



Underestimation of perceived number at the time of saccades

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ABSTRACT

Saccadic eye movements produce transient distortions in both space and time. Mounting evidence suggests that space and time perception are linked, and associated with the perception of another important perceptual attribute, numerosity. Here we investigate the effect of saccades on the perceived numerosity of briefly presented arrays of visual elements. We report a systematic underestimation of numerosity for stimuli flashed just before or during saccades, of about 35% of the reference numerosity. The bias is observed only for relatively large arrays of visual elements, in line with the notion that a distinct perceptual mechanism is involved with enumeration of small numerosities in the ‘subitizing’ range. This study provides further evidence for the notion that space, time and number share common neural representations, all affected by saccades.

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1. Introduction

Most adult humans can count. However, there also exists an approximate non-verbal system they share with infants and other animals: a direct visual sense of number. When verbal counting is prevented, we can still see and estimate the numerosity of large sets of items, although with a margin of error (Whalen, Gallistel, & Gelman, 1999). This error increases with increasing set size, following Weber’s law (Ross, 2003; Whalen et al., 1999), a defining feature of perceptual processes. Evidence suggests that numerosity can be extracted independently from other stimulus features, such as texture density (Ross & Burr, 2010). And like all primary sensory properties, numerosity is susceptible to adaptation: the prolonged exposure to a more numerous visual stimulus makes the current stimulus appear less numerous, and vice versa (Burr & Ross, 2008).

The perception of small sets of items (up to 4 or 5) seems to involve a system that is at least partially separate from estimation. Enumeration in this range (the ‘subitizing’ range) is immediate and error-free (Kaufman, Lord, Reese, & Volkman, 1949), and may rely on tracking each individual item (Feigenson, Dehaene, & Spelke, 2004) rather than by the extraction of a statistic for the whole visual display. Much evidence (e.g. Revkin, Piazza, Izard,

Cohen, & Dehaene, 2008) suggests that naming numbers in the subitizing range involves processes distinct from those used in estimation. For example, number estimation is relatively immune to performing an attentional demanding dual task, while subitizing suffers considerably under these conditions (Burr, Turi, & Anobile, 2010).

A good deal of evidence suggests that number and space are strongly linked. Perhaps the best known example is the SNARC effect (Spatial Numerical Association of Response Codes), where subjects respond faster to smaller numbers presented to left hemi-space, and larger numbers to right hemi-space, suggesting that a “mental number line” maps onto spatial representations from the right to left hemisphere (Dehaene, Bossini, & Giraux, 1993). The association between space and numerosity is strengthened by neuropsychological observations. The Gerstmann syndrome (Gerstmann, 1940; Roeltgen, Sevush, & Heilman, 1983) is characterized by impaired numerical abilities (acalculia) as well as spatial deficits (finger agnosia, disorientation of right and left space, and agraphia). Neglect, a visuo-spatial deficit leading to inattention for the left hemi-space (Bisiach & Vallar, 2000) is associated to a similar inattention for small numbers, arguably the left side of the “number line” (Zorzi, Priftis, & Umiltà, 2002). And amblyopia, a visual condition closely associated with poor spatial resolution and spatial distortions, also affects numerosity judgments outside the subitizing range (Sharma, Levi, & Klein, 2000).

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Monkey physiological and human imaging studies suggest that both numerosity and space are represented in the posterior parietal lobe, particularly the Horizontal segment of the Intra-Parietal Sulcus (HIPS) (for a review see Dehaene, Molko, Cohen, & Wilson, 2004). The posterior parietal cortex encodes spatial information for the guidance of eye and hand movements (Andersen, Snyder, Bradley, & Xing, 1997; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Lesions in this area are associated with numerical deficits in patients (Dehaene & Cohen, 1997; Molko et al., 2003) and stimulation by repetitive TMS was found to interact with the SNARC effect (Oliveri et al., 2004). fMRI evidence also shows tuning for quantity in the human HIPS (Eger et al., 2009; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Studies in non-human primates have identified neurons tuned to numerosity in homologous areas: Ventral Intra-Parietal (VIP) (Nieder, Diester, & Tudusciuc, 2006) and Lateral Intra-Parietal (LIP) (Roitman, Brannon, & Platt, 2007). Selectivity to numerosity is consistently found also in a lateral pre-frontal region (Nieder, Freedman, & Miller, 2002) and in the somatosensory cortex (Sawamura, Shima, & Tanji, 2002).

There is some experimental evidence to link numerosity and space to another perceptual dimension, time. Trained animals (rats or pigeons) discriminate stimuli based on their timing or numerosity with equal sensitivity and the administration of methamphetamine produces equal distortions of temporal and numeral judgments (Meck & Church, 1983). In double-task experiments, counting tasks interfere with timing judgments and vice versa (Brown, 1997). And a link between time and space has been repeatedly suggested in recent years, based on the observation of spatially localized alterations of perceived time (Burr, Tozzi, & Morrone, 2007; Johnston, Arnold, & Nishida, 2006) and on the observation of similar spatial and temporal distortions at the time of saccadic eye movements (Burr & Morrone, 2006; Morrone, Ross, & Burr, 2005). The same posterior parietal areas implicated in numerosity and space processing have been proposed to play a role in the encoding of temporal intervals. Single neuron responses in the posterior parietal cortex are modulated by judgments of short (<2 s) intervals (Leon & Shadlen, 2003) and neglect could be associated to an overestimate of the duration of stimuli presented in neglected space (Basso, Nichelli, Frassinetti, & di Pellegrino, 1996). Psychophysical and neurobiological studies collectively support the idea of functional overlap or interaction between neural circuits processing number, time and space. These interactions have been integrated in a proposed 'theory of magnitude', in which spatial, temporal and numerical units of measurement share a common neural basis in the PPC possibly interacting with pre-frontal cortex, basal ganglia and cerebellum (Walsh, 2003; see also Burr, Ross, Binda, & Morrone, *in press*).

The present study investigates the effects of saccades on numerosity perception. Saccades are rapid gaze shifts that we make very frequently to scan the visual scene and foveate objects of interest that are known to affect both space and time perception. Visual stimuli briefly flashed just before or during a saccade are systematically misperceived, displaced in both space (Honda, 1989) and time (Binda, Cicchini, Burr, & Morrone, 2009a). Furthermore, both space and time are compressed at the time of saccades (Morrone, Ross, & Burr, 1997; Morrone et al., 2005; Ross, Morrone, & Burr, 1997). Transient changes of neural activity accompany these perceptual distortions. In many areas, and most prominently in areas surrounding the intra-parietal sulcus, the receptive fields of visual neurons shift in anticipation of saccades, displacing visual spatial representations (Duhamel, Colby, & Goldberg, 1992).

The notion that spatial, temporal and numeral representations share a neural substrate impinging on the posterior parietal cortex, together with the impact of saccades on areas that include the intra-parietal sulcus, raises the possibility that perceived numerosity may also be affected by saccades. An interaction between eye

movements and numerosity is indicated by a recent fMRI study. Brain activity was measured separately while subjects performed two tasks: they made leftward or rightward saccades, or summed or subtracted numerical quantities. A classifier was able to predict the direction of saccades based on the multi-voxel pattern of brain activation during the saccade task. Most interestingly, the same classifier could also predict which numerical operation was being performed, providing direct evidence for an interaction between changes in eye position and the processing of numerical quantities (Knops, Thirion, Hubbard, Michel, & Dehaene, 2009). A behavioral study investigated the effect of saccades on the ability to manage numerical quantities and found an increase in reaction times when subjects were asked to compare the magnitude of two numerals presented while subjects made an eye movement – but no such effect was observed if the task was unrelated to the magnitude of the numbers and merely required subjects to indicate whether the numerals were even or odd (Irwin & Thomas, 2007).

Here we investigate the effect of saccades on perceived numerosity by asking human subjects to estimate the number of visual elements presented perisaccadically. In a series of experiments, we test two ranges of numerosity, small (between 0 and 7, including the 'subitizing' range) and larger numerosities (up to 30). We find that the larger numerosities are systematically underestimated during saccades, showing that perisaccadic perception is a prominent example of the strong links between space, time and number. All three dimensions are subject to a similar distortion, a compression of stimulus magnitude. These data have been published in abstract form (Binda, Ross, Burr, & Morrone, 2009b).

2. Methods

A total of nine observers (all but two naive to the aim of the study) volunteered to participate in the experiments after giving informed consent. Each observer participated in one or more parts of the experiment. All had normal or corrected-to-normal vision. Experimental procedures were approved by the local ethics committees and are in line with the declaration of Helsinki.

Experiments took place in a dark and quiet room. Subjects sat with head stabilized by a chin rest 30 cm from a monitor screen. The screen subtended $70^\circ \times 50^\circ$, of which the central area of 20° diameter was occupied by the stimuli (except for one experiment, Fig. 5). The large display relative to the area occupied by the stimuli was chosen to minimize the masking effects from the borders of the screen, known to accompany the displacement of retinal images during real and simulated saccades (Derrington, 1984). Stimuli were presented on a CRT color monitor (Barco Calibrator) driven at a resolution of 464×532 pixels and a refresh rate of 120 Hz by a visual stimulus generator (Cambridge Research Systems VSG2/5) attached to a PC and controlled by Matlab (Mathworks, Natick, MA).

2.1. Task and procedure

Trials began with subjects fixating a 0.5° black dot presented 10° left of screen center, at eye-level (see Fig. 1). After a variable delay (2200 ± 200 ms), the fixation point was extinguished and the saccadic target (another 0.5° black dot) appeared 10° to the right of screen center. Subjects saccaded towards the target as soon as it appeared (see Fig. 1). In a control condition, the fixation spot remained visible throughout the trial and subjects maintained fixation. Eye movements were recorded by means of an infrared limbus eye tracker (ASL 310), with the infrared sensor mounted below the left eye on wrap around plastic goggles through which subjects viewed the display binocularly. The spatial resolution of the system was $0.5\text{--}1^\circ$ (manufacturer specifications). The PC sampled

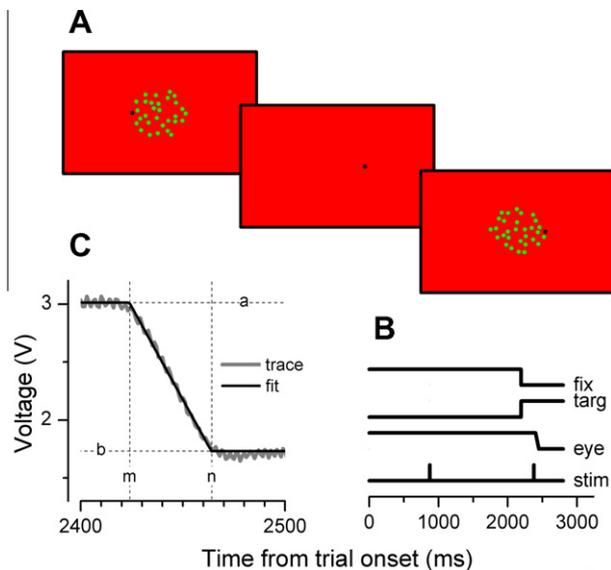


Fig. 1. Stimulus (A) and presentation sequence (B) for numerosity measurements. The fixation point (fix) appeared 10° left of the screen center; after an average delay of 2200 ms, it was replaced by the saccadic target (targ), 10° right of center, to which subjects saccaded. Two random arrays of visual elements were flashed for one monitor frame in the central area of the screen (20° diameter) separated by 1500 ms: the reference stimulus (comprising a fixed number of elements, presented well before the saccade) and the test stimulus (with variable numerosity and presented at about the time of the saccade onset). Panel C shows an example eye trace (gray line) recorded in a sample trial, plotting the voltage output of the eye tracker against the time from the trial onset. Traces were fit with a three-line-segment function (black line – see Eq. (1) Methods); the best fitting parameters m and n estimate the saccade onset and offset respectively; a and b are set by the voltage levels acquired during the pre- and post-saccadic epochs.

eye position at 1000 Hz and stored the trace in digital form. At the end of each trial, the saccadic onset was estimated by fitting the eye trace with a three-line-segments function with the form:

$$\hat{y} = \begin{cases} a & t < m \\ a + \frac{b-a}{n-m} \cdot (t-m) & m \leq t < n \\ b & t \geq n \end{cases} \quad (1)$$

where t is time from the trial onset. The three segments correspond to the pre-saccadic, saccadic and post-saccadic epochs. The point of intercept between the first and the second segment (m) yields an estimate of the saccadic onset; n estimates the saccade offset and a and b are set by the voltage levels acquired during the pre- and post-saccadic epochs (see Fig. 1C for an example of the fit and a graphic representation of the parameters).

In a later offline analysis, the experimenter checked the quality of saccades and discarded trials where fixation was unsteady or a corrective saccade occurred (about 2% of trials). The total number of trials eliminated was less than 7%.

For three subjects and one stimulus type, we studied an additional condition where no actual eye movement was executed but the retinal image displacement caused by a saccade was simulated by displacing the whole field of view with a rotating mirror. We used a similar procedure to Morrone et al.'s (1997). Subjects viewed the monitor screen through a small mirror (4 × 3 cm) positioned 27 cm from the monitor and about 3 cm from the subject right eye (left eye patched). The mirror was moved with the same dynamics as a human saccade by a galvanometric motor under the control of the VSG, producing a 20° saccade-like leftward shift of the entire scene. The duration and velocity of the mirror rotation were monitored (by eye tracker) throughout the experiment to confirm that the dynamics were similar to saccades. We also monitored subjects' eye movements (with a second eye tracker)

to confirm that they maintained steady fixation. Before each experimental session the position, the orientation and the range of rotation of the mirror were calibrated.

At a randomly chosen time relative to saccade (or mirror-swing) onset, the test stimulus – a 2D array of elements randomly distributed within a 20° diameter circle – was presented for one monitor frame (about 8 ms). In discrimination tasks, subjects compared the numerosity of the test stimulus with that of another random array of elements (the reference stimulus) presented 1.5 s beforehand (see Fig. 1B) – note that, unlike true 2AFC procedures, the temporal order of the test and reference stimuli was fixed. The numerosity of the reference stimulus remained constant within a session; across sessions, we varied the reference numerosity ($n = 30, 15$ or 10) to assess the effect of the density of visual displays and control for potential confounds arising from the apparent compression of visual space known to occur at the time of saccades (see Section 4 for more details). The number of elements of the test was varied from trial to trial using the adaptive QUEST procedure (Watson & Pelli, 1983). Except for their numerosity, the test and the reference stimuli were identical and both were flashed for one monitor frame.

2.2. Stimuli

Four different types of stimuli were employed. In the first series of studies, all stimuli were green¹ (Luminance: 55 cd m⁻²; C.I.E. coordinates: $x = 0.286$; $y = 0.585$), displayed on a dimmer red background (Luminance: 18.1 cd m⁻²; C.I.E. coordinates: $x = 0.624$; $y = 0.344$). The elements of the reference and the test stimulus were circular dots of 1° diameter displayed in random (non-overlapping) positions within a 20° diameter circle. In the second study the elements were short, horizontal, non-overlapping lines (2° by 0.25°), presented randomly within the circle with the additional constraint that each occupied a different vertical position. For the study reported in Fig. 5, the elements were horizontal lines extending over the entire screen (70 by 0.25°), with vertical semi-random position constrained so no two lines could be closer than 0.5°. These later stimuli were randomly chosen red or green bars, equiluminant to the yellow background (Luminance: 18.1 cd m⁻²; C.I.E. coordinates: $x = 0.470$; $y = 0.452$). The equiluminant point of individual subjects was checked with standard flicker-photometry procedure.

2.3. Analyses

Each trial was ranked by the delay of the test presentation relative to saccadic onset, then binned appropriately (average 50 trials per bin, minimum 20 trials) for separate analysis. The proportion of trials of each bin in which the test was perceived as more numerous than the reference was plotted against the test numerosity, yielding psychometric curves like the ones in Fig. 2. The Psignifit Matlab package (Wichmann & Hill, 2001a, 2001b) fit data with cumulative Gaussian functions and provided estimates of the fit parameters and their standard errors (based on 1000 Montecarlo simulations). The median and the standard deviation of the fits were taken as estimates of the PSE (the perceived test numerosity) and JND (the precision of the judgment) respectively. Linear fits and other statistical analyses were performed with Origin pro 8 (OriginLab, Northampton, MA, USA) and SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA). For the statistical comparison of perisaccadic and fixation values (Fig. 4) we used a bootstrap t -test (one-tailed, based on 5000 Montecarlo stimulations) – we started from the distributions of PSE values for the perisaccadic and the fixation conditions (each comprising 5000 values) and took

¹ For interpretation of color in Figs. 1–5, the reader is referred to the web version of this article.

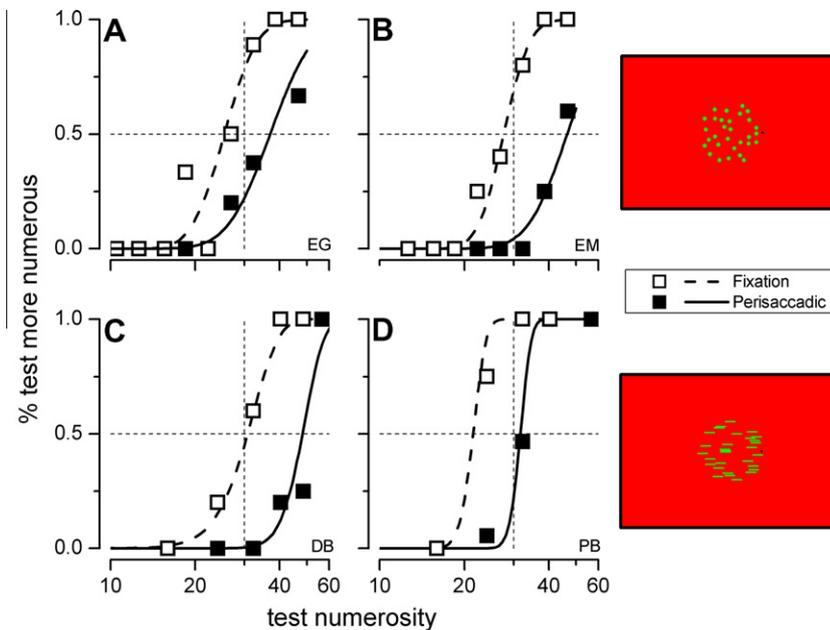


Fig. 2. Psychometric curves from four example subjects for numerosity judgments, for two stimulus types. The test and reference stimuli were random arrays of green dots (A and B) or short horizontal lines (C and D), presented on a red background (see insets – note that elements are slightly out of proportion, made thicker to ensure visibility); the reference numerosity was 30. The proportion of trials where the test stimulus was reported to be more numerous than the reference is plotted against the element number of the test stimuli A–D: hollow symbols report results for the fixation condition; filled symbols refer to trials in which the test stimulus was presented between 25 and 0 ms before the saccade onset. PSE is given by the 50% point (horizontal dashed lines). Vertical dashed lines report the reference numerosity. Note that, during steady fixation, perceived numerosity varied across subjects and was not necessarily veridical. One subject (author PB) consistently showed a bias towards overestimating the numerosity of the second stimulus in fixation conditions.

the ratio of the two; we computed the probability of the value 1 being part of the distribution, which yielded an estimate of the p -value. The same procedure was repeated for JNDs.

2.4. Numerosity naming

As in the experiments described above, subjects fixated a dark spot presented 10° to the left of the screen center and, when this jumped to a new location 10° right of the screen center, they followed it with a saccade (except in a control steady-fixation condition). At about the time of the saccade onset, a random array of short horizontal green lines (2° by 0.25° , each appearing at a different vertical position and inscribed in a circular patch of 20° diameter located at the center of the screen) was flashed against the red background. On each trial, the numerosity of the stimulus was randomly sampled from a uniform distribution of the integers between 0 and 7 (extremes included). At the end of trials, a number pad appeared on the screen together with the mouse pointer and subject clicked on the figure corresponding to their estimate of test numerosity.

Five subjects were tested in this experiment. The mean and standard deviation of perceived numerosity were computed for each subject and then averaged across subjects to give the values reported in Fig. 7. For the saccade condition, only trials in which the stimulus was presented less than 25 ms before or after the saccade onset were considered. Note that this temporal window is wider than that used to define perisaccadic trials in the numerosity-estimation experiments ($-25; 0$ ms); using this smaller temporal window made estimates more noisy but it did not change the pattern of results.

3. Results

In a first experimental condition, we measured numerosity during saccades and fixation for random, non-overlapping arrays of

small disks, with reference numerosity of 30. Fig. 2A and B shows psychometric functions during fixation and just before (less than 25 ms) saccadic onset for two of the three subjects tested. The perisaccadic curves are shifted rightwards relative to fixation, resulting in PSE values considerably higher than those observed during steady fixation (indicating that the perceived numerosity of this test had been reduced). Note that perceived numerosity during steady fixation was not necessarily veridical (the PSE did not coincide with the reference numerosity, indicated by the dashed vertical lines). The increase in perisaccadic PSE relative to fixation was a factor of 1.46 ± 0.17 for subject EG, 1.68 ± 0.15 for subject EM, and 1.61 ± 0.16 for subject PB (data not shown).

Fig. 3 plots for the two subjects of Fig. 2A and B the PSE of the psychometric curves and their JND (the precision of the judgments) as a function of the time of test presentation relative to the saccadic onset. When the test appeared more than 50 ms before the saccade, PSE and JND values are similar to those observed in fixation conditions (dashed horizontal lines). In a small temporal window around the onset of the saccade, PSEs increase as the test presentation approaches the saccadic onset, indicating a progressive underestimation of the test numerosity. Just after the saccade, PSE values are reset to baseline.

A possible confound is that the observed perisaccadic reduction of perceived numerosity may be secondary to another perceptual distortion known to occur at the time of saccades, the perisaccadic compression of visual space (Ross et al., 1997). Perisaccadically flashed visual stimuli are mislocalized towards the saccadic target, and this could in principle cause the elements in the test stimulus to overlap perceptually (Morrone et al., 1997), effectively reducing their apparent numerosity. This seems unlikely, as subjects reported seeing the whole field of dots move towards the saccadic target, but to be certain we repeated the experiments with short horizontal lines located in different vertical locations so that no compression of space (in the direction of the saccade) would make them overlap. As Fig. 2C and D shows, this change in the stimulus

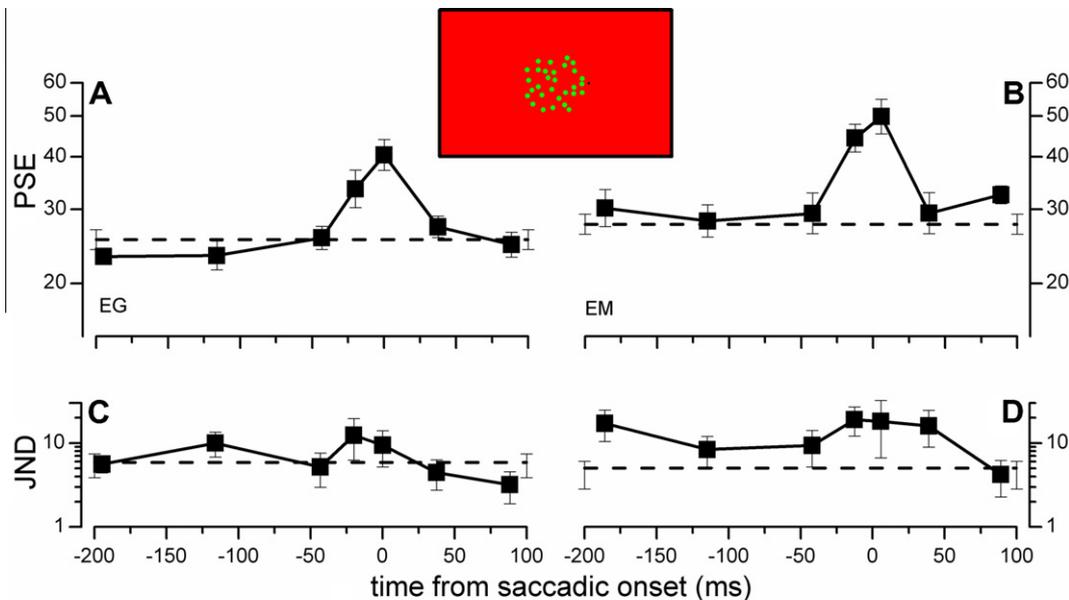


Fig. 3. Timecourse of the numerosity underestimate for the two subjects of Fig. 2A and B. Stimuli were random arrays of green dots on a red background (inset) with reference numerosity of 30. Trials were ranked by the delay of test presentation relative to the saccade onset in bins. The estimated PSEs (A and B) and JNDs (C and D) of each bin are reported as a function of the test presentation time relative to the saccadic onset. The dashed lines report values for fixation trials. Error bars report standard errors as computed by bootstrap with 1000 repetitions.

configuration did not affect the result. Both tested subjects underestimated numerosity of perisaccadic stimuli. The perisaccadic PSE was about 1.5 times the PSE during steady fixation in all subjects and for both stimulus configurations (perisaccadic vs. fixation PSE ratios were 1.60 ± 0.21 for subject DB and 1.48 ± 0.06 for subject PB).

We also repeated the measures with a reference numerosity of 15 (halving the average density of the display) and again observed a reduction of perceived numerosity of similar magnitude. Fig. 4 shows example psychometric curves from one subject (panel A) in saccade and fixation conditions, and plots (Fig. 4B) the ratio of saccade to fixation PSEs and JNDs for all the four tested subjects, as a function of the delay of test presentation from the saccade onset (symbols). A Gaussian function was fit to all the individual subjects data, providing an indication of the central tendency of the data (thick line in Fig. 4; see figure legend for the equation and the fitting parameters). As with the other experiments, the PSE for stimuli presented at saccadic onset is about 1.6 times larger than that observed during fixation, and the effect rapidly disappears as the delay between the stimulus presentation and the saccade onset increases. A bootstrap *t*-test (one-tailed, 5000 repetitions) confirmed that, in all subjects, the ratio of perisaccadic to fixation PSE was larger than 1 across all the perisaccadic intervals (black symbols, $p < 0.05$; gray symbols indicate non-significant comparisons). The JNDs (given by the slope of the psychometric curves) tend to be higher perisaccadically than during fixation, implying lower precision of the judgments. However, the dependence of JND values from the time of stimuli presentation is much less orderly than for PSE values and only in few cases did the comparison of perisaccadic to fixation JND values reach statistical significance.

Fig. 4 also reports the results from the “simulated saccades” condition, where subjects made no eye movements, but a saccade-like retinal displacement was simulated by rapid rotation of a mirror (see Section 2). The PSE of the psychometric function (crossed circle symbols in Fig. 4A) is very similar to that measured in steady-fixation conditions, indicating that the reduction of perceived numerosity observed at the time of saccades does not

emerge as a byproduct of the change of retinal image or spurious motion produced by saccades. None of the PSEs (Fig. 4C) differed significantly from unity.

Saccades reduce sensitivity to low-frequency stimuli modulated in luminance but not in chromaticity (Burr, Morrone, & Ross, 1994; Ross, Burr, & Morrone, 1996), and this could conceivably have affected perceived numerosity. It seems unlikely, as both dot and line stimuli had a strong high-spatial frequency component, with both luminance and chromatic contrast, resistant to perisaccadic suppression. However, to further rule out this possible complication, we repeated the study with stimuli defined only in chromatic contrast: equiluminant horizontal lines, straddling the entire screen width, distributed randomly across the central 20° of the screen, never closer to each other than 0.5° . The reference numerosity was reduced to 10 so to allow a properly randomized distribution of the elements. As with all the other types of stimuli, in this condition we found a reduction of perceived numerosity when the test stimulus was presented perisaccadically (Fig. 5).

Fig. 6 summarizes the results from all numerosity-estimation experiments, plotting (in log–log coordinates) PSEs and JNDs observed for perisaccadic presentations against the corresponding values observed in steady-fixation conditions. PSEs (panel A) are distributed along a straight line of near unity slope (slope = 0.99 ± 0.07 in log–log coordinates) and intercept 1.56 (0.19 ± 0.08 log-units). This means that the ratio between perisaccadic and fixation PSEs was constant – at a factor of 1.56 – for all subjects, irrespective of stimulus numerosity or configuration. Saccades produce a reduction of perceived numerosity of about 35%. However, PSEs for the simulated-saccade condition lay on the equality line, implying no change in perceived numerosity. The linear regression of perisaccadic against fixation JNDs (on log coordinates) also had near-unity slope (1.07 ± 0.21), with intercept of 1.76 (0.25 ± 0.26 in log–log), indicating that perisaccadic JNDs were, on average, higher than fixation. The simulated-saccade JNDs also tended to be higher than the fixation estimates.

We also studied the relationship between PSE and number of elements in the display and density. The obvious correlation between PSE and element number remained strong and significant

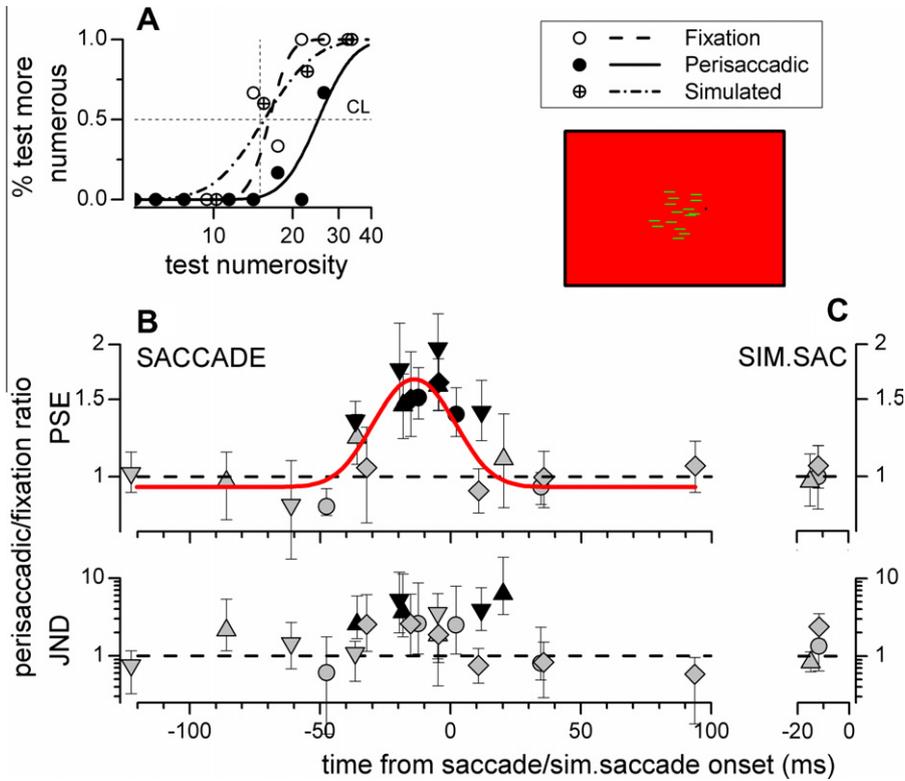


Fig. 4. Numerosity judgments for stimuli comprising 15 short horizontal lines (see inset). (A) Hollow symbols reports psychometric curves during steady fixation; filled black symbols, just before a real saccade and crossed circles just before a simulated saccade. Panel B reports PSE (top row) and JND (bottom row) from individual subjects (different symbol-shape for the four tested subjects) in the real saccade condition as function of delay of stimulus presentation from the saccade onset (abscissa). PSEs and JNDs are both normalized by dividing by the values observed during steady fixation. Data points significantly larger than 1 (one-tailed bootstrap *t*-test, $p < 0.05$) are shown in black, non-significant data points are gray. PSE data from all subjects were fit with a Gaussian function with the form $y = y_0 + \frac{A}{w\sqrt{\pi/2}} \exp\left(-2\frac{(x-x_c)^2}{w^2}\right)$ and best fitting parameters: $y_0 = 0.95 \pm 0.04$; $x_c = -13.98 \pm 2.29$; $w = 27.61 \pm 4.49$; $A = 24.91 \pm 4.78$ (estimated σ : 32.51; estimated height: 0.72, adj. R^2 0.63). Panel C reports normalized PSE and JND values in the simulated-saccade condition. Error bars were computed by bootstrap.

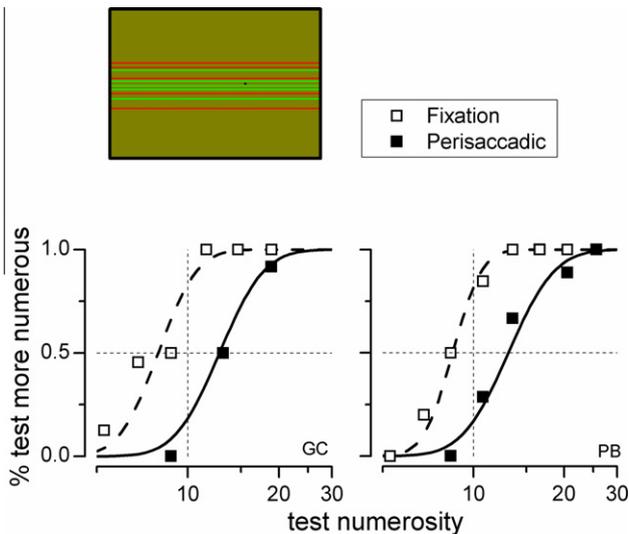


Fig. 5. Psychometric curves for two observers for numerosity estimation of long horizontal lines, randomly red or green and equiluminant to the yellow background (inset). Hollow symbols report performance during steady fixation; filled symbols for test stimuli presented less than 25 ms before the saccade onset. Dashed vertical lines indicate the reference numerosity (10).

when we controlled for the density of the displays (partial correlation values were 0.76 and 0.71 for fixation and perisaccadic PSEs respectively, and the corresponding significance values were $p = 0.01$ and $p = 0.02$). However, the partial correlation between

PSE and density values with numerosity controlled was low and non-statistically significant (0.142 and 0.204, $p \gg 0.05$).

In the final experiment we studied the effect of saccades in the subitizing range. The stimuli (short horizontal lines) were similar to the other experiments, except that the number of elements was much smaller (0–7), and only the test was presented: subjects reported perceived numerosity on a number pad. Fig. 7A plots average perceived numerosity as a function of stimulus number (note that unlike in the previous figures, the ordinate reports the subjects' estimate of stimulus numerosity, not the PSE), with Fig. 7B showing the Weber fraction (the standard deviation of the judgments divided by stimulus number). Hollow symbols refer steady fixation trials, filled symbols to trials in which the stimulus was flashed less than 25 ms before saccadic onset. No systematic errors of estimation were observed for this low number range, at least up to 6. Stimuli with seven items tended to be underestimated in the perisaccadic interval, suggesting a trend towards the perisaccadic underestimation for larger numerosities.

Interestingly, although there was no systematic bias for these low element numbers, the precision of the judgments (Weber fraction) was far worse for perisaccadic stimuli than in steady-fixation conditions, particularly for low numbers of elements. Errors began to be made for 2 and 3 elements, well within the subitizing (error-free) range, causing the Weber fraction for these small numerosities to be significantly worse perisaccadically than during fixation. This is consistent with the fact that subitizing, but not estimation, requires attention (Burr et al., 2010). Saccades are known to be strongly linked to changes in attention (Deubel & Schneider, 1996).

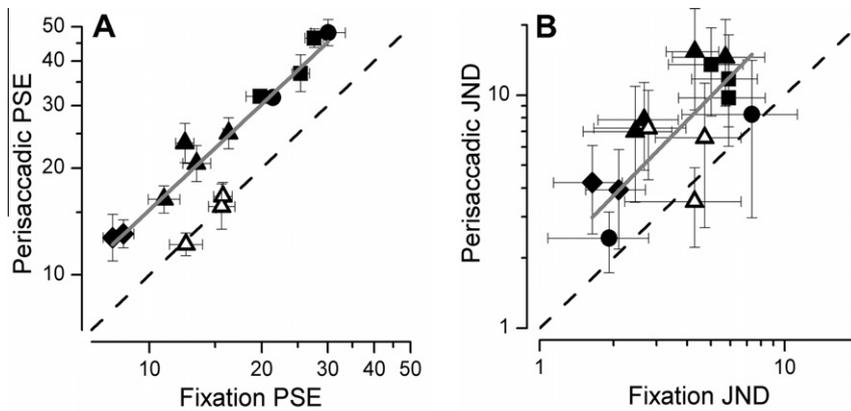


Fig. 6. Summary of data for all numerosity-judgment experiments. Data collected with different stimuli are reported with different symbols. PSEs and JNDs for test stimuli presented between -25 and 0 ms before the saccade onset are plotted against the corresponding values during fixation, on log-log scale. The dashed black lines have unitary slope. The thick gray lines are linear fit to the PSE and JND data (real saccades vs. fixation). Hollow symbols report data from the simulated-saccade condition.

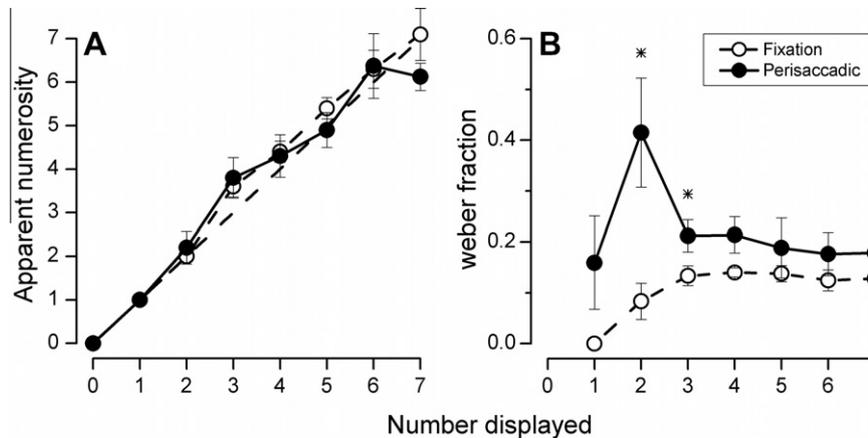


Fig. 7. Numerosity judgments of a random array of short lines. (A) Perceived numerosity averaged across subjects. (B) Weber fractions (ratio of the standard deviation of the judgments to the tested number). Hollow symbols: fixation; filled symbols: stimulus presented within 25 ms of saccadic onset. One-tailed paired t -tests were performed between fixation and perisaccadic values; asterisks for significant difference at $p < 0.05$.

4. Discussion

The perception of briefly presented visual stimuli is known to be distorted at the time of saccadic eye movements: stimuli are mislocalized towards the endpoint of the saccade and their spatial separation is underestimated (Lappe, Awater, & Krekelberg, 2000; Morrone et al., 1997; Ross et al., 1997); stimulus time is also systematically misperceived (Binda et al., 2009a) and the perceived temporal separation between two perisaccadic stimuli is underestimated (Morrone et al., 2005). Here we show that saccades affect yet another perceptual attribute of briefly flashed visual stimuli, numerosity. Random arrays of visual elements (dots, short lines or long lines) are systematically perceived as less numerous when flashed just before the onset of a saccade. The underestimate is about one third of the actual numerosity of the stimuli; it remains constant over a threefold increase of stimulus numerosity (10–30), irrespective of the size, shape and color of the elements composing the display. However, for small numerosities (<7) the effect is not observed.

In line with the recent study of Ross and Burr (2010), we find that numerosity estimates were uninfluenced by the density of the displays. Stimulus density varied by more than an order of magnitude, yet perceived numerosity remained veridical during fixation and compressed perisaccadically by 35% (Fig. 6A).

We consider and reject the possibility that perisaccadic compression of numerosity is secondary to other distortions at the time

of saccade, such as spatial compression (Morrone et al., 1997; Ross et al., 1997) that could squeeze elements closer together, causing potential overlap. In nearly all trials the subjects reported a mislocalization of the stimuli, usually displaced as a whole, but they were always able to perform the numerosity task. In the studies with short and long lines, the lines were arranged so as to remain distinct even with the strongest possible spatial compression along the direction of the saccade. Compression in the direction orthogonal to the saccade has also been reported, but only in the far periphery of the visual field (more than 20° away from the fixation point, Kaiser & Lappe, 2004), where we presented no stimuli. Also, if the underestimate of stimulus numerosity was in any way caused by the apparent compression of the stimulus area, it should have been more prominent for the high than the low-density displays. Inspection of Fig. 6A and the analysis of partial correlation between PSE values and density demonstrate that this is not the case.

Another potential confound is saccadic suppression, the perisaccadic reduction of visibility for luminance-modulated stimuli of low spatial frequency (Burr et al., 1994; Ross et al., 1996). Reduced stimulus visibility could reduce the likelihood of each element in a display to be seen and consequently counted. However, our stimuli should show very little saccadic suppression, having a strong high-spatial frequency component modulated in both luminance and chromaticity. And for the study of Fig. 5, the

stimuli were equiluminant, which are not suppressed during saccades (Burr et al., 1994).

A crucial control condition was to measure numerosity with saccades simulated by fast mirror movement. This had no effect on perceived numerosity, demonstrating that the distortion of apparent numerosity is contingent on the active execution of a saccade, and does not result from visual changes produced by the rapid rotation of the eyes.

While the perceived numerosity of displays with largish (>10) element numbers was reduced during saccades, less numerous displays were perceived accurately (if somewhat imprecisely). This is consistent with much evidence suggesting a dissociation between the perceptual processing of large and small sets of items (Burr et al., 2010; Revkin et al., 2008).

Precision thresholds, or JNDs, were higher in both the subitizing and the estimation range, and also during the simulated saccades. However, unlike the change in perceived numerosity, the increase of JNDs was not sharply tuned for time of stimuli presentation relative to saccadic onset. This suggests that, contrary to the systematic underestimation, the increased imprecision of numerosity judgments was not specific to the execution of the saccade but was more generally related to the deployment of attention to an additional task (movement of the eyes) or to an additional event (the whole field motion produced by the rotation of the mirror). Previous work has shown that thresholds increase in conditions of divided attention, most prominently in the subitizing range (Burr et al., 2010).

Walsh (2003) has proposed that a single magnitude system is responsible for the approximate computation of quantity, be it number, space or time. Behavioral, neuropsychological and neurophysiological data on patients, healthy human subjects and non-human primates suggest that space, time and number are represented by partially overlapping neural circuits, the posterior parietal cortex playing a pivotal role (Dehaene et al., 2004; Leon & Shadlen, 2003; Simon et al., 2002). Our data, combined with previous studies on visual perception at the time of saccades, provide further evidence for the association of these three perceptual attributes. When we execute saccades, space, time and numerosity are all subject to a similar distortion: the stimulus magnitude along all three dimensions is transiently reduced – see Burr et al. (in press) for a fuller more speculative discussion of this issue.

Saccades produce dramatic transient alterations of neural responses. The receptive fields of visual neurons shift in anticipation of saccades, displacing visual spatial representations which may underlie the stability of perception across eye movements (Burr & Morrone, 2010, in press; Ross, Morrone, Goldberg, & Burr, 2001). This phenomenon is observed in many visual areas (Nakamura & Colby, 2002) but it is most prominent in higher-level regions (Duhamel et al., 1992), particularly in the intra-parietal areas involved in the representation of numerical magnitude (Dehaene et al., 2004). This suggests a tantalizing hypothesis: saccades may alter the representation of numerosity by transiently changing the response properties of numerosity-tuned neurons, possibly those with a gradient response, reported in LIP (Roitman et al., 2007). At present, the effect of saccades on visual responses of single neurons has only been investigated with for their spatial properties: it remains to be established whether the encoding of other stimulus features, such as time and number, are also subject to transient perisaccadic changes. And it also remains unclear why compression of these important perceptual attributes – space, time and number – occurs. Possibly it is a consequence of the system becoming overloaded at the time of saccades by important tasks related to mediating perceptual stability.

Our experiments demonstrate that saccades affect the perception of number directly, not indirectly through the distortion of other perceptual attributes. Neural regions representing the

numerosity of sets of visual elements have been shown to respond to other format of number representation as well, such as Arabic numerals (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Piazza, Pinel, Le Bihan, & Dehaene, 2007). Experiments testing whether saccades also interfere with these alternative numerical formats are currently in progress.

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