or individual dot locations) did not affect the degree of integration, even though they would be expected to break object continuity. The apparent discrepancy between these results and the effects of blanking described above could reflect the fact that the feature relevant to the task (numerosity) was not disrupted.

4.4 Conclusion

In situations where rapid decisions are required, the maintenance and use of pre-saccadic visual information could convey substantial benefits to an observer. When the post-saccadic information is congruent with the pre-saccadic memory, incorporating pre-saccadic information into perceptual judgements makes them both faster and more accurate. Indeed, the pre-saccadic input can directly influence the way that a post-saccadic stimulus is perceived, with the degree of influence dependent on the relative reliability of each view and the extent to which continuity of the relevant features can be established. In this way, the perceptual system makes the most of the information that it has available, improving both the efficiency and the continuity of our visual perception, despite the interruption of the saccade. Future work should investigate how transsaccadic integration operates in complex environments, where establishing object correspondence is often challenging, and the limited nature of transsaccadic memory is likely to impose an important constraint on what can be integrated.

5 Correcting Eye Movement Errors

Saccades, like every movement of the body, are subject to variability and inaccuracy. A number of mechanisms, operating on different timescales, exist to compensate or correct for saccade errors. When an eye movement fails to bring gaze precisely to the desired saccade target, it is often followed by a fast and automatic second eye movement, known as a corrective saccade, which typically brings gaze closer to the intended goal (Becker and Fuchs 1969). When the motor signal required to generate a particular eye movement changes – for example, as the result of fatigue or, on a longer timescale, advancing age (Warabi et al. 1984; Munoz et al. 1998; Hopp and Fuchs 2004; Dowiasch et al. 2015) – adaptation processes counter these effects to prevent systematic errors from developing (Herman et al. 2013). In this section we will look at how the storage of pre-saccadic visual information can contribute to immediate corrective saccades and longer-term recalibration of eye movements to minimize future errors.

5.1 Corrective Saccades

Debate about the role of both post-saccadic visual feedback and remembered pre-saccadic visual information in the initiation of corrective saccades has persisted for decades (Tian et al. 2013). Central to this discussion is the suggestion that the latency of some corrective saccades (which can be as short as 50 ms; Schut et al. 2017) is incompatible with a role for post-saccadic vision (Weber and Daroff 1972; Becker 1976). While some authors observed corrective saccades even when the saccade target was obscured (Barnes and Gresty 1973; Shebilske 1976; Ohl et al. 2013), others found that the absence of post-saccadic visual feedback eliminates their occurrence (Bonnetblanc and Baraduc 2007). Deubel et al. (1982) showed that introducing a brief blank after the saccade, followed by the reappearance of the saccade target, inhibited secondary saccades, as if delaying them until the return of visual feedback. Recent studies have attempted to draw a distinction between rapid (50–200 ms) corrective saccades that are pre-prepared based on the motor outflow and slower (200–300 ms) corrective saccades that are guided by visual feedback (Tian et al. 2013; Schut et al. 2017).

When available, post-saccadic visual information improves the accuracy of corrective saccades so that they compensate for about 70% of the error in the primary saccade (Prablanc et al. 1978; Tian et al. 2013), an increase from around 50% when only non-visual signals are available (Munuera et al. 2009; Tian et al. 2013). While many studies of corrective saccades have presented single saccade targets in darkness, in more naturalistic environments locating the saccade target in the post-saccadic scene is likely to require memory. Hollingworth et al. (2008) presented subjects with a circular array of coloured stimuli and exogenously cued one item as the saccade target. During the saccade, the array was rotated so that gaze landed in-between the cued target stimulus and another un-cued distractor. Participants consistently made corrective saccades to the item that had been cued rather than the distractor, even though both were equidistant from fixation and distinguishable only by reference to pre-saccadic appearance (Fig. 4a). This indicates that features of the saccade target (in this case, its colour) were stored in memory before the saccade and used post-saccade to reidentify the target and generate a corrective eye movement (see also Richard et al. 2008).

Hollingworth and Luck (2009) confirmed the role of VWM in this experiment by adding a concurrent task in which participants were instructed to remember the colour of a central stimulus in addition to making a saccade to a cued item in the periphery. As before, the array was rotated during the saccade so that gaze landed between the cued target and a distractor. When the distractor object matched the colour of the item the participants had been instructed to hold in memory, corrective saccades were slower and more frequently directed towards the distractor instead of the target, compared to when the distractor was an irrelevant colour.

One important caveat to these experiments is that participants were given an explicit instruction to fixate the object indicated by the cue and could not move on to the next trial until that goal had been accomplished. This is likely to have motivated participants to remember the target colour in order to complete the task quickly. In one experiment, Hollingworth et al. (2008) instructed participants to look away from the target (to an outer ring) if they perceived a movement of the array. They found that in many cases observers made a corrective saccade to the target before fixating the ring, suggesting they were unable to suppress the corrective eye movement. While this indicates that memory-guided corrective saccades can occur involuntarily, it does not clarify whether the act of memorizing the saccade target's features was itself automatic. Other lines of evidence do however support the idea that a saccade target is automatically assigned priority in memory (Bays and Husain 2008; Hanning et al. 2015; Tas et al. 2016; Ohl and Rolfs 2017).

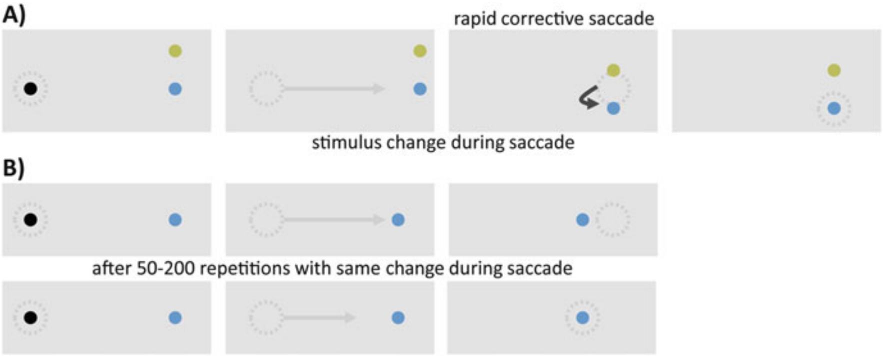

Fig. 4 Experimental methods for investigating correction and updating of saccades. (**a**) When a change is made to the display during an eye movement so the saccade lands at the midpoint between two stimuli, subsequent corrective saccades tend to be directed towards the stimulus that matches the surface features of the intended target. (**b**) When the saccade target is consistently displaced by the same distance over many trials, the saccade amplitude gradually adapts until gaze lands on the post-saccadic position of the target

5.2 *Saccadic Adaptation*

When saccade targets are systematically shifted during eye movements (Fig. 4b), so that the landing position consistently falls short of the target, then saccade amplitudes change progressively until gaze once again terminates close to the target on average (Hopp and Fuchs 2004; Pélisson et al. 2010; Prsa and Thier 2011). Subsequently eliminating the target shift will result in saccades overshooting its location, indicating that an adaptation of the saccade motor programme has taken place. Adaptation can be observed even when observers are unaware of the displacements of the target.

While it was initially proposed that corrective saccades provide the feedback required to adjust saccade amplitude (Albano and King 1989), the elegant demonstration of saccadic adaptation in the absence of corrective eye movements (Wallman and Fuchs 1998; Noto and Robinson 2001) demonstrated a role for visual feedback. Importantly, rather than the distance of the target from the fovea (Miller et al. 1981; Wallman and Fuchs 1998; Hopp and Fuchs 2004), saccadic adaptation is driven by a discrepancy between the predicted and actual location of the visual target in the post-saccadic image (Bahcall and Kowler 2000; Wong and Shelhamer 2011; Collins and Wallman 2012; Herman et al. 2013). For example, Collins and Wallman (2012) demonstrated that even when the trial-by-trial retinal error was identical across two experimental sessions, manipulating the predicted target position resulted in different magnitudes of saccadic adaptation.

These results suggest that memory for the pre-saccadic location of the saccade target is important for saccadic adaptation, but an influence of surface properties of the target initially proved difficult to establish. Bahcall and Kowler (2000) presented inward-shifting circular targets and outward-shifting square targets on alternating trials and found no evidence of adaptation. Similarly, after adaptation to a consistently displaced green cross, Deubel (1995) reported that the adaptation state persisted even when the target was changed to a red circle. In both cases, adaptation seems insensitive to visual features of the target. However, when the target is replaced during the saccade by two objects displaced in opposite directions, one visually matching the saccade target and the other distinct from it, saccadic adaptation is observed in the direction of the object that matches the pre-saccadic target (Madelain et al. 2010).

One explanation for the seeming discrepancy between studies is that saccadic adaptation is influenced by object continuity. When only a single object is present after the eye movement, there is no ambiguity as to the intended saccade target, and feature changes are ignored. In contrast, when a new object appears during the saccade, determining which object matches the intended target requires a comparison of surface features against memory of the pre-saccadic input.

When subjects are instructed to saccade to target objects that are presented overlaid on background images, consistent displacements of the background typically fail to induce saccadic adaptation (Ditterich et al. 2000; Robinson et al. 2000; Madelain et al. 2013). Only when observers are forced to rely on the background information – such as when the saccade target is blanked (Madelain et al. 2013) or when the target is itself defined as a specific location within a structured background (Deubel 1991; Ditterich et al. 2000) – do background displacements reliably induce adaptation. So, saccadic adaptation appears to be based on identification of the saccade target in the post-saccadic image where possible, but when this fails, comparisons to other pre-saccadic information may contribute (Herman et al. 2013). From the perspective of VWM, these findings are consistent with the evidence discussed above that the saccade target is compulsorily encoded into memory with high precision. When multiple objects are present, the saccade target will likely have the largest weight in assessing the accuracy of the eye movement because of its greater reliability. However, in its absence, other nearby objects or identifiable components of visual texture may be used.

5.3 Conclusion

The pre-saccadic content stored in VWM plays an important supporting role in correcting inaccurate eye movements, both through secondary saccades and adaptation of motor signals. While memory for the pre-saccadic location of the saccade target has the dominant influence, surface feature information and memory for nontarget objects both may be called upon when the location of the target in the post-saccadic scene is ambiguous. Future research could explore the dissociation between perception of transsaccadic change and saccadic adaptation, perhaps from the perspective of optimal decision where the cost of errors differs between the two mechanisms.

6 Discussion

By enabling the retention of visual information across the disruption of a saccade, VWM provides a means through which we can link pre- and post-saccadic information. This supports vital perceptual and oculomotor functions including detecting changes that occur during a saccade, permitting visual processing of stimuli to bridge a saccade, and correcting and compensating for errors in saccade endpoint. We note a number of consistent themes across the studies reviewed above that have investigated these different functions of transsaccadic memory.

The saccade target appears to have a unique status with respect to each of the functions we have considered. However, in every case we have also seen evidence that other elements of the visual scene are stored and compared across a saccade and can take on a dominant role when post-saccadic information about the saccade target is unavailable or compromised. While some theories have proposed that the saccade target is processed in a qualitatively different way from other items, we suggest that enhanced visual processing (Deubel and Schneider 1996) and prioritized encoding of the saccade target into VWM (Bays and Husain 2008) before the eye movement may be sufficient to account for its dominant influence on behaviour. According to this view, it is simply that the most precise and reliable evidence to survive the saccade is related to the target of the eye movement.

6.1 Optimality

One recurring theme is a shift away from heuristic models of processing (Gigerenzer and Brighton 2009) and towards models based on optimal inference (Knill and Pouget 2004). At one extreme, the process by which our perceptual system utilizes pre-saccadic representations has been depicted as a series of decisions unfolding in time after the saccade. In these models, the use of different sources of information hinges on the outcomes of preceding decisions, such that only subsets of the information present feed in to any decision. An example from the SSD literature would be the proposal that precise localisation information is always available after an eye movement but only consulted in certain circumstances, for example, if the saccade target cannot immediately be located. Another example is the (refuted) hypothesis that saccadic adaptation is driven solely by displacement of the target from the fovea. Both procedures would necessarily be suboptimal because some available, relevant information is not integrated into the decision-making process.

The contrasting hypothesis would be that all sources of information (from vision, memory, proprioception, and efference copy) are integrated in a statistically optimal manner (weighting each according to its reliability) to generate a single coherent and consistent set of estimates about the likely states of the observer and the world. These estimated states would determine our perception of changes in the environment, integrate pre- and post-saccadic features of object judged not to have changed, and drive corrective saccades and recalibration of oculomotor commands. According to Bayesian principles, these inferences would be based not only on the immediately available inputs but also on a lifetime of experience in how objects behave in everyday environments, expressed in the form of statistical priors.

While optimal inference models have been shown to capture aspects of transsaccadic processing better than heuristic models – for example, parsimoniously describing effects of saccade magnitude and direction on saccadic suppression of displacement (Niemeier et al. 2003) – the picture presented above is unlikely to be fully accurate. First, due to the complexity of the computations, in most cases exact Bayesian inference cannot feasibly be achieved by neural systems, meaning that an approximation of the optimal process is the most we can expect to find (Siegelmann and Holzman 2010; Penny 2012; Rich et al. 2015; Zhang et al. 2016). Second, there are experimental indications that different processes weigh information differently. For example, the information driving saccadic adaptation appears at least partially dissociable from the information contributing to awareness of the displacement of the saccade target (Souto et al. 2016). Also, limited feature integration appears to occur even between objects that observers judge changed or distinct (Wittenberg et al. 2008; Demeyer et al. 2010b). One possibility is that these dissociations arise from optimizing decisions under different cost functions, for example, our perceptual systems may be less averse to erroneously integrating two different objects than they are to failing to detect a change.

One area in need of more investigation is the role that previous experiences – prior information – have on how different sources of information are evaluated and used across a saccade. It is important to recognize that these priors may reflect not only our experience of the natural world but also the specific context described by a psychophysical experiment. During one trial of a typical study, participants briefly view a sparse, static visual image on a computer display before making a single saccade to an instructed location. While their judgements will undoubtedly be informed by experience of objects in the everyday world, it also seems reasonable to assume that participants are learning about the behaviour of these particular blobs of light as the experiment progresses. The extent to which mechanisms such as transsaccadic integration are malleable, and on what timescales, must be established for us to relate conclusions drawn from laboratory observations to natural vision.

6.2 Object Correspondence

Another clear theme to emerge from our review is the important role of object correspondence in determining how pre-saccadic visual information is used after the saccade. For each of the VWM functions considered, we have found evidence that changes to features of an object that are secondary to the task nonetheless modulate the influence of pre-saccadic memory. For example, the displacement of a target orthogonal to the saccade can relieve saccadic suppression of its shift in the direction of the saccade (Wexler and Collins 2014). Inferring which objects in one image correspond to objects in another is a challenging computational problem that remains unsolved in computer vision and machine learning. An object could move location, but otherwise remain the same object, and thus although seen at an unexpected location should still inherit remembered information about its content. Similarly, one feature of an object may unexpectedly change – such as a multicoloured LED lamp changing colour – without affecting other features such as shape and location. However, at other times these changes may correspond with the disappearance of one object and the appearance of an entirely new object, where inheritance of the previous properties would be undesirable. Beyond being simply present or absent, single objects can also be perceived to split into smaller objects, or objects can merge to form a single object.

The need to weigh up evidence for every possible such combination of changes to objects in a scene is part of the reason that full Bayesian inference is infeasible. Understanding what compromises the visual system makes to approximate optimal inference is an important avenue for future research.

6.3 Memory Limitations

As discussed in the Introduction, our ability to detect changes across an eye movement, or explicitly recall what we saw before our eyes moved, is typically found to reflect the limited capacity of VWM. Recent developments in our understanding of VWM have led to the idea that its limits are best expressed in terms of a limited resource, flexibly allocated to objects to determine the resolution of their storage (Ma et al. 2014). However, the implications of this new view of VWM for transsaccadic processing have received only preliminary investigation. For example, we know that the saccade target receives a disproportionate share of resources, but what factors influence the size of this share, and how are the remaining resources distributed between other elements of complex visual scenes?

A final consideration is that, while there is strong evidence that the shorter-lived forms of visual persistence contribute little or nothing to our explicit awareness of transsaccadic changes in real scenes, the possibility that they play a part in implicit processes, including transsaccadic integration and saccadic adaptation, has not been definitively ruled out. The critical test will be whether these processes are subject to the same strict resource limits as explicit change detection, indicating a reliance on VWM alone. These open questions, like many of those uncovered in this review, will only be answered by moving beyond single target displays to study more complex and naturalistic scenes.

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