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Time order reversals and saccades

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ABSTRACT

Ballistic eye movements, or saccades, present a major challenge to the visual system. They generate a rapid blur of movement across the surface of the retinae that is rarely consciously seen, as awareness of input is suppressed around the time of a saccade. Saccades are also associated with a number of perceptual distortions. Here we are primarily interested in a saccade-induced illusory reversal of apparent temporal order. We examine the apparent order of transient targets presented around the time of saccades. In agreement with previous reports, we find evidence for an illusory reversal of apparent temporal order when the second of two targets is presented during a saccade – but this is only apparent for some observers. This contrasts with the apparent salience of targets presented during a saccade, which is suppressed for all observers. Our data suggest that separable processes might underlie saccadic suppressions of salience and saccade-induced reversals of apparent order. We suggest the latter arises when neural transients, normally used for timing judgments, are suppressed due to a saccade – but that this is an insufficient pre-condition. We therefore make the further suggestion, that the loss of a neural transient must be coupled with a specific inferential strategy, whereby some people assume that when they lack a clear impression of event timing, that event must have happened less recently than alternate events for which they have a clear impression of timing.

1. Introduction

Humans make frequent eye movements, bringing images of contemporary interest onto the foveae so they can be examined with greater resolution. These movements often involve ballistic switches of fixation between widely separated points – a saccade. Such movements cause a blur of movement across the two-dimensional surface of the retinae, but this usually goes unnoticed as the visual system suppresses awareness of retinal motion blur signals (Burr, Morrone, & Ross, 1994; Latour, 1962; Thiele, Henning, Kubischik, & Hoffmann, 2002; Volkmann, 1962).

Saccades do not just result in perceptual suppression of retinal motion blur signals, they also result in a number of curious perceptual phenomena. For instance, stimuli flashed around the time of a saccade can appear displaced toward the saccade target (Honda, 1989; Lappe, Awater, & Krekelberg, 2000; Matin, Clymer, & Matin, 1972; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997) and space itself can seem contracted (Morrone et al., 1997; Ross et al., 1997). Of most interest here, however, is an illusory reversal of temporal order (Binda, Cicchini, Burr, & Morrone, 2009; Morrone, Ross, & Burr, 2005).

The apparent order of two sequential flashes presented around the time of a saccade is reportedly subject to an illusory distortion (Binda et al., 2009; Morrone et al., 2005). If the first of the two flashes is presented ~50 ms *before* saccade onset, and the second lags the first by up to ~50 ms, an illusory reversal of order can ensue. The saccade-related timing of this phenomenon corresponds well with the critical timing for a maximal suppression of saccade-generated motion blur signals (Wurtz, 2008).

As yet it is unclear how temporal order is encoded. In part, this is likely because the determination of temporal order is an inferential process tapping multiple sources of information. The times at which signals reach cortex is demonstrably important (Arnold & Wilcock, 2007; Hirsh & Sherrick, 1961; Roufs, 1963), but this is not the exclusive determinant of perceived timing. Additional influences are apparent, for instance – the physical timing at which two signals seem to coincide is subject to change (Arnold & Yarrow, 2011; Fujisaki, Koene, Arnold, Johnston, & Nishida, 2006; Vroomen, Keetels, de Gelder, & Bertelson, 2004), suggesting subjective timing

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reflects an experience-based appraisal of recent timing relationships.

Illusory order reversals around the time of saccades have previously been linked to processes underlying the perceptual suppression of saccade-generated motion blur signals (Binda et al., 2009). Accordingly, illusory order reversals should be universal, as it would seem that all people with normally functioning vision typically fail to become aware of saccade-generated motion blur (Burr et al., 1994; Latour, 1962; Thiele et al., 2002; Volkmann, 1962). We assessed this hypothesis by examining the suppression of apparent target salience around the time of a saccade, and by measuring the apparent order of sequential stimuli in the same time frame. We find that both salience and subjective temporal order are subject to modulations with a matched time-dependence, but that while saccade-related salience suppressions are evident for all participants, only a subset evidence illusory order reversals.

2. Methods

Eleven volunteers took part in Experiment 1, including the first, second and last authors (P1, P2 and p11). Participant identifiers are consistent across experiments, so data labelled as having been collected from P1 in successive experiments relates to the same person. Five participants completed all experiments (P1–P5). The studies reported here were approved by the local ethics committee of the University of Queensland and were in accordance with Declaration of Helsinki. Participants gave informed consent prior to the beginning of the experiments. All participants had normal or corrected-to-normal visual acuity and colour vision.

Visual stimuli were generated using a ViSaGe stimulus generator from Cambridge Research Systems (Rochester, United Kingdom) driven by MATLAB 7.5 software and displayed on a gamma-corrected 19″ Sony Trinitron G420 monitor at a resolution of 1024 × 640 pixels and a refresh rate of 120 Hz. Stimuli were viewed from 114 cm with the head placed in a chin rest. Responses were recorded via mouse button presses. Eye movements were recorded using a high speed (250 Hz) HS-VET video eye tracker from Cambridge Research Systems.

2.1. Experiment 1: temporal order reversals for luminance defined stimuli

Each trial began with participants fixating a circular white dot subtending 0.3 degrees of visual angle (dva) at the retina. This was centred 11 dva to the left of centre on the display. After a variable period (0.9 s ± 0.25) the initial fixation point disappeared and a black saccade target (0.3 dva diameter) appeared 11 dva to the right. Participants were asked to saccade and fixate the new target as soon as it appeared. Two sequential horizontal bars (19.3 × 1 dva) were shown after saccade target onset, one 4 dva above the saccade target, the other 4 dva below. Both bars were horizontally centred on the display and shown for 8.33 ms (1 frame) with an onset asynchrony of 50 ms. Order of presentation (above then below, or below then above) was determined at random on a trial-by-trial basis (see Fig. 1).

The display background was grey (CIE $x = 0.30$, $y = 0.32$, $Y = 22$ cd/m^2) and flashed bars were green (CIE $x = 0.28$, $y = 0.34$, $Y = 39$ cd/m^2). After each test participants first reported if they had seen both bars and then, if they had, which of the two bars they thought had been first presented.

During a block of trials the delay between onset of the saccade target and onset of the first bar (50, 100 or 150 ms) was manipulated according to the method of constant stimuli, with each of three delays sampled 25 times each in random order, for a total of 75 individual trials. Each participant completed at least 2 blocks of trials (mean = 4.5 blocks, *SD* = 2.2). Additional blocks were completed as required, until at least 10 trials were recorded in which the first bar (regardless of the position of the bar) had onset in each of 10 time windows relative to saccade onset. The first of the relevant time windows extended from 90 to 70 ms *before* saccade onset, with 9 successive windows each beginning 20 ms after the last and extending for 20 ms, such that the final window extended from 70 to 90 ms *after* saccade onset. Individual data were collated across blocks of trials.

We determined the proportion of trials, falling into each of the 10 designated time bins, in which the participant had erroneously reported order relative to the physical test presentation. Any trials in which participants blinked before saccade target onset, or in which they had reported not seeing one of the two flashed bars, were repeated with a new randomisation, in terms of bar positions.

2.2. Results

Fig. 2 shows the proportion of trials, for each designated time bin, in which participants *successfully* identified physical test order. A repeated-measures ANOVA revealed a significant main effect of saccade onset time ($F_{8,\ 72} = 2.54$, $p = 0.017$). Order judgments concerning events happening well before or after a saccade onset were typically accurate, whereas timing was often misjudged when the first of two successive bars onset within a ‘critical window’ of ∼70–30 ms *before* saccade onset. The minima correct performance coincided with a time bin extending from 50 to 30 ms *before* a saccade onset, which corresponds with a second bar timing that is approximately synched with saccade onset. These data are well-matched, in terms of temporal dependence, with illusory order reversals reported by Binda et al. (2009), Kitazawa et al. (2008), and Morrone et al. (2005).

It should be noted, however, that on average across participants temporal order did not reverse *reliably*. Instead performance, averaged across participants, was close to chance for the critical time bin (−50 to −31 ms; see Fig. 2). Post-hoc pairwise comparisons (adjusted for multiple comparisons) showed that at −40 ms before the saccade, the proportion of reversals was higher than that obtained in all other time bins except for −20 and −60 ms, conditions adjacent to the peak timing for order reversals. Post-hoc tests did not detect any other pairwise differences.

2.3. Experiment 2: perceived salience about the time of saccades

Details regarding Experiment 2 were as for Experiment 1, with the following exceptions.

Nine participants, including the first two authors, took part in this experiment. One of the two bars, the Comparison, was dimmer (30 cd/m^2) than the Standard bar (33 cd/m^2). On each trial participants were asked to indicate which of the two flashed bars had seemed more salient. A block of trials involved 60 presentations of the Standard leading and 60 presentations of the Comparison leading. Participants completed at least 4 blocks of trials (mean = 5 blocks, *SD* = 0.5) until at least 18 trials had fallen within each time bins of interest. Individual data were collated across multiple trial blocks, separately for Comparison leading and for Standard leading presentations.

2.4. Results

Fig. 3 shows the proportion of correct salience judgments as a function of the initial test presentation relative to saccade onset, for trials wherein the Comparison was presented first. Bear in mind that the comparison was physically dimmer than the Standard, so an incorrect salience judgment in this context indicates that the