Vision during saccadic eye movements

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Abstract

The perceptual consequences of eye movements are manifold: each large saccade is accompanied by a drop of sensitivity to luminance-contrast, low-frequency stimuli, impacting both conscious vision and involuntary responses, including pupillary constrictions. They also produce transient distortions of space, time and number, which cannot be attributed to the mere the motion on the retinae. All these are signs that the visual system evokes active processes to predict and counteract the consequences of saccades. We propose that a key mechanism is the reorganization of spatiotemporal visual fields, which transiently increases the temporal and spatial uncertainty of visual representations just before and during saccades. On the one hand, this accounts for the spatiotemporal distortions of visual perception; on the other hand, it implements a mechanism for fusing pre- and post-saccadic stimuli. This, together with the active suppression of motion signals, ensures the stability and continuity of our visual experience.

The world seems to stay put, despite continual saccadic eye movements that actively reposition our gaze, two to three times a second. The problem of visual stability during eye movements is an old one, already formulated in the clear terms by 11th century Persian scholar Alhazen: "For if the eye moves in front of visible objects while they are being contemplated, the form of every one of the objects facing the eye … will move on the eyes as the latter moves. But sight has become accustomed to the motion of the objects' forms on its surface when the objects are stationary, and therefore does not judge the objects to be in motion" (Alhazen 1083). To date, the problem is far from solved; it can be broadly divided into two separate issues: why do we not perceive the *motion* of the retinal image produced as the eye sweeps over the visual field? – and how do we cope dynamically "on-line" with the continual changes in the retinal image produced by each saccade to construct a stable representation of the world from the successive "snapshots" of each fixation? This review highlights the progress made in the last decades in these fields; we focus on large saccades: for smooth pursuit eye movements please see the recent review by Schutz and colleagues (Schutz et al. 2011); for small saccades and drift (fixational eye movements) please refer to another recent Annual Review of Vision Science (Rucci & Poletti 2015).

Active, Selective Saccadic Suppression

One major component of the general problem of visual stability is why the fast-motion of the retinal image generated by the movement of the eyes completely escapes notice: comparable wide-field motion generated externally is highly visible, and somewhat disturbing (Allison et al. 2010, Burr et al. 1982). It has long been suspected that vision is somehow suppressed during saccades (Holt 1903), but the nature of the suppression has remained elusive. Now it is clear that the suppression is neither a "central anaesthesia" of the visual system (Holt 1903), nor a "grey-out of the world due to fast motion" (Campbell & Wurtz 1978, Dodge 1900, Woodworth 1906), as this motion is actually visible, extremely so at low spatial frequencies (Burr & Ross 1982). What happens is that some stimuli are actively suppressed by saccades, while others are not: stimuli of low spatial frequencies, presented very briefly and in optimal conditions to discard retinal painting, are very difficult to detect if flashed just prior to a saccade, while stimuli of high spatial frequencies remain equally visible, as shown in figure 1A (Burr et al. 1982, Volkmann et al. 1978). *Equiluminant* stimuli (varying in colour but not luminance) are not or minimally suppressed during saccades (Braun et al. 2017, Gu et al. 2014), and can even be enhanced (Burr et al. 1994, Diamond et al. 2000, Knoll et al. 2011, Uchikawa & Sato 1995), implying that the parvocellular pathway, essential for chromatic discrimination, is left unimpaired, while the magnocellular pathway is specifically suppressed (Fig 1A). These results are corroborated by poor sensitivity to motion perception (Burr et al. 1982, Burr et al. , Shioiri & Cavanagh 1989), with suppression taking place at the input of the motion detection

signals (Burr et al. 1999) and not at level of conscious motion perception. Poor sensitivity does not mean complete blindness to motion. Indeed, some residual perception of motion can be elicited due to retinal painting: during the saccade, stationary stimuli are represented on a moving retina and therefore produce a retinal motion signal, which may be perceived (Castet et al. 2002), consistent with the idea that the motion suppression does not occur at high decision levels; for the same reason, stimuli moving at very high speed (invisible in fixation) produce a slower retinal motion during a saccade in the stimulus direction, and may become visible (Castet & Masson 2000). Neither of these phenomena is evidence against the reduction of magnocelluar sensitivity during saccades and neither shows how good (or poor) motion perception is during saccades. They both are consistent with the hypothesis that magnocellular activity is strongly but not completely suppressed during saccades – which we suggest could be enough to reduce the salience of the strong full-field motion that would otherwise have a distracting and disruptive effect on perceptual continuity.

Saccadic suppression follows a specific and very tight time course, illustrated in Fig. 1B (replotted from Diamond et al. 2000), which is very different from saccadic enhancement for equiluminant stimuli (fig 1C 1F replotted from Knoll et al. 2011). Sensitivity for seeing low spatial frequency, luminance-modulated brief stimuli declines 25 ms before saccadic onset, reaches a minimum at the onset of the saccade, then rapidly recovers to normal levels 50 ms afterwards. The suppression effect is multiplicative and homogeneous at all eccentricities (Knoll et al. 2011), in contrast to what was previously postulated (Mitrani et al. 1970). Does the suppression result from a central non-visual "*corollary discharge*" signal (Wurtz 2008), or does it result simply from visual "masking" effects? This would seem unlikely, as great care was taken to ensure a uniform surround. However, the question is important. In order to be certain that the saccade itself was essential for the suppression, we simulated saccadic eye movements, by viewing the stimulus setup through a mirror that could be rotated at saccadic speeds. When the background was uniform, with minimal visual references, the simulated saccades had little or no effect on sensitivity (open symbols of Fig. 1B).

But that is not to say that under more natural conditions masking does not occur. When the test stimulus is embedded within a textured screen, simulated saccades do decrease contrast sensitivity (Fig. 1D). This pattern of results has also been observed with more natural signals, like real scenes (Dorr & Bex 2013), pointing to visual masking contributing to suppression in the presence of a visual background. Interestingly during simulated saccades and in the presence of a masking background (noise or natural scenes), high spatial frequencies are suppressed like low ones, strengthening the suggestion that real saccades and masking effects tap different mechanisms. Before the saccade, the two cooperate with similar dynamics. After saccadic offset, however, the

two mechanisms behave very differently: the suppression lasts for much longer for masking, compared to a real saccade (Fig.1D). This suggests that after the saccade, sensitivity is greater than that expected with comparable motion without the saccade, implying a post-saccadic facilitation. The timing for this post-saccadic facilitation is very similar to that observed for equiluminant stimuli. Interestingly, for the equiluminant stimuli, the simulated and real saccade produce the same effects (closed and open symbols of Fig 1F), indicating that the facilitation is related to the spurious retinal motion and not to an active mechanism associated with the saccade. This is true also for small perisaccadic suppression sometime observed also for equiluminat gratings presented at peripheral eccentricities (see figure 5C in Braun et al. 2017, Knoll et al. 2011)

Fig 1 about here

That luminance-contrast suppression is different for real saccades and simulated saccades shows that suppression results at least in part from an active, extra-retinal signal. The interaction between this active suppression signal and the spurious retinal motion generated by the eye movement must occur exactly at the crucial time: at saccadic onset. Given that saccadic reaction times are long and variable, the temporal synchronization between suppression and saccade onset may be not easy to achieve. Recently we observed that saccadic suppression is systematically embedded in a series of oscillations of contrast sensitivity that fluctuate rhythmically in the delta range (at about 3 Hz), commencing about one second before saccade execution and lasting for up to one second after the saccade. Synchronization of internal rhythms leading to perceptual oscillation are consequences of many events, like any abrupt sensory signal or attentional shift and even a decision process (Engel et al. 2001, Schroeder et al. 2010, VanRullen & Koch 2003) }.To avoid that the oscillation could be induced by exogenous signals (like flashing the saccadic target) we asked the subjects to perform saccades at their own (slow) pace and we eliminated nearly all visual cues. The results show that saccadic preparation and visual sensitivity oscillations are coupled and we suggest that the coupling might be instrumental in temporally aligning the initiation of the saccade with the visual suppression (Fig 1C reproduced from Benedetto & Morrone 2017). Interestingly the timing of the first post-saccadic peak in detectability (Fig 1C) correspond very well with the facilitation observed in Fig 1D and in Dorr & Bex (Dorr & Bex 2013), and is consistent with the boost of visibility at low frequency displayed for long duration observed by Boi et al (Boi et al. 2017). The facilitation, which may help to achieve an optimal recruitment of information at the various spatial scales of analysis (Boi et al. 2017), is a result of an ongoing oscillation (see Fig 1C) generated by the synchronization of endogenous internal rhythms.

Additional evidence in support of the idea that saccade planning actively modulates visual sensitivity comes from developmental studies. The amount of suppression at saccadic onset varies with age, and is much stronger in adolescent children of 12-14 years than in adults (Bruno et al. 2006), even though motion perception and masking are largely adult-like by that age (Maurer et al. 2005, Parrish et al. 2005). This suggests that the mechanisms mediating suppression are still developing into late adolescence. As the saccadic motor system is also not completely mature during adolescence (Fischer et al. 1997), this is further evidence that the extra-retinal signal responsible for mediating the saccadic suppression may be linked to the motor system.

Psychophysical studies indicate that saccadic suppression occurs early in the visual system (Burr et al. 1994), at or before the site of contrast masking (Watson & Krekelberg 2011), and before low-level motion processing (Burr et al. 1999). Thilo *et al.* (2003) addressed this question more directly with a clever electrophysiological technique. Replicating an old study by Riggs *et al.* (1974), they showed that visual phosphenes produced by electrical stimulation of the eye are suppressed during saccades. But phosphenes of cortical origin — V1 or V2 — generated with the technique of transcranial magnetic stimulation (TMS) were not suppressed. This strongly suggests that saccadic suppression occurs early, before the site of generation of cortical phosphenes, probably within the lateral geniculate nucleus (LGN), or perhaps within V1 itself. An fMRI (Sylvester et al. 2005) study that measured BOLD activity of LGN while subjects made saccades over a field of constant illumination (to avoid the generation of spurious retinal motion) showed a clear suppression in both LGN and V1, reinforcing early suggestions of saccadic suppression in the dark in V1 (Bodis-Wollner et al. 1999, Paus et al. 1995). Interestingly, the amplitude of the BOLD responses in V1 decreases as the stimuli were presented closer to the saccadic onset, following a dynamic similar to that observed psychophysically (see stars in Fig 1B taken fromVallines & Greenlee 2006), again suggesting an early site of action.

Although evidence for suppression at these early stages, V1 and LGN, is strong, there is also fMRI evidence for later post-thalamic modulation of responses. For example, the BOLD response to luminance stimuli is relatively suppressed compared with that to chromatic stimuli during saccades, but the attenuation varies across areas (Kleiser et al. 2004), strong in MT – as expected – but also strong in V4, a cortical area receiving more parvocellular than magnocellular input (Watson & Krekelberg 2009). That saccadic suppression occurs at multiple different levels should not be surprising. Many basic sensory phenomena, such as gain-control, do not occur at a single site but at virtually every possible location: photo-receptors, retinal ganglion cells, LGN cells and cortex (Shapley & Enroth-Cugell 1984). Indeed, the parallels between saccadic suppression and contrast gain control are strong, suggesting that they may share similar mechanisms. During saccades, the

temporal impulse response to luminance, but not to equiluminant stimuli, becomes faster and more transient (Burr & Morrone 1996). These results suggest that saccadic suppression may act by attenuating the contrast gain of the neuronal response, causing a faster impulse response (Shapley & Victor 1981). Changing contrast gain makes neurons less responsive to low contrast stimuli, decreasing the effectiveness of the spurious signals caused by the saccade, hence facilitating the recovery to normal sensitivity. This would certainly be an elegant and economical solution to the problem of saccadic suppression, taking advantage of mechanisms already in place.

The idea that gain control explains both the suppression and rapid recovery during saccades has been implemented in a model that simulates quantitatively the time course of contrast sensitivity in normal and simulated saccade (Diamond et al. 2000). Interestingly, changing response gain is one of the few mechanisms that can explain simultaneously many saccadic suppression properties. It can account for the similarity in sensitivities of real and simulated saccade in presence of a noise background, but not with homogeneous background; and it can explain the dependence of suppression from input noise (Watson & Krekelberg 2011). It can also explain the post-saccadic enhancement; the change of the impulse response function (Burr & Morrone 1996), and also the change in the strength of masking between brief pre- and post-saccadic stimuli (Burr et al. 1994). Interestingly, all these properties observed measuring human sensitivities (peri-saccadic gain modulation, suppression followed by facilitation with dynamic similar to those observed by simulated saccades) have been also observed at level of single unit of monkey V1 (McFarland et al. 2015). Both sets of evidence (for a complete review of single unit evidence, please refer to Wurtz 2008) agree in suggesting the role of an internal signal that modulates response gain also at thalamic levels. By operating on gain-control mechanisms, saccadic suppression would serve two important roles: the suppression of image motion, which would otherwise be disturbing, and the rapid return to normal sensitivity after the saccade.

Spatial and Temporal Distortions of object localization During Saccades

Besides the (relatively) simple problem of suppressing the motion caused by the fast-moving image on the retina, the brain must also take into account the saccadic movement when determining the instantaneous position of objects in space. Like Alhazen, Helmholtz (1866) recognized that "the effort of will involved in trying to alter the adjustment of the eyes" could be used to help stabilize perception. Models based on similar ideas of compensation of eye movements were proposed by Sperry (1950) in the 1950s with the concept of corollary discharge and by Von Holst and Mittelstaedt (1954) of efference copy: the effort of will of making the eye movements (corollary

discharge or efference copy) is subtracted from the retinal signal, to cancel the motion produced by the eye-movement and stabilize perception. Now we know that retinal motion signals cannot be easily compensated, given the sophisticated analysis performed by motion detectors. However, there is evidence for the existence of a corollary discharge signal that must be instrumental in maintaining visual stability: both neurophysiological (reviewed by Sun & Goldberg 2016, Wurtz 2008), and psychophysical. The latter is primarily related to the perisaccadic distortions of visual space perception. The first report dates back to the 1960s, when Leonard Matin and others reported large transient changes in spatial localization at the time of saccades. When asked to report the position of a target flashed during a saccade, subjects mislocalized it, primarily in the direction of the saccade (Honda 1991, Mateeff 1978, Matin & Pearce 1965). Later, Mateeff and Honda measured the time-course of this effect and showed that the error starts about 50 ms before the saccadic onset and continues well after fixation is regained. The error before the saccadic onset has been taken as an indication of the existence of a slow and sluggish corollary discharge signal that compensates partly for the eye movement: the internal representation of the position and the actual position of the gaze do not match, resulting in errors in the localization of a briefly presented visual target. But localization errors can be more complex: when examined in photopic conditions, visual space is not so much shifted in the direction of the saccade, but *compressed* towards the saccadic target (see Fig 2A, reproduced fromMorrone et al. 1997, Ross et al. 1997).

Fig. 2 about here

Objects flashed at saccadic onset to a range of positions, from close to fixation to positions well beyond the saccadic target, are all perceived at or near the saccadic target. The effect is primarily parallel to the saccade direction (Ross et al. 1997), although a small compression is also observed in the orthogonal direction (Kaiser & Lappe 2004, Zimmermann et al. 2015, Zimmermann et al. 2014c). These results are intriguing because they indicate that the process described mathematically as a simple translation of the internal coordinate system is not plausible: perhaps the system cannot perform the transformation of space, without additional perceptual costs. The peri-saccadic compression of space is so strong that four bars, spread over 20 degrees, are perceived as fused into a single bar (Ross et al. 1997). Discrimination of shape (Matsumiya & Uchikawa 2001) or colours (Lappe et al. 2006 , Wittenberg et al. 2008) of the bars is still possible, but counting them and perceiving them in separate positions is not. The fact that the feature itself is not lost or compressed suggests that the mislocalization occurs at a relatively high level of analysis, after feature extraction.

What causes the different perisaccadic behaviours, mislocalization or compression? It has been suggested that saccadic compression occurs only when visual references are present. However, several studies have shown that visual references *per se* (like scattered points on the monitor) do not affect localization of a perisaccadic probe, which is only affected by two kinds of stimuli: the saccade target, and/or another perisaccadic stimulus with matching visual features (Cicchini et al. 2013, Zimmermann et al. 2014c). The saccade target is the focus of perisaccadic compression and no compression is observed when the saccade target is withheld (Zimmermann et al. 2014c). A saccade without saccade target is an uncommon scenario, but it is typically encountered in experiments using the double-step saccade paradigm (Zimmermann et al. 2015). Subjects are instructed to move their gaze sequentially trough two positions, and their markers are removed well before the eye movement sequence is initiated. Flashed stimuli presented at about the time of the second saccade are localized quasi-veridically, showing no compression (Fig.2B) – whereas stimuli presented at about the time of the first saccade are subject to the usual pattern of mislocalization, drawn toward the saccade target (as in Fig.2A). Another condition claimed to be exempt of compression is when stimuli are presented in complete darkness (Awater & Lappe 2006, Lappe et al. 2000). However, in this case, the pattern of localization errors may be complicated by an additional phenomenon: a mislocalization of the saccade target itself (Awater & Lappe 2006, Morrone et al. 2005a), which might be drawn toward the flashed bar – implying that compression is still strong, only anchored to a different stimulus.

Perhaps the strongest influence on the localization of a perisaccadic flashed stimulus is exerted by another similar stimulus flashed in close temporal proximity. Almost irrespective of where the two stimuli appear, they are usually perceived as co-localized and, in some special cases, this leads to annulling the perisaccadic mislocalization (Morrone et al. 1997, Park et al. 2003, Pola 2007, Zhang et al. 2004). For example, no mislocalization occurs when the perisaccadic stimulus is preceded by a prolonged continuous or flickering stimulus with similar features (Sogo & Osaka 2001, Watanabe et al. 2005). We performed a systematic study of these interactions, using pairs of flashed stimuli separated by 80 ms. In one of the experiments, the probe was flashed at a fixed location (same as in Fig.2A, green bar), but was followed by a "reference" stimulus at variable spatial separation (due to the 80 ms temporal distance, the reference was always post-saccadic, and always seen clearly and stably). We found that the two bars interacted with each other, and were mostly perceived as superimposed at the same position. This strong attraction is observed within a very broad range (Fig. 2C) of spatial separations, as large as the saccade itself (about 20º of horizontal space), and across a large range of temporal separations, 200-300 ms, about four times the saccadic duration. Consistent results have also been obtained with a completely different

technique, classification images: this estimates the spatio-temporal window over which stimuli are integrated, and shows that during saccades this is enlarged and slanted in space-time (Panichi et al. 2012). On the other hand, relative independence of mislocalization was found between stimuli of different shapes presented at different temporal intervals (Hamker et al. 2008), displaced orthogonally to the saccade (Morrone et al. 1997, Sogo & Osaka 2002) or of incongruent orientations (Cicchini et al. 2013). These findings suggest that the visual system has a mechanism for maintaining positional constancy of objects across saccades, within a large but well defined spatiotemporal receptive field. Perisaccadic compression may be a by-product of this mechanism, attempting to fuse perisaccadic stimuli with any sensible visual signal available after the saccade that may potentially match the pre-saccadic stimuli: in the lack of a better match, the saccade target might serve as an attractor, given the large amount of attentional resources that it absorbs during saccadic programming (Deubel & Schneider 1996, for review see Kowler 2011).

The key feature of the spatiotemporal interaction field in Fig. 2C is its orientation in space-time: the field is slanted along the trajectory of spurious retinal motion. We suggest that this reflects the action of transiently altered neuronal receptive fields. Visual detectors with spatiotemporally oriented receptive fields are very common in the primate brain. They are fundamental for the computation of motion trajectories, particularly for perceiving the form of the moving object, which would otherwise be subject to heavy motion smear (Burr 1980, for review seeBurr & Thompson 2011). All models of motion perception, from Reichardt's (1957) classic proposal, involve non-linear combination of systematically delayed signals, which generates a spatiotemporal orientation of receptive fields. An analogous strategy may be used to stabilize visual images during saccades, as transiently oriented receptive fields could serve to effectively eliminate the spurious motion signals caused by the movement of the eyes. This profound alteration of neural receptive fields may be crucial to achieve perceptual stability. The perisaccadic extension in space and in time is so large that pre- and post-saccadic information can both activate the same detector, allowing for the integration of images from the two successive fixations. Importantly, only congruent information, concerning similar features, will take place.

This mechanism for perisaccadic fusion of congruent information could be implemented by the "remapping receptive fields" observed in many visual cortical cells (Duhamel et al. 1992). We do not discuss how and where in the brain this phenomenon is observed, thoroughly reviewed by Wurtz (2008). What we would like to highlight is the computational mechanism that might support the formation of a such a spatio-temporal receptive field oriented along the saccadic direction, as seen in Fig.2C. At least two elements are necessary: one is an intention-to-move or "corollary discharge" signal, necessary to give the direction and amplitude of the saccade to which the

interaction field must be parallel. And the other is, like in Reichardt's model, a temporal delay of visual processing, which varies with stimulus position, and determines the space-time orientation of the field.

Although not in the focus of the initial investigations, there is now good evidence that atypical delays are a key feature of perisaccadic visual processing. Binda et al (2009) showed that the perceived time at saccadic onset (measured by matching an auditory tone) is delayed by about 100 ms. This perceived delay is consistent with the delay of the "remapped" response observed by Nakamura et al (2002) and Wang et al. (2016): visual activity at the "future" post-saccadic position of the receptive field typically emerges with a much longer latency than typical visual responses, and the onset of the response is often locked to the time of the saccade execution – rather than to stimulus presentation (Sommer & Wurtz 2006). This delay also implies that stimuli presented at saccadic onset are coincident with stimuli presented soon after saccades, and this could facilitate the interpretation of their position in the post-saccadic coordinate system, in a form of *post-diction* (Eagleman & Sejnowski 2000). Possibly related is the phenomenon of chronostasis, where the perceptual report is of time "stopping" at the end of a saccade, transiently freezing the state of the world with each saccade (Yarrow et al. 2001). However chronostasis is observed also during simulated saccades, suggesting that a strong component of the phenomenon may be passive and related to stimulus visibility and masking (Knoll et al. 2013). On the other hand, the peri-saccadic time-interval distortion (Fig. 3A) is tightly linked to saccade execution, like spatial mislocalizations; and we found that the size of the perceptual temporal delay is correlated – on a trial by trial basis – with the size of mislocalization errors. All this fits with the idea that temporal delay is one of the mechanisms explaining spatial perception during saccades, and it is also consistent with the long temporal extension of the peri-saccadic receptive field (Fig. 2C), which extends well after the saccade is completed. Two independent proposals model the temporal and spatial effects together, assuming a travelling wave of activity moves in the remapping direction, from the original to the future location of the receptive field over the short time preceding the saccade: a concept proposed in Binda et al. (2009) and formalized in Wang et al. (2016)

Fig. 3 about here

Delay is not the only temporal distortion seen perisaccadically; about 50 ms before saccade the opposite effect is observed, with a latency reduction of about 20 ms (Fig.3A) (Binda et al. 2009). This may seem a small effect, but it is sufficient to produce the most dramatic alteration of the sense of time: an inversion of the perceived temporal sequence (Binda et al. 2009, Kresevic et al. 2016, Morrone et al. 2005b, Yabe et al. 2014), as exemplified in Fig. 3B. Again this is consistent with the neurophysiology of visual responses, as the pre-saccadic latencies of remapping neurones in areas

MT and MST are shorter before real saccades than simulated saccades (Price et al. 2005). Temporal inversion before the saccade and post-diction around the saccade also affect the perceived duration of perisaccadic events (Morrone et al. 2005b). When asked to compare the perceived duration of a temporal interval presented around the time of a saccade with one presented 2 secs afterwards, subjects judged it much shorter, about half the duration (Fig. 3C). The time course of the temporal distortion is quite tight and, after taking into account the duration of the stimuli and the effect of contraction, similar to that of the spatial compression; temporal and spatial compression may well be manifestations of a common neural cause, possibly the same distortion in the space-time metric induced by the transient orientation of the interaction field (Fig. 2C).

Another key feature of the latter is its spatial tolerance: it extends over several degrees in space (perisaccadic spread over the y-axis in Fig. 2C). This suggests that localization during saccades is variable or imprecise – so much that a probe at any given position can be seen as co-localized with a reference more than 20 deg away from it (for a 20 deg saccade). Perisaccadic loss of localization precision is consistent with much evidence that visual spatial information is degraded at the time of saccades, and with modelling work showing that perisaccadic perception is well accounted for by optimal cue integration (Niemeier et al. 2003). One example is the evidence obtained by testing multisensory integration of audio-visual spatial cues during saccades. Auditory stimuli are usually far more difficult to localize in space than visual stimuli: when vision and sound are in conflict, vision dominates (the "ventriloquist effect") as predicted by optimal integration. However, when visual stimuli are artificially degraded by blurring, audition can dominate (Alais & Burr 2004), again consistent with optimal integration. As saccades have little effect on auditory space perception (Harris & Lieberman 1996), optimal integration predicts that, perisaccadically, audition should transiently become dominant over the degraded visual localization signals. Indeed audio-visual stimuli (bars and beeps presented together in the same spatial position) are mislocalized much less than visual stimuli presented alone, in line with the idea that visual information is given a low weight during saccades (Binda et al. 2007). This model assumes that the multisensory integration occurs after visual signals are subject to mislocalization, and this is also supported by showing that the time-course of visual mislocalization is unaltered when the perceived time of the visual stimuli is displaced forward or backward due to an auditory temporal cue (Binda et al. 2010).

Optimal integration and loss of visual precision may also explain the phenomenon of "saccadic suppression of displacement" (Bridgeman et al. 1975). This is another form of insensitivity occurring during saccades that, despite its name, should not be considered as a manifestation of saccadic suppression of contrast sensitivity, but as a form of spatial stability: where matching pre- and post-saccadic stimuli are seen at the same spatial position, even when a large displacement is

introduced during the saccade (for review, see Zimmermann et al. 2014b). Neimeier et al. (2003) suggested that this is simply a consequence of near-optimal integration of retinal and extra-retinal corollary discharge signals; and a similar concept has been recently proposed by Crevecoeur and Kording (2017). In all cases, the key concept is that visual information is imprecise during saccades, and therefore weighted less, ultimately favouring spatially stable, continuous perception. In fact, the large interaction field depicted in Fig. 2C implements a mechanism for saccadic suppression of displacement (it allows for co-localizing trans-saccadic stimuli across large displacements), essentially supporting spatial stability. However, it is important to point out that this transient reorganization of visual receptive fields is only the first step towards building a stable spatiotopic visual representation, which probably relies on additional coordinate transformations of spatial mechanisms anchored in external coordinate system (for reviews, see: Burr & Morrone 2011, Burr & Morrone 2012, Melcher & Morrone 2015, Zimmermann et al. 2014b).

What accounts for the large range of spatial integration and consequent spatial imprecision? One possibility is that the visual signal itself is degraded. Another possibility, which we favour, is that the noisiness and sluggishness are properties of the corollary discharge signal: which does not (and probably cannot) exactly reproduce the dynamics of the eye movement (Crevecoeur & Kording 2017). This is in line with computational work as well as with experimental work attempting to manipulate the reliability of corollary discharge signals, e.g. by studying rapid sequences of eye movements as in the double-step paradigm. There is evidence suggesting that the two steps are planned in parallel before the initiation of the sequence, and that a single corollary discharge signal is issued at the beginning of the movement. If this were the case, lack of a corollary discharge signal during the second saccade would explain both the absence of compression (Fig.2B) and also, crucially, that perceptual stability is challenged during this second saccade, supporting the concept that compression reveals a mechanism important for trans-saccadic stability (Zimmermann et al. under review).

Our proposal is that all these spatiotemporal distortions of localization are consequence of the mechanisms aimed at maintaining perceptual stability across saccades, which depend on the action of "intention to move" or "corollary discharge" signals. Others have questioned this idea, showing that qualitatively similar phenomena may occur away from saccades, simply in connection with a visual disturbance that partially resembles the fast retinal motion during the eye movement (Zimmermann et al. 2014a). However, those effects are small compared with the effects of saccades: spatial compression during saccades reduces the distance among stimuli by nearly 100% or more, whereas the maximum compression observed with masking is about 50% (Zimmermann et al. 2014a); similarly, the temporal compression effect in Morrone et al. (2005b) was as strong as

50%, whereas it never goes beyond 20% in the masking experiments by Zimmermann et al. (2014a). Like for saccadic suppression, we do not question that masking effects accompany the execution of a saccade. Simply, we note that these effects are not nearly large enough to explain the distortions observed during the saccade.

Peri-saccadic changes of high-level visual and cognitive processes

The process of establishing a spatio-temporal continuity of visual perception appears to impact on higher level functions as well: not just spatial and temporal localization, but also numerosity, size perception and mental calculation. This provides one of the most robust pieces of evidence on the existence of a shared "metric" for quantity (Walsh 2003), which overlaps the neural representation of motor actions, and accompanying intention to move or corollary discharge signals (Burr et al. 2010a). Several investigators have postulated links between space, time and number, often from circumstantial and somewhat weak evidence. Much relies on the coincidence of neural areas (e.g. intraparietal cortex) and on small advantages in reaction times that can often be put down to congruency effects. The fact that reaction times are faster to small numbers on the left and larger numbers on the right does not necessarily imply a hardwired connection. On the other hand, the effect of saccades appears to be congruent and synchronized: always an underestimate of magnitude, always peaking at saccade onset, always recovering with the same dynamics (after accounting for the stimulus duration itself). Spatial and temporal compression consist in underestimating distance: in space and time. These are accompanied by an underestimation of numerosity (Binda et al. 2011, Burr et al. 2010a), a primary sensory feature (Burr & Ross 2008), perceived independently of other spatial attributes like texture and size (Cicchini et al. 2016). This means the same number of dots is perceived as less numerous if transiently flashed perisaccadically. To demonstrate this, we asked subjects to compare the number of elements in a random test array flashed at the time of a saccade to that of a reference stimulus presented well before the saccade (Binda et al. 2011). Figure 4A illustrates how apparent numerosity varied with time relative to the saccade. Well before or after the saccade, numerosity estimation is veridical, but near saccadic onset there is a large and systematic underestimation of number – perceived numerosity is nearly halved. The time course of the compression follows closely those of space and of time. As with saccadic compression of space and time, there is no underestimation of number when simulating the saccade with a fast mirror motion (Binda et al. 2009, Binda et al. 2011, Morrone et al. 1997). Importantly, the spatial displacement and compression of the individual elements cannot account for the effect, as shown by a series of control conditions as well as by a subsequent study using symbolic representations of numerical quantity (Binda et al. 2012). In the latter, we show that numerical magnitude is misestimated even when it is represented by digits that subjects had to sum

or subtract (Fig.4B). When the saccade was made during the mental arithmetic (i.e. the digits were displayed before the saccade, between the appearance of the saccade target and the onset of the saccade) the result was systematically underestimated (Binda et al. 2012): a "compression" of about 10%, proportionally similar for large two-digit figures and smaller one-digit figures.

Fig. 4 about here

How would mental arithmetic be affected by spatiotemporal remapping? One possibility is that action and number (quantity) representation impinge on the very same circuit, as also suggested by other lines of evidence where the execution of a repetitive action, tapping, influences the perception of numerosity: our perception of how many dots are on the screen, depends on how many times we tapped (Anobile et al. 2016, Arrighi et al. 2014). Of course, saccades (and other actions) also impact on more general-domain abilities, like short-term memory and attention. These functions certainly have an effect on complex cognitive tasks, but again, evidence to-date suggests that the effects of saccades are much stronger that the effects of dividing or diverting attention (e.g. for numerosity: Burr et al. 2010b)

Indexing Intention and Attention through Pupil Diameter

The studies discussed in the previous sections highlight the importance of considering the role of attention in eye movements (for a full discussion of attentional modulation during saccades please refer to Kowler 2011, Zhao et al. 2012). Disentangling the effect of attention and eye movements has been a continual effort since Kowler and colleagues accepted the challenge in 1995 (Deubel & Schneider 1996, Kowler et al. 1995, Sheliga et al. 1995). However, recent research into movements of intrinsic muscles controlling the pupils of the eyes suggests that attention and intention may be efficiently and implicitly tracked by measuring pupil diameter.

The light response was historically considered a low-level reflex without any cognitive component (Loewenfeld 1993), preserved across many vertebrates and even some invertebrates (Douglas et al. 2005). However, recent studies have shown that the light response in humans is far more than a reflex, and reveals what you attend to, how you interpret what you see and how you intend to act (Binda & Murray 2015a). For example, a recent series of studies have demonstrated a previously unappreciated role of attention in modulating the pupillary light response: the pupils constrict when a light is flashed, but it constricts more if the subject's attention is directed towards the light source, either voluntarily in human participants (Binda & Murray 2015b) or by microstimulation of a FEF cell with receptive field covering the light source, in non-human primates (Binda & Gamlin 2017, Ebitz & Moore 2017); and, conversely, when illumination remains

constant, attending to a light source is sufficient to evoke a pupillary constriction (Binda et al. 2013, Binda et al. 2017).

Saccades provided one of the first pieces of evidence that the pupillary light reflex incorporate complex information of likely cortical origin: it was shown in the 60s that the pupil constriction in response to a flash is markedly reduced if the flash occurs during a saccade, and is thereby subject to saccadic suppression (Lorber et al. 1965, Zuber et al. 1966). We recently resumed this research comparing the suppression of pupillary responses with the suppression of visual perception (Benedetto & Binda 2016). Although both are systematic strong effects, peaking at about the time of saccade onset, we were surprised to find a lack of correlation between the two. The pupil response could be depleted (as shown comparing the coloured traces in Fig.1E) in trials where the stimulus was detected, and it could strong and brisk in trials where the stimulus was suppressed from awareness. This is not the first case where perisaccadic visual stimuli evoke different conscious and sub-conscious vision. For example, stimuli suppressed from awareness can still affect subsequently presented visual stimuli, like in the "shape contrast" paradigm where a line presented perisaccadically and made invisible due by saccadic suppression is nonetheless effective at biasing the apparent shape of a subsequently presented ellipse (Watson & Krekelberg 2009). Also, several experiments have shown different patterns of perisaccadic mislocalization when participants indicate their response by a verbal report or with a blind ballistic motor action, like pointing (Burr et al. 2001, Hallett & Lightstone 1976a, Hallett & Lightstone 1976b, Hansen & Skavenski 1977, Hansen & Skavenski 1985, Morrone et al. 2005a). Pupillary light responses are an extreme example of non-conscious responses, being completely automatic and escaping voluntary control (Loewenfeld 1993). Taken together, these dissociations suggest that two (or more) partially independent pathways for visual processing exist (Goodale & Milner 1992, Mishkin et al. 1983), each independently interacting with corollary discharge information, and differently weighted for different types of tasks.

Close examination of the timecourses in Fig.1E suggests that there is more in the perisaccadic pupil behaviour besides the suppression of light responses. The pupils dilate before the saccade; although small and transient, this pupil change has been found to predict the timing of the impending saccade (Mathot et al. 2015b). This dilation is linked to the arousal change associated with any decision, including that of making an eye movement, and as such it is emerging as an important component of the orienting response: the turning of gaze, head and attention in the direction of a sudden stimulus (Wang et al. 2015, Wang & Munoz 2015).

A more evident yet more mysterious component of the perisaccadic pupillary modulation is the large pupil constriction that immediately follows the saccade (see black trace in Fig.1E). This resembles the short-lived constriction that is evoked by any non-luminance modulated visual stimulus, including contrast modulations and motion transients. Could this constriction be a response to the retinal motion occurring during the saccade – affecting the pupil even while escaping conscious perception (Mathot et al. 2015a)? Or, is it possible that this small pupil modulation is a read-out of one of the extra-retinal signals that participate in mediating saccadic suppression? It is interesting to note that the very same pupillary constriction is elicited by eye-blinks, which are associated with perceptual suppression similar to saccades (Hupe et al. 2009). Current experimental data is insufficient to draw any conclusion, and future experiments might tackle the problem with the same tools that have proved informative for the study of conscious vision during saccades, e.g. simulated saccades. It may also help in dissociating the effect of attention and intention during the programming and execution phase of a saccade and their consequences on vision.

Conclusion

Vision is always clear and stable, despite continual saccadic eye movements that reposition our gaze and generate spurious retinal motion. The brain actively anticipates the consequence of a future saccade to efficiently compensate for the shift in gaze and to prevent motion perception. Selective suppression is directed towards the motion mechanisms, to suppress the otherwise compelling motion early in processing, while stability across saccades is guaranteed by the integration of post- and pre-saccadic information across a slanted spatiotemporal field. However, these changes take place at the cost of precision of visual localization, which becomes poor, and impact on multiple dimensions, such as numerosity and multisensory perception. The internal and predictive signals that orchestrate these profound changes of peri-saccadic visual mechanisms can be efficiently measured by pupillometry, which provides a new tool to dissociate active vision from conscious perception.

Acknowledgements

Figure 1 (large)

Effect of saccades on human contrast sensitivity and human BOLD and pupillary responses (reproduced with permission from Benedetto & Binda 2016, Diamond et al. 2000, Knoll et al. 2011, Vallines & Greenlee 2006). **A.** Contrast sensitivity function for luminance (blue symbols) and red/green equiluminant grating (orange symbols) presented for 5ms during fixation (open symbols) or parallel to the saccade (filled symbols). **B.** Luminance contrast sensitivity as function of presentation time from saccadic onset (blue symbols). The open blue circles show measurements made in identical conditions for a simulated saccade using a rotating mirror. The stars plot the exponential of the V1 BOLD amplitude under the hypothesis that BOLD amplitude is proportional to log contrast sensitivity. **C.** Performance in detect a small contrast increment of a brief sinusoidal grating presented in +-1 sec from the onset of a voluntary saccade performed between two stable saccadic targets. The suppression is embedded on a slow perceptual oscillation. **D.** As for Fig. B except that the background was a high-contrast random check pattern. The grey shaded area indicates the region where sensitivity was greater during the saccade than in fixation. **E.** Saccadic suppression also influences pupillary responses. A flash of 62 cd/m^2 shown against a background of 37.2 cd/m^2 evokes weaker pupil constriction when presented perisaccadically (blue) than post-saccadically (red) – triangles on the x-axis show the presentation time of the flashes, and the peak pupil response takes about 500 ms to develop. Notably, a saccade executed in the absence of any visual flash (black) is sufficient to evoke a small transient pupil constriction. **F.** Equiluminant contrast sensitivity during real (filled symbols) and simulated saccade (open symbols).

Figure 2 (small)

Effect of saccades on apparent bar position (reproduced from Cicchini et al. 2013, Ross et al. 1997, Zimmermann et al. 2015). **A.** Perceived position of green bars, briefly flashed on a red background at various times relative to the onset of a reflexive saccade from −10 to +10˚. **B.** As in **A** but during the second of a two-step saccade sequence aimed at a memorized target. **C.** Spatiotemporal map of interactions (relative distance) between a perisaccadic probe bar presented between −20 and 0 ms at screen position 0˚ (black symbol) and a similar reference bar presented at random position and time: the abscissae and the ordinate report the temporal and spatial position of the reference bar. The grey and black lines show, respectively, the position of the fovea and of the saccade target. The left insets show schematically the position and shape of the stimuli and of the saccadic and fixation targets at the time of the saccade.

Figure 3 (small)

Time is also altered during saccades (reproduced with permission from Burr et al. 2010a, Binda, 2009 #102). **A.** Perceived time of a bar, reported relative to two auditory markers, as function of the delay from the saccadic onset. The histogram on the left shows the probability of perceiving the bar in each time bin. **B.** Perceived duration of an interval marked by two visual flashes (separated by 100 ms and plotted as function of the average flash delay from the saccade onset). Subject reported it by comparing the perisaccadic interval duration with a post-saccadic interval of variable duration: marked by another two visual flashes, presented 2 seconds after the saccade. **C.** Perceived temporal order of two visual stimuli: the probability of reporting the correct temporal order of presentation for two short bars, separated by 20 ms, is plotted as function of the average delay from saccadic onset. Chance performance is 0.5. The dashed line reports performance during fixation.

Figure 4 (small)

Saccadic distortions extend to our sense of number (reproduced from Binda et al. 2012, Binda et al. 2011). **A.** Numerosity of a cloud of dots, flashed at variable times from the saccade, and reported by comparing it with a similar cloud of dots shown post-saccadically. **B.** underestimation also characterizes numerosity represented symbolically. A pair of numerals (one-digit or two-digits) were shown at variables time from the saccade, which subjects had to sum or subtract and judge the results relative to a subsequently presented probe digit.

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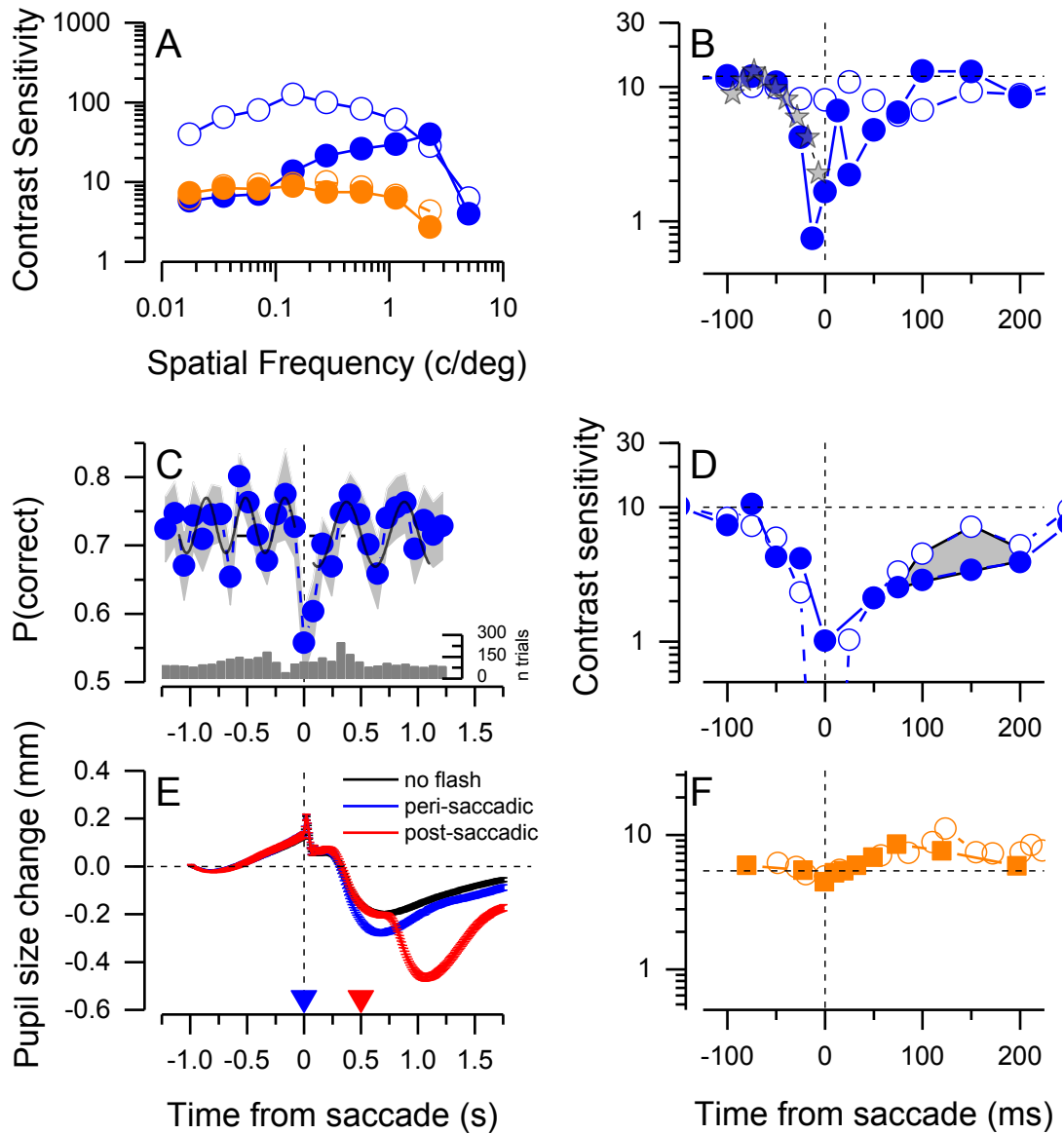Zuber BL, Stark L, Lorber M. 1966. Saccadic suppression of the pupillary light reflex. *Exp Neurol* 14: 351-70
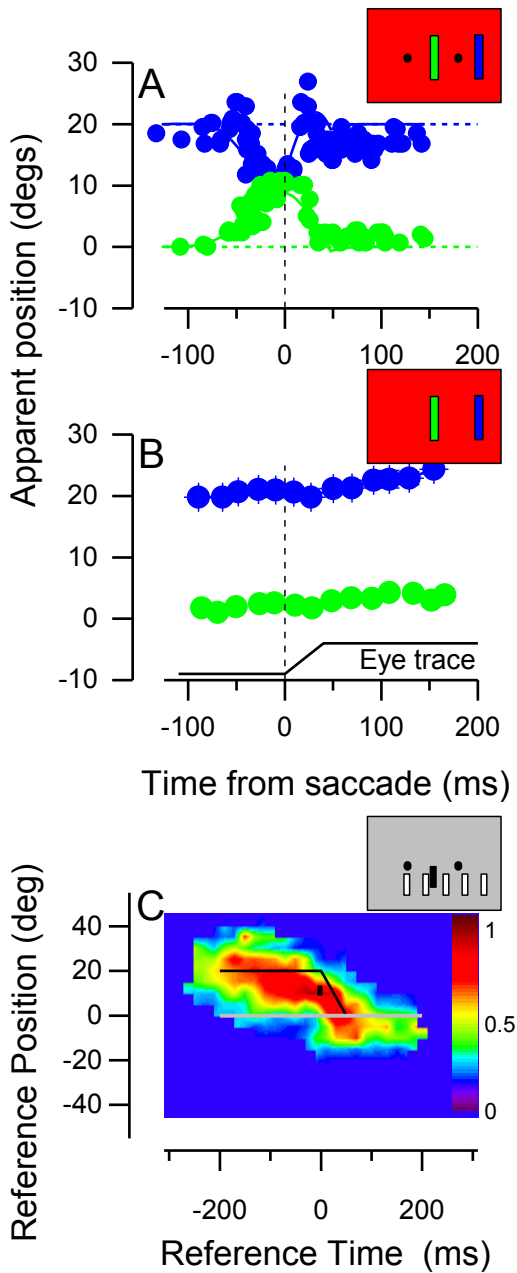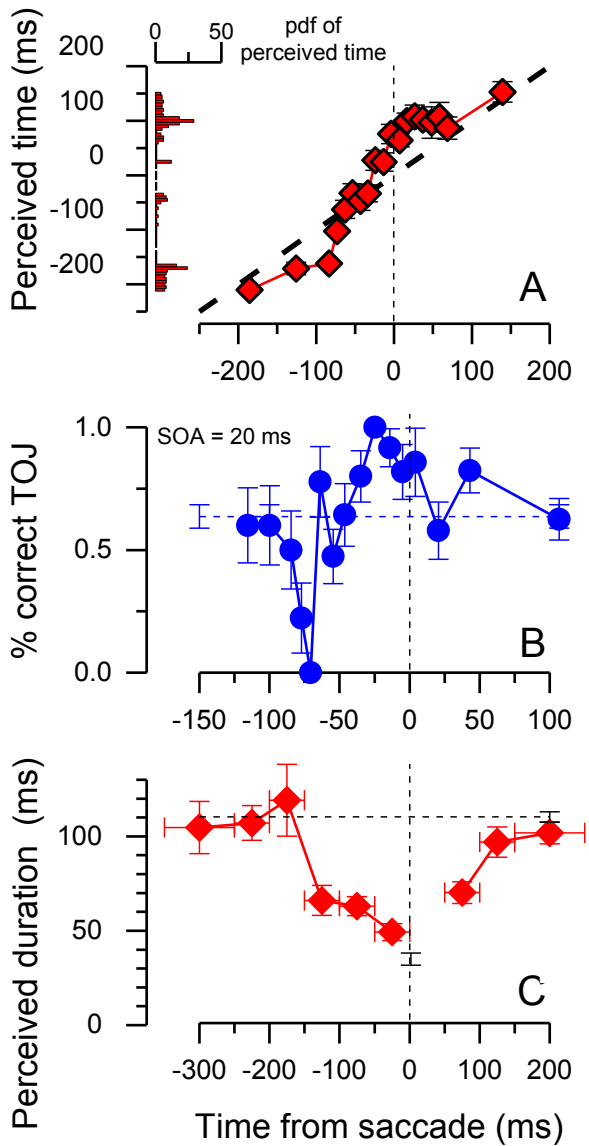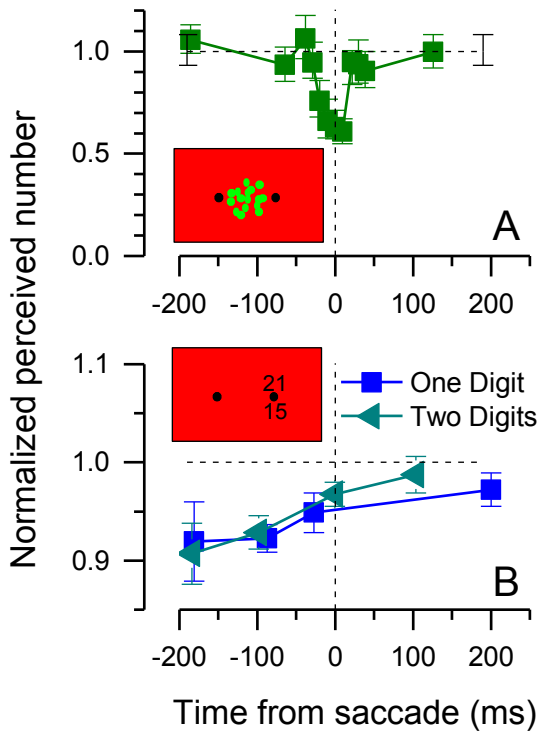
Fig. 1

Fig. 2

Fig. 3

Fig. 4