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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

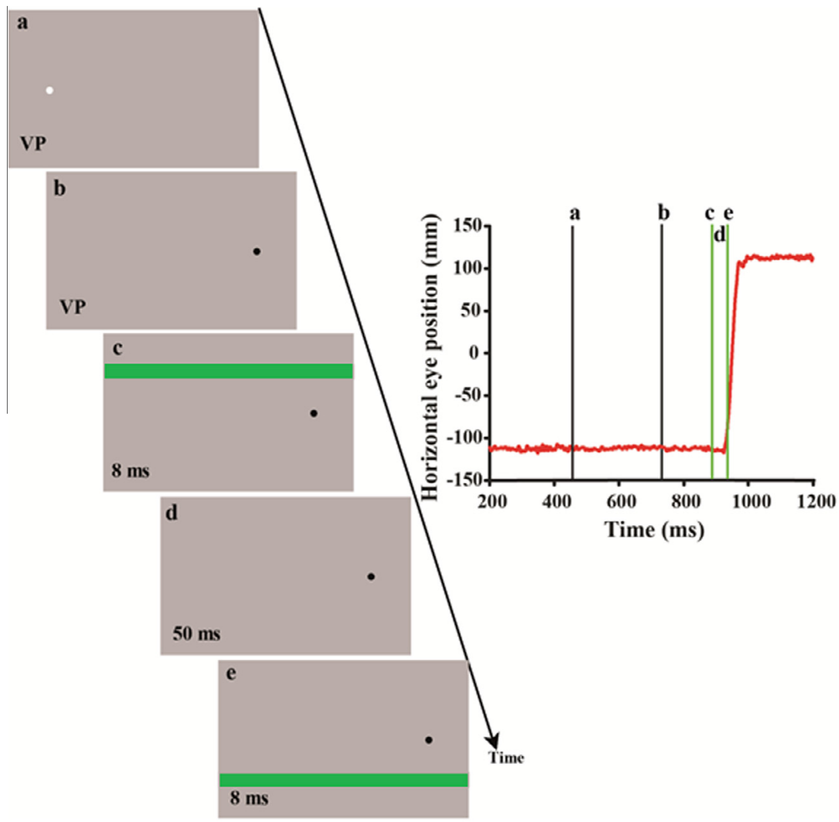

Fig. 1. Left – Schematic of the time course of events during a trial in Experiments 1 and 2. Right – Eye movement trace from a typical trial. Events depicted on the left (a. initial fixation onset, b. saccade target onset, c. first bar presentation, d. 50 ms ISI, e. second bar presentation) are marked and labelled on the eye trace. The red line traces the horizontal gaze coordinate over time. The timing of the saccade onset (red line begins moving upwards) and offset (red line begins tracing along horizontal axis again) can be inferred from examining the red line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

participant felt the second *physically brighter* stimulus was less salient than the initial *dimmer* stimulus.

A repeated measures ANOVA was conducted on these data to assess the effect of saccade onset time on perceived salience when a physically brighter – Standard – bar was presented second. There was a significant main effect of saccade onset time ($F_{8,\ 64} = 10.90$, $p < .0001$). The pattern of results was consistent with the apparent salience of physically brighter inputs being maximally reduced in the 50–30 ms pre-saccade onset time bin, a timing that corresponds well with the second (brighter) bar being presented in synchrony with the saccade onset. It is important to note that all participants experienced a reduction in apparent salience for brighter bars presented at or about the time of saccades, reflected in minimal accuracy when identifying the timing of the physically brighter bar when its presentation coincided with the critical −40 ms time bin (see Fig. 3).

2.5. Experiment 3: persistent tests with sudden onsets

One possible explanation for perisaccadic reversals of perceived order in Experiment 1 was that a subset of participants used stimulus appearance as a proxy for timing in conditions of uncertainty. Stimuli in Experiment 1 were transient, like those in similar experiments conducted by other authors (Binda et al., 2009; Morrone et al., 2005). While potentially visible, the apparent salience of targets presented during a saccade can be diminished. This is apparent from our analyses of apparent contrast as a function of saccade time in Experiment 2. Thus, in Experiment 1, if people had picked the most salient target as most proximate in time when uncertain of temporal order, an illusory reversal of timing might have ensued that was simply a bias reflecting temporal uncertainty, which in turn was maximal at the time of saccades.

To assess this hypothesis, in Experiment 3 we ask participants to judge the temporal order of bars that suddenly onset but then remain visible on the display screen. The appearance of such stimuli is believed to be determined by protracted analyses, and thus should not be impacted by transient saccadic suppressions (Blakemore & Campbell, 1969). If apparent reversals of order (evidenced by some participants in Experiment 1) were due to modulations of apparent salience, we would therefore expect them to be eliminated in this experiment.

Details for Experiment 3 were as for Experiment 1, with the following exceptions.

There were seven participants, including the first two authors. Whereas stimuli in Experiments 1 and 2 were transient, in Experiment 3 stimuli would suddenly onset at times matched to previous experiments, but then persist until the participant had made a judgement regarding test onset order.

2.6. Results

A repeated measures ANOVA was conducted to compare the effect of saccade onset time on accuracy of test onset order judgements. There was a significant main effect of saccade onset time ($F_{8,\ 48} = 5.17$, $p < .001$). Contrary to the hypothesis, the pattern of results was very similar to that of Experiment 1, as is apparent from an inspection of Fig. 4, in comparison to Fig. 2. Averaged across participants, onset order sensitivity was maximally reduced when initial tests were presented from 50 to 30 ms ($M = .49$, $SD = .22$) and from the 30 to 10 ms ($M = .49$, $SD = .25$) before sac-

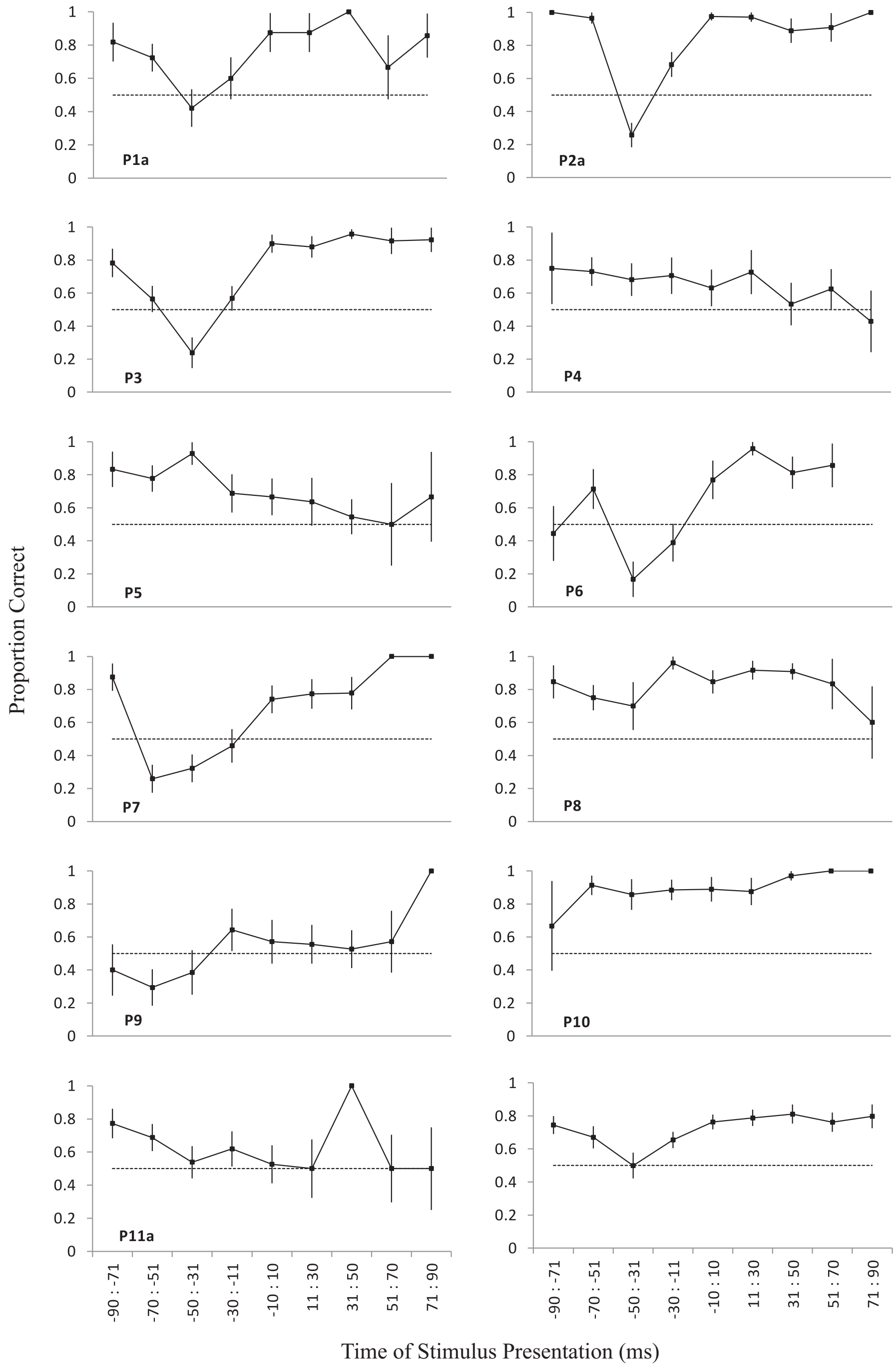

Fig. 2. Individual data from Experiment 1, depicting proportion of correct order judgments as a function of initial bar onset time relative to saccade onset. Error bars depict binomial standard error. Dashed horizontal lines denote chance performance. Data averaged across participants is depicted in the bottom right, where error bars depict ±1 SEM. Suffix 'a' signifies author data.

cade onset. These data show that temporal order reversals still occurred at the predicted time bins, suggesting they are unlikely to be fully explicable in terms of participants adopting the salience of stimuli as a proxy for event timing under conditions of uncertainty.

2.7. Experiment 4: order reversals and saccade length

In Experiment 2, the optimal presentation time for inducing illusory reversals of salience was matched to the optimal time for inducing illusory order reversals. This could have indicated that a sub-set of participants had used apparent salience as a proxy for timing when uncertain of temporal order. The results of Experiment 3 refute this possibility. Illusory order reversals were still reported for targets that onset in the critical time bin, despite stimuli being persistent and therefore seeming to have equal salience. Moreover, a subset of participants reported illusory order reversals on a proportion of trials (>60% of trials in that time bin) that seems to preclude simple insensitivity, and random responding, as an explanation.

Given the discrepancy between our findings, suggesting temporal insensitivity and guessing about timing, and previous findings, suggesting a universal order reversal effect (Binda et al., 2009), we decided to investigate whether more robust reversals could be eli-

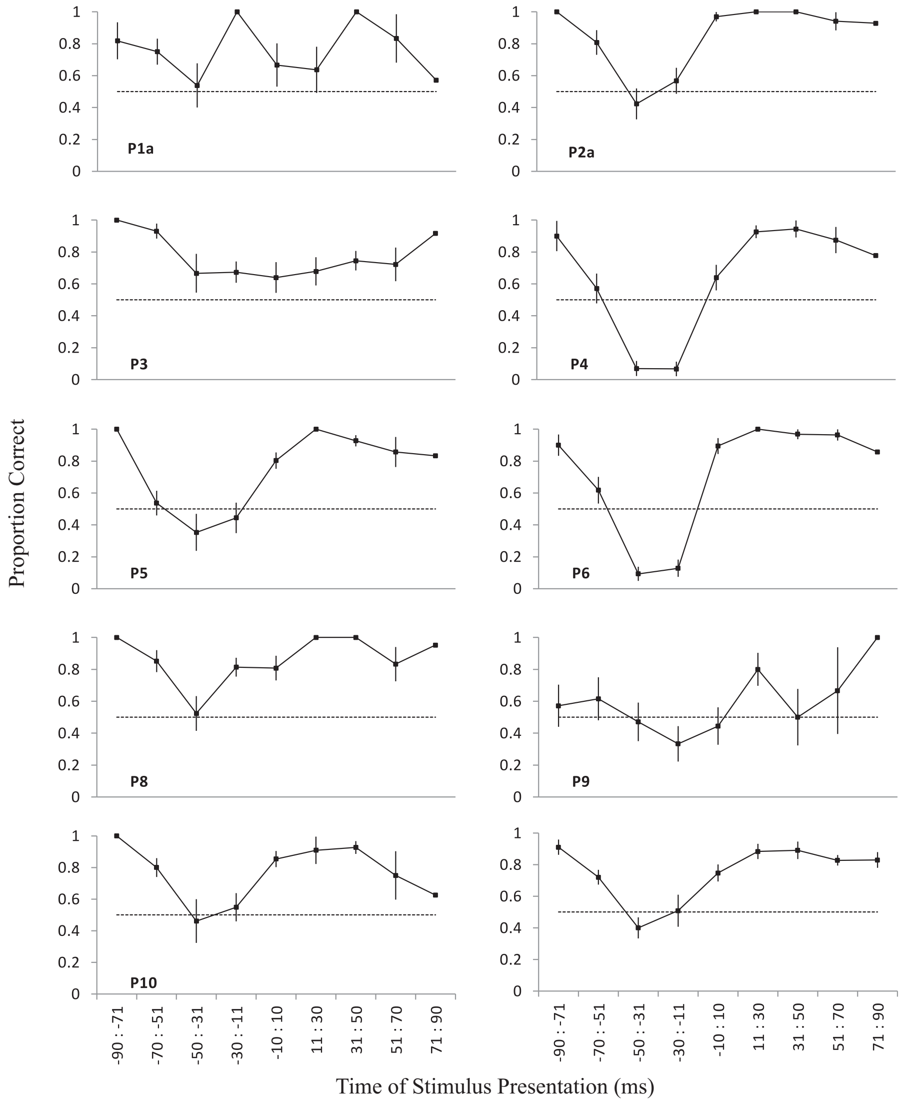

Fig. 3. Results of Experiment 2. Proportion of correct salience perception responses as a function of test presentation time relative to saccade onset when the comparison bar (dimmer) was presented first. Error bars depict binomial standard error. Bottom right graph shows averaged data where error bars depict ±1 SEM. Suffix 'a' signifies author data.

cited using longer saccades. Previous research on this phenomenon has employed larger saccades (30 dva, Binda et al., 2009; 24 dva, Kitazawa et al., 2008), as compared to 22 dva in our preceding experiments.

Details regarding Experiments 4 were as for Experiment 1, with the following exceptions.

Seven participants, including the first two authors, took part in Experiment 4. Participants made saccade movement toward a proximate (6 dva from fixation) or distal (29 dva from fixation) target in different blocks of trials. Block order was counterbalanced across participants.

2.8. Results

A paired-samples *t*-test confirmed that long saccades were more persistent ($M = 104$ ms, $SD = 5.97$ ms) than short saccades ($M = 57.7$ ms, $SD = 2.69$ ms; $t_6 = 27.44$, $p < 0.0001$).

To compare the time spans across which order reversals occurred, we normalised the proportion of reversals in each time bin to the peak of order reversals. Then, we added the normalised values from the bin before the peak to the bin just after the peak (three bins including the bin where the peak occurred, value = 1). Given the small number of participants and the nature of the measurement (normalised proportions), we adopted a conservative approach and tested for a difference between means of the normalised values using the Wilcoxon test (exact *p* value reported). The sum of the normalised values was 2.12 ($SD = 0.24$) for the short saccade and 2.61 ($SD = 0.23$) for the long saccade as shown in Fig. 5. The Wilcoxon test revealed a statistically significant difference between these means ($z = 2.36$, $p = 0.017$).

3. General discussion

Here, we have examined the determinants of illusory order reversals around the time of saccades. Consistent with previous reports, in Experiment 1 we found that when stimuli were presented just before a saccade, performance deteriorated and participants erroneously reported order reversals (Morrone et al., 2005). Intriguingly, however, our data suggest order reversals are not universal, as only a subset of participants (5 of 11) reported these at a rate below chance performance (see Fig. 2). Data from other participants, and data averaged across participants, was suggestive of

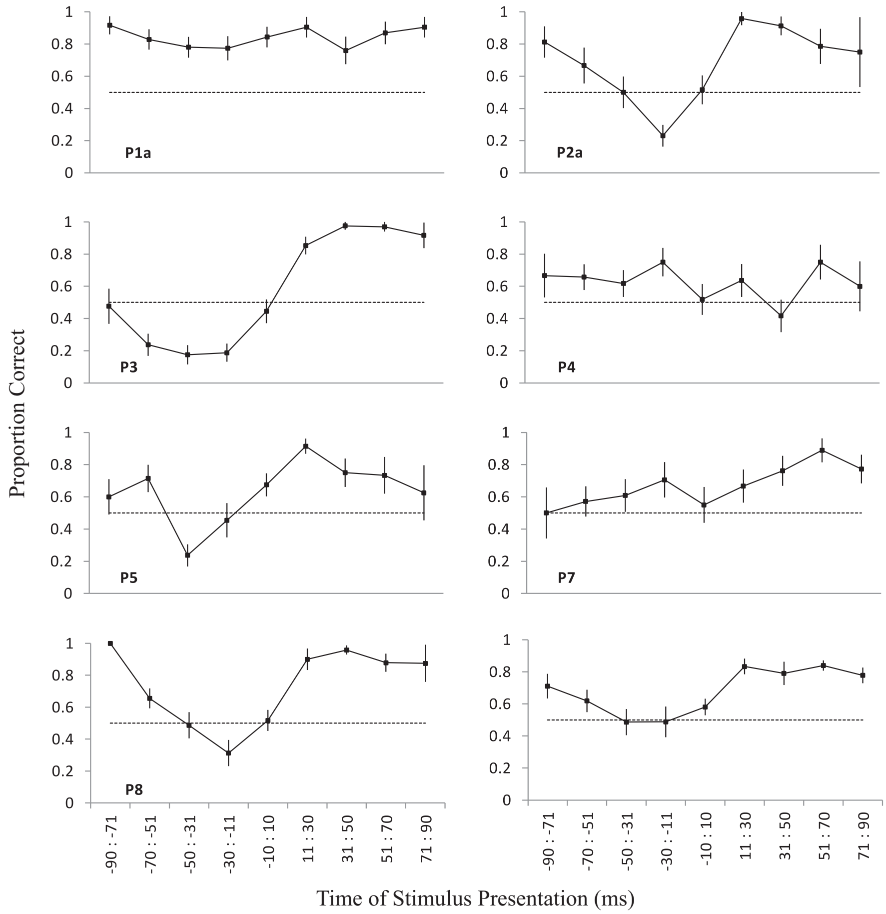

Fig. 4. Results of Experiment 3. Proportion of illusory order reversals as a function of initial bar presentation time relative to saccade onset when the flashed bars remained on the screen until a response was made. Error bars depict binomial standard error. Bottom right graph shows averaged data where error bars depict ±1 SEM. Suffix 'a' signifies author data.

chance performance (50%). Overall, these data are indicative of insensitivity, as opposed to a systematic universal reversal of subjective order.

In Experiment 2 we showed that the time course of salience modulations, about the time of saccades, is well-matched to reports of illusory order reversals. This effect was, however, apparent for all participants – consistent with this being a universal consequence of saccades. This prompted us to speculate that order reversals might result from a subset of participants using stimulus salience as a proxy for timing when uncertain. The results of Experiment 3 refuted this suggestion, as illusory order reversals still occurred when subjective salience changes were eliminated.

Experiment 4 used longer saccades (29 dva) than we had used in earlier experiments (22 dva). Results were analogous to those reported by Kitazawa et al. (2008). In their study, Kitazawa and colleagues had employed a saccade length of 24 dva (compared to our 29 dva). Their results were reminiscent of our own – order reversals were observed, but not universally.

What implications do our data have for the existing explanation of illusory order reversals? Binda et al. (2009) have proposed that saccade related temporal inversions and saccade related reductions of salience have a common cause – namely the suppressive process associated with saccades. Our data are consistent with saccade related salience reductions being experienced by all people with normally functioning visual systems, but are inconsistent with saccade related temporal inversions being similarly universal. This suggests the latter phenomenon might require an addition fact relative to saccadic suppression. What might the nature of this fact be?

One possibility is that saccade related salience modulations and order reversals share a common cause, but salience modulations are simply more pronounced and are therefore easier to measure than illusory order reversals. According to this rationale, it might be possible to adopt a set of stimulus parameters that would deliver more robust, universal, order reversals. To investigate this possibility, future studies should investigate the contingency of order reversals on stimulus settings, wherein our stimuli differed from those that elicited more robust order reversals in other studies – such as an increased target eccentricity (see Binda et al., 2009). It is additionally possible that the time-course and extent of saccade related suppression is variable across participants. The duration and extent of saccadic suppression experienced by some people might have been sufficient to induce order reversals for events separated by 50 ms, but other people might experience lesser suppression and only experience reversals for events at smaller separations.

We choose a 50 ms offset between sequential events as this was within the range of offsets that seemed optimal for inducing illusory order reversals in a previous study (Morrone et al., 2005; 20–76 ms, see Fig. 4a and b, p. 952). This timing is also commensurate with the critical timing for a maximal suppression of saccade-generated motion blur signals (Wurtz, 2008). It remains possible, however, that this timing was sub-optimal for some participants, and that smaller temporal separations should be used (see Binda et al., 2009).

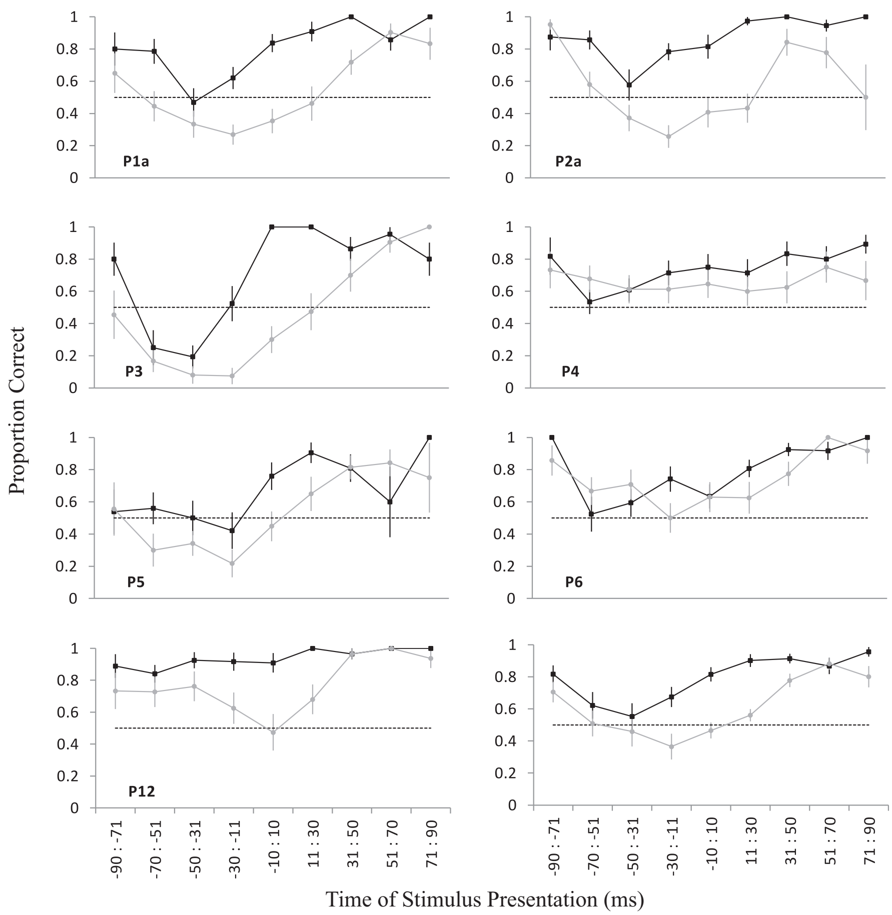

Fig. 5. Results of Experiment 4. Proportion of incorrect temporal order judgements for short saccades (black) versus long saccades (grey). Error bars depict binomial standard error. Bottom right graph shows averaged data where error bars depict ±1 SEM. Suffix 'a' signifies author data.

Another possibility is that in addition to saccadic suppression, a subset of people evidence illusory order reversals as they adopt a particular inferential strategy. Due to saccadic suppression, the neural onset transient for a stimulus presented during a saccade is mitigated, potentially causing temporal ambiguity. This could necessitate an inferential process when attempting to judge the timing of the impacted, relative to other events. Some participants might infer that the temporally ambiguous stimulus has onset prior to the saccade. Others might make the opposite inference, but this would not readily be apparent, as it would just enhance veridical reports of event order. Still other participants might simply guess at event order. Summing across equal numbers of such participants would produce order reports, about the time of saccades, which are consistent with chance. This would seem to be a good description of our data.

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