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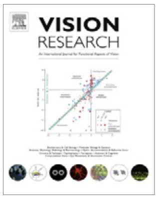

Underestimation of perceived number at the time of saccades

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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.

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, & Volkmann, 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, & Umilta, 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 prefrontal 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 where 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° × 50°, 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 0.5–1° (manufacturer specifications). The PC sampled