Spatial consequences of bridging the saccadic gap

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Abstract.

We report six experiments suggesting that conscious perception is actively redrafted to take account of events both before and after the event that is reported. When observers saccade to a stationary object they overestimate its duration, as if the brain were filling in the saccadic gap with the post-saccadic image. We first demonstrate that this illusion holds for moving objects, implying that the perception of time, velocity, and distance traveled become discrepant. We then show that this discrepancy is partially resolved up to 500 ms after a saccade: the perceived *offset* position of a post-saccadic moving stimulus shows a greater forward mislocalization when pursued after a saccade than during pursuit alone. These data are consistent with the idea that the temporal bias is resolved by the subsequent spatial adjustment to provide a percept that is coherent in its gist but inconsistent in its detail.

Introduction

How does conscious experience emerge from the temporal flow of sensory input? Clay, cited by James, introduced the concept of the "specious present" to characterize an extended temporal window within which ongoing events can influence an apparently instantaneous perceptual experience (James, 1890). Since that time there has been a lively debate regarding whether perception is feedforward and immediate, accurately reflecting the physical timing and neural delays of stimulus processes, or post-hoc and reinterpretive (Dennett & Kinsbourne, 1992; Libet, Wright, Feinstein, & Pearl, 1979; Zeki & Bartels, 1998).

Illusions such as the flash-lag effect and somatosensory saltation have been taken to imply that the perception of an event can be influenced by *subsequent* sensory information (Eagleman & Sejnowski, 2000; Geldard & Sherrick, 1986) These results suggest that the brain imposes a delay between sensation and perception in order to accommodate all potentially relevant input. There is also evidence from phenomena such as forward masking that prior events can influence subsequent ones by enhancing or degrading stimulus processing (Foley & Boynton, 1993; Posner, 1980; Raymond, Shapiro, & Arnell, 1992). The question we ask here is whether both effects can ever occur together as predicted by the concept of the specious present. That is, can our reports about past events be better characterized as a sequence of temporal snapshots in which events interact both forwards and backwards in time throughout the window, rather than as a continuous stream of sensory input?

We addressed this question with a modification of the saccadic chronostasis illusion. In saccadic chronostasis, observers experience the temporal interval immediately following a saccade as longer than a comparable control interval (Yarrow, Haggard, & Rothwell, 2004a; Yarrow, Haggard, Heal, Brown, & Rothwell, 2001; Yarrow, Johnson, Haggard, & Rothwell, 2004b). The target stimulus changes form or color during the saccade, but observers feel they have seen it in its changed state since before the time of saccade initiation. This mechanism may contribute to our experience of visual continuity across eye movements by filling in the saccadic gap caused by retinal blur and saccadic suppression (Ross, Morrone, Goldberg, & Burr, 2001). Four main lines of evidence support this interpretation. Firstly, the size of the illusion grows with the duration of the preceding saccade (Yarrow et al., 2001). Secondly, the illusory bias is constant for saccades of a given size regardless of the type of saccade that is made (Yarrow et al., 2004b) or the duration of the stimulus that is fixated (Yarrow et al., 2004a). Thirdly, when subjects make temporal order judgments comparing a brief auditory tone and the initial perception of a post-saccadic target stimulus, their judgments are biased in a manner consistent with advanced awareness of the post-saccadic stimulus (K.Y, L.W., P.H. & J.C.R., submitted). Finally, the chronostasis illusion disappears when the spatial continuity of the saccade target is noticeably compromised (Yarrow et al., 2001).

These results suggest that an illusory timeline for perceptual events is recalled following a saccade. However, we do not know whether this distortion affects only perceived time, or can also influence other perceptual dimensions such as spatial location. Events on the timeline are repositioned, but the properties of the intervening percept that fills the saccadic gap are unknown. In the experiments reported here, we altered the

typical saccadic chronostasis procedure by asking subjects to saccade to a *moving* target.

If the target is perceived to have been present from before the saccade, there will be a

discrepancy between its perceived duration and its veridical trajectory. The laws of

physics dictate a specific relationship between position, velocity, and time. The saccadic

chronostasis illusion means that the post-saccadic object will have an extended *subjective*

duration, which will therefore be inconsistent with its veridical path of motion. Will the

brain adjust spatial perception to resolve this discrepancy? Visual perception does not

always respect the logical relation between physical space, time and velocity. In the

waterfall illusion, for example, an object may clearly appear to move with only very

minor changes in perceived position (Nishida & Johnston, 1999). Hence the brain might

not attempt to produce a coherent perceptual experience after a saccade. Alternatively, it

might achieve spatiotemporal coherence by various means. Figure 1 provides a schematic

summary of some possible resolutions, and their consequences for perceived onset

position, offset position, or velocity. The present experiments tested for each of these.

Our results suggest that the brain may be willing to adjust its interpretation of the

individual events comprising a recent sensory episode in order to have the episode as a

whole make sense.

Experiment 1. Our first experiment was designed to establish whether chronostasis

occurred for moving stimuli. If so, the illusion might be accompanied by a *temporally*

aligned adjustment to spatial perception (see Figure 1 parts a and b). Experiment 1 tested

the hypothesis that antedating would be accompanied by the perception of an illusory

spatial trajectory filling the saccadic blank period (Figure 1a).

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Materials and Methods

Participants. Eight subjects (5 male, mean age 28.9, SD 6.6) participated. Two were authors, the other six were naïve to experimental hypotheses. Five more were tested and subsequently rejected because their temporal judgments were unreliable (logistic regressions lacked significant slope). Note that these rejections did not depend on the pattern of means these subjects produced (which was in the same direction as the group that was included) but rather on the consistency of their temporal judgments in what was clearly a challenging task.

Apparatus. Subjects sat before a 22" CRT color monitor refreshing at 100 Hz. Eye to screen distance was maintained at 41 cm using a chin/forehead rest. Horizontal eye movements were recorded from the left eye and vertical eye movements from the right lower eyelid using an infra-red eye tracker (Applied Science Laboratories Eye-trac model 310) and sampled at 200 Hz (12 bit A/D card; National Instruments DAQ 1200). Visual stimuli were black, red or grey on a white background (average luminance 91 cd/m^2). They consisted of crosses and circles (subtending 1.2º of visual angle) and a clock face (7º radius, hour marks extending 1º inwards). Crosses and circles moving within the clock face followed a trajectory 5º in radius.

Design. A two factor (2 x 2) repeated-measures design was employed. Factor 1 compared trials involving saccades with constant pursuit (control) trials. Factor 2 varied the

decision subjects made (temporal or spatial). Subjects completed 50 randomly interleaved trials from each condition in a single block of 200 trials. Rejected trials (see procedure, below) were repeated at the end of the block.

Procedure. Figure 2 shows the stimulus events/ trial structure for control and saccade conditions. In saccade trials, subjects initially fixated a peripheral black cross. A clock face on the opposite side of the screen (20° distant at its centre) contained a target black cross at a random start position. A message indicated whether a temporal or spatial judgment would be required. After subjects started the trial with a mouse key press, the target black cross followed a clockwise circular trajectory with an angular velocity of 0.4 cycles per second (12.6º visual angle per second). Subjects maintained fixation at the initial black cross until it turned grey (500 ms after the key press) then make a speeded saccade to the target black cross. The eye movement signal was continuously monitored so that the black cross could be replaced with a black circle 5º into the saccade. Delays arising from online control (approximately 2-23 ms based on sampling and screen refresh rates) meant that this change actually occurred 5.5-11.5º into the saccade. The black circle then continued to move with the same velocity for a variable duration (200-800 ms). After this time it changed color to red (the reference stimulus) moving for a further 500 ms before disappearing. The red circle began and finished with the same velocity as the preceding black circle, but its velocity profile varied randomly from trial to trial to prevent distance covered providing a cue for temporal judgments. Velocity increased or decreased by up to half the baseline speed, reaching and returning from this maximum perturbation in a sinusoidal manner. Subjects pursued the circle to its disappearance.

In saccade temporal judgment trials, subjects indicated whether they saw the black circle for more or less time than the red circle. The black circle's duration was selected randomly from a condition-specific adaptive distribution containing values between 200 and 800 ms in 20 ms steps. The distribution was initially uniform, in the region 340-660 ms, but was updated after each accepted trial according to the generalized P'olya urn model (type IV, k = 8) (Rosenberger & Grill, 1997). In saccade trials, each trial's duration value was corrected post hoc to match the time the black circle was on screen following target foveation by subtracting the time the eye was in motion following the triggered change to a circle. Subjective duration estimates were then obtained using logistic regression. Saccade start/end points were calculated automatically using a velocity criterion. Trials in which corrective or catch-up saccades exceeding 3° occurred were rejected. Running averages of reaction time (RT) and saccade duration for the last ten saccade trials were maintained (initially 200/60 ms for RT/saccade duration respectively) and were used in control trials (see below). Trials were rejected when eye movements were initiated anticipatorily, or too slowly (> running average RT +300 ms).

In saccade spatial judgment trials, subjects used a scroll bar to position a black circle on the clock face in the position at which they had first seen it. The value recorded was adjusted (as in temporal judgment trials) to produce a localization error relative to the black circle's position when first foveated. Localization errors were averaged across trials, with trials rejected as above.

In control (constant pursuit) trials, subjects initially fixated the cross within the clock face so that no saccade was required. Following a key press, the cross began to move, turning grey 500ms later for a duration determined by the running average RT

from the saccade conditions, then disappeared for a duration determined by the running average saccade duration. The variable-duration black circle then appeared (at a position consistent with continuous motion) with subsequent stimulus presentation and subject responses as per saccade trials. Control trials were rejected if a saccade exceeding 3° was detected. Direction of saccade (saccade conditions: left to right and vice versa) or position of the clock face (control conditions: left or right) alternated every trial.

Results and discussion

Results are shown down the left-hand side of Figure 3. For duration judgments (3a, top) subjective duration estimates represent the duration for which the post-saccadic black circle had to be displayed *following foveation* in order to be judged of equal duration to the 500 ms reference. Judgments were fairly accurate in the control condition, but the duration estimate was significantly lower in the saccade condition (mean chronostasis effect = 110 ms; $t = 4.24$, $df = 7$, $p = 0.004$) indicating that the black circle underwent illusory temporal extension. We assumed that the moving circle could not be perceived for the purposes of estimating duration until it was foveated (because of saccadic suppression). The validity of this assumption affects the size, but not the direction of the effect. Mean saccade durations were 69 ms, and the change from a cross to a circle occurred on average 29 ms into the saccade, implying that the black circle was effectively seen 41 ms before saccade initiation (and 70 ms before its actual appearance was triggered in mid saccade).

For position judgments, the localization errors shown in Figure 3a (bottom) are given in units of milliseconds rather than degrees of visual angle in order to allow easy comparison with duration judgments (conversion based on the 12.6°/sec mean velocity). In saccade trials, the localization error represents the average difference between the judged position at which the black circle was first seen and the actual position it occupied when first foveated. The black circle was initially mislocalized forwards by 0.69° of visual angle (equivalent to 55 ms). In control trials, mislocalization was in the same direction, but larger on average. This bias differed significantly from zero in the control condition (t = 3.71, df = 7, p = 0.008) and showed a clear trend in the saccade condition (t = 2.33, df = 7, p = 0.052), being individually significant in six out of eight cases. The two conditions also differed significantly from one another (t = 2.98, df = 7, p = 0.02). Our calculation of the effect's magnitude depends upon the same assumption about saccadic suppression employed in the duration judgment data (we calculated bias relative to foveation position rather than physical onset position). However, once again the direction and presence of the bias is clear. Calculating bias relative to the position at which the mid-saccadic stimulus change occurred in saccade trials would add approximately 40 ms to the effect, enhancing it to a level similar to that obtained in control trials.

These data demonstrate a temporal bias when saccading to a moving stimulus, accompanied by a spatial bias relating to its initially perceived position. Although the spatial bias was smaller in saccade compared to control trials, its forward direction is incompatible with the perception of an illusory trajectory at a time consistent with the temporal illusion (Figure 1a). The spatial bias found during pursuit in our control

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condition is consistent with previous reports (Jordan, Stork, Knuf, Kerzel, & Musseler, 2002; Kerzel, Jordan, & Musseler, 2001; Mateeff, Yakimoff, & Dimitrov, 1981). Ours is, however, at least to our knowledge, the first study to investigate where a moving/pursued object is initially perceived *following a saccade*. We found a forwards bias similar to that obtained when an object appears at an unpredictable spatial location (Frohlich, 1923). This localization error seems surprising, given that the position of a moving object appears to be very well anticipated across saccades when assessed in terms of either displacement detection thresholds (Gysen, De Graef, & Verfaillie, 2002) or the degree of preparedness of the pursuit system (Lisberger, 1998).

Experiment 2. Rather than constructing an interpolated trajectory to fill in the period of the eye movement, the brain might produce a static image of the post saccadic stimulus at a location near where it was first foveated (Figure 1b). One prediction of such an account is that at the point the cross is perceived to change into the (momentarily stationary) black circle it would have to jump forward (see the discontinuity in the position trace and upwards arrow in the velocity trace of Figure 1b). In this case, we would expect subjects to perceive a slight forwards jump in the stimulus, whereas no such discontinuity would be perceived if the black circle actually jumped *backwards* at the moment it first appeared. In the latter case, the initially foveated circle would occupy the same spatial position that the peripheral cross had occupied when the saccade began.

Materials and methods

Seven of the eight subjects from Experiment 1 and one new subject completed 60 trials each (mean age 27.0, SD 4.1, five male). One subject had to repeat the experiment (initial logistic regression p > 0.05). The procedure was identical to that used in the saccade conditions of Experiment 1 except that on each trial, at the instant the black circle replaced the black cross during the saccade (5º plus delay into the eye movement) the black circle was moved forwards or backwards. Hence this stimulus jumped slightly rather than maintaining a continuous trajectory. Both circles were now presented for 500 ms. Subjects judged whether the black circle had jumped forwards or backwards. The magnitude of the jump was selected randomly (-300 to +300 ms, equivalent to -3.78 to + 3.78º visual angle) from an adaptive distribution (initially uniform, -160 to +160 ms).

Results and Discussion

On average, subjects perceived continuity when the black circle was displaced backwards by 24 ms (standard deviation 36 ms), equivalent to 0.3º visual angle, a value that was in the predicted direction but did not differ significantly from zero (t = 1.87, df = 7, p = 0.104). We cannot therefore conclude that subjects perceived a discontinuity (forwards jump) in the stimuli's trajectory at the transition from pre to post-saccadic stimulus, in line with the perception of a static image filling the period of the eye movement.

Experiment 3. Having failed to find evidence that spatial perception was adjusted at a time consistent with the temporal illusion demonstrated in Experiment 1, we now

investigated possible adjustments to *subsequent* spatial perception. One possibility is that subjects misperceive the velocity of a moving stimulus seen after a saccade, such that the distance it covers is appropriate for its perceived duration. Perceived velocity might fall to a constant sub-veridical level across the duration of the post-saccadic stimulus with a subsequent sudden increase in speed (see Figure 1c) or follow some more complex and smooth profile. The temporarily reduced velocity would compensate for the additional duration associated with temporal antedating, while avoiding any spatial mislocalization of post-saccadic events. We tested this possibility using a nulling procedure.

Materials and methods

The procedure is illustrated in Figure 4a. Both the procedure and subjects were identical to those used in Experiment 2 with the following exceptions. Subjects completed four blocks of trials. The black circle appeared at the correct location (i.e. did not jump) but the velocity profiles of both the black and the red circles were initially perturbed in the region zero to two times baseline velocity (in steps of 0.1 x baseline velocity) at each of five points (start, ¼, ½ and ¾ of the way through, and end for each circle). Intervening velocity values were determined using spline fits (one per circle). Subjects could adjust the velocity at one or more points from trial to trial by setting positive or negative scores relative to the unknown initial perturbations (steps of 0.1 x baseline velocity, but no scale specified). They terminated the block (after a minimum of ten acceptable trials) when they considered that both circles moved smoothly and with a velocity equal to that of the preceding black cross.

Results and Discussion

Based on Experiment 1, subjects should perceive the black circle as having a greater duration than the red circle. If a biased velocity judgment helps achieve spatiotemporal coherence, they should therefore see the black circle moving at a lower average speed than the red circle when it actually moves with the same velocity (because it covers less distance in the same amount of *perceived* time). Hence, to achieve a percept of smooth constant motion they ought to increase the black circle's velocity, setting it to a higher average speed than the red circle. The results are shown in Figure 4b. Averaged across the visible period of circle motion (non-greyed areas in Figure 4b) subjects adjusted velocity to a very similar level for the black and red circles (1.27 versus 1.22 times baseline velocity respectively). These values did not differ from one another ($t = 0.78$, $df = 7$, $p = 0.461$) but did differ from the actual speed of the preceding peripheral black cross (black circle: $t = 4.88$, $df = 7$, $p = 0.002$; red circle: $t = 2.6$, $df = 7$, $p = 0.036$). The experiment had a power of 0.74 (two-tailed) to detect a difference that could account for the full 110 ms temporal bias found in Experiment 1. We cannot assert that chronostasis influenced subsequent perception based on these data, but were it shown reliable in a larger sample, the small trend towards higher adjustments for the black circle than the red circle could account for around 29 ms of this temporal bias. Subjects did perceive both circles as moving slower than the preceding cross (viewed in peripheral vision) when velocities were actually identical, but this result is incidental to our

hypothesis, being an example of the classic Aubert-Fleischl phenomenon (Aubert, 1886; Fleischl, 1882).

Experiment 4. We next assessed whether spatiotemporal coherence was achieved by biasing subjects' perception of the *offset* position of the saccade target object (the change of circle color from black to red). A change in perceived position at this point implies an alteration in the extent of the perceived trajectory for the post-saccadic object. An alteration to the time at which the onset of the saccade target is perceived would thus be compensated by a spatial alteration occurring at its offset (Figure 1d).

Materials and Methods

The eight subjects from experiments 2 and 3 completed Experiment 4, with two further subjects tested but rejected. Procedurally, Experiment 4 was identical to Experiment 1 except that in spatial judgment trials subjects judged the position at which the circle changed color from black to red, rather than the position at which it was first perceived.

Results and discussion

Results are shown down the right-hand side of Figure 3. The duration judgment task is unchanged from Experiment 1 and shows an identical pattern of results, with the large difference between control and saccade conditions (chronostasis effect of 146 ms; t

= 3.95, df = 7, p = 0.006) indicating that the black circle's duration was overestimated. Average saccade durations (66 ms) and trigger times (average display change 25 ms into the saccade) were also similar to our first experiment. For position judgment trials, however, results were quite different. The forwards mislocalization bias was larger in the saccade condition than in the control condition (difference of 37 ms, equivalent to 0.47º visual angle; t = 4.45, p = 0.003) indicating that the change from a black circle to a red circle was perceived to occur later when this change marked the offset of an epoch initiated during a saccade and subject to illusory temporal extension.

Hence, combining the results from experiments 1 and 4, we can infer that the black circle underwent a smaller onset spatial mislocalization but a greater offset spatial mislocalization in saccade compared to control conditions. This observation was confirmed statistically using a 2x2 ANOVA with one between subjects factor (onset/offset judgments) and one within subject factor (saccade/control conditions; f = 22.45, df = 1,14, p < 0.001). This result is consistent with subjects having perceived an extended trajectory for the black circle following a saccade.

Experiment 5. In the first four experiments, we tested a number of possible ways in which the brain might achieve spatiotemporal coherence following a saccade to a moving stimulus, and found a statistically reliable and potentially compensatory spatial effect occurring at the end of a 500 ms post-saccadic stimulus. Having inferred a mechanism that compensated for a temporal bias by adjusting subsequent spatial vision, we considered what timecourse this mechanism would be effective over. Presumably visual consciousness is not infinitely malleable in response to temporally distant saccade-

contingent effects. Before progressing to test the window over which compensation

would occur (Experiment 6, below) we first had to verify that the temporal effect

(chronostasis) occurred at post-saccadic stimulus durations across our intended test range.

We therefore introduced a variant task requiring an absolute temporal estimate. This

procedure allowed us to determine efficiently whether the temporal bias varied with the

duration of the stimulus that was being judged. It also tested our tacit assumption that it

was the duration of the post-saccadic stimulus that was being influenced (as opposed to

that of the reference).

Materials and Methods

The procedure and subjects were identical to those used in Experiment 3 with the

following exceptions. The red circle was omitted. Presentation was blocked, with four

temporal judgment blocks of 20 trials each (10 saccade and 10 control, pseudorandom

order). The black circle was displayed for 260-750 ms (in 10 ms divisions) with 2

randomly selected presentations in each 100 ms bin per block (i.e. 2 presentations

between 250 and 350 ms etc.). Subjects judged the duration for which they had seen the

black circle on a 1-1000 ms scale. Examples of a stationary black circle presented for

300, 400, 500, 600 and 700 ms were given at the beginning of each block and on request.

Error scores were calculated as the difference between the duration presented (following

foveation for saccade trials) and subjects' judgments, and were averaged across trials.

The velocity of the black circle was randomly adjusted from trial to trial. The velocity

profile was set at five points (start, ¼, ½ and ¾ of the way through, end). At each point, a

random perturbation from 0.5 to 1.5 x baseline velocity was applied (in steps of 0.1 x

baseline velocity).

Results and Discussion

The results are plotted in Figure 5. On average, judgments in the control condition

underestimated the actual presentation time by 42 ms. In contrast, judgments in the

saccade condition exceeded the time for which the black circle had been foveated by 72

ms, a significant difference of 114 ms ($t = 8.58$, df = 7, $p < 0.001$). For each subject, we

used linear regression to determine the relationship between actual stimulus durations and

judged durations in control and saccade conditions. Mean slopes did not differ ($t =$

0.22, df = 7, $p = 0.833$) but mean intercepts differed significantly by 115 ms ($t = 2.90$, df

$= 7$, $p = 0.023$). These results indicate that the temporal bias was present and of a similar

size for post-saccadic stimulus durations ranging from 250 to 750 ms.

Experiment 6. We next employed a procedure similar to the position judgment conditions

of Experiment 4, but with post-saccadic stimuli lasting either 250 or 750 ms before the

change to a red circle, in order to assess the maximum duration over which chronostasis

would have a knock-on effect on spatial perception.

Materials and Methods

A new sample of 12 subjects (5 male, mean age 27.6, SD 4.0) completed an experiment that differed from Experiment 4 only in the following respects. Position judgments were made in all trials, with control/saccade trials performed with a black circle duration of either 250 or 750 ms duration (40 trials per condition randomly interleaved). The red circle now moved with constant velocity. In control trials, the initially fixated cross did not begin to move at once. It remained stationary, turned grey, disappeared, and was replaced by the black circle, which immediately began to move, thereby more accurately matching the period of pursuit between control and saccade conditions.

Results and Discussion

The results are presented in Figure 6. A 2x2 repeated measures ANOVA showed a significant interaction between post-saccadic stimulus duration and the presence/absence of a saccade (f = 6.30, df = 1, 11, p = 0.029). Follow-ups indicated that the mislocalization bias was significantly larger when the circle changed color 250 ms after a saccade initiated pursuit than when this change occurred after 250 ms of pursuit from fixation (32 ms difference, equivalent to 0.40º visual angle; t = 2.53, df = 11, p = 0.028). No such difference emerged when the post-saccadic stimulus remained black for 750 ms (11 ms trend in the opposite direction, equivalent to 0.14º visual angle; t = 1.48, df = 11, p = 0.166). These results contrast with those of Experiment 5, where the chronostasis (temporal) effect occurred with a consistent magnitude over this whole range.

General Discussion

We conducted six experiments to determine 1) if a temporal bias existed for moving targets seen following a saccade, and 2) whether the brain modified spatial perception, perhaps in order to achieve spatiotemporal coherence. Regarding point 1, experiments 1, 4 and 5 provided converging evidence from two different tasks that the duration of a moving stimulus pursued after a large saccade was indeed overestimated compared to an identical stimulus pursued from fixation. This bias is comparable in size with that obtained when saccading to a stationary target, and shows a similar constancy across post-saccadic stimulus durations (Yarrow et al., 2004a; Yarrow et al., 2001). It is therefore likely to result from the same antedating mechanism.

We showed clear evidence for a saccade-contingent spatial bias in experiments 4 and 6. In Experiment 4, subjects judged the position at which the post-saccadic stimulus (black circle) changed to the reference stimulus (red circle). The critical event (the change of color) always occurred during smooth pursuit. Subjects displayed a greater forwards bias around 500 ms after a saccade than when no saccade had been made (i.e. there was an additional bias in the saccade condition over and above the standard forwards mislocalization found in the control condition). In Experiment 6, the same judgment was made when the color change terminated the post-saccadic stimulus either 250 or 750 ms after the saccade. The control conditions revealed the familiar forward localization bias (discussed earlier) and also showed a slight increase in this bias with time since smooth pursuit initiation. The saccade conditions revealed an additional spatial

adjustment riding atop this baseline bias for the 250 ms condition but not after 750 ms. Hence the picture emerging from the two experiments together is of a robust saccade-contingent forwards spatial bias that is present up to 500 ms after a saccade, but not beyond. We suggest that this bias may result from a compensatory mechanism operating to provide coherence between spatial and temporal aspects of visual perception. Perceived time is extended, and perceived trajectory is extended in partial compensation.

We have shown that the perception of stimulus offset position is biased, and suggested that this adjustment is a compensation for a temporal effect. It is noteworthy that the nonsignificant trends found in both experiments 2 and 3 were also in a direction consistent with temporal overestimation of the post-saccadic target. Such contributions would complement, not contradict our interpretation of the stimulus offset effects. They would simply represent additional examples of the brain's ability to adjust perception in order to compensate for a post-saccadic temporal bias.

In our experiments, subjects judged the temporal or spatial features of stimuli some seconds after seeing them. Therefore, if the two are related as we have suggested, we cannot be certain whether the brain adjusts subjective time first, and adjusts subsequent spatial perception as a consequence, or alternatively arrives at a combined spatiotemporal interpretation after some delay. Our results are consistent with a hierarchical relationship between temporal and spatial representations, because spatial adjustments are made to achieve coherence with perceived time. However, we did not address the inverse possibility of temporal effects resulting from changes in perceived position. Nevertheless, our results do suggest that spatiotemporal coherence takes precedence over purely spatial accuracy.

Could a difference in the quality of pursuit occurring at the time of the change of stimulus color explain our results? Smooth pursuit already functions at full gain immediately after a saccadic eye movement (Lisberger, 1998). It is also very likely to have been operating efficiently on the majority of control trials: the shortest latency used in Experiment 6 (250 ms) gave little time to initiate pursuit, but the pursuit system rapidly adapts to predictable target movements away from fixation even when such targets require complex perceptual judgments (Wells & Barnes, 1999). The change in mislocalization bias between the 250 ms and 750 ms control conditions of Experiment 6 suggests that this bias accumulates over a critical period of pursuit, and we might expect pursuit to be better established after a saccade than in control trials for the 250 ms condition. However, this cannot explain our results across experiments. In Experiment 4, subjects undertook prolonged pursuit prior to color change in the control condition (approx 1300 ms) compared to 500 ms of post-saccadic pursuit, but the bias was larger in the latter case. Only if pursuit was substantially *worse* in the saccade conditions of both experiments, and this poor pursuit *increased* the size of the mislocalization bias, could differences in pursuit explain our results. The first part of this conjecture is undermined by the available evidence on post-saccadic pursuit (Gardner & Lisberger, 2002) while the second part is contrary to the results from the control conditions of Experiment 6.

While our explanation of the effects we have observed is logically coherent, two aspects of this account remain speculative rather than proven. Firstly, we suggest that the spatial bias we have observed at stimulus offset, being opposite in direction to the bias observed at stimulus onset, suggests an extended perceived trajectory. However, we have not required subjects to directly estimate the extent of post-saccadic trajectories. Perhaps

more importantly, we have suggested that this spatial adjustment is a compensation for a biased perception of duration. The fact that the two biases co-occur in a logically coherent manner does not prove that they are actually related, although it is consistent with such a relationship. Is the spatial bias really compensatory? Future research might seek to provide direct evidence for the relationship we have suggested, such as a correlation between the effect sizes for the temporal and spatial effects we report using a much larger group of subjects. It might be possible to obtain even stronger evidence by intervening in some way to disrupt the temporal (chronostasis) effect (for example with trans-cranial magnetic stimulation) and assessing whether the spatial effect is similarly disrupted.

In summary, we have demonstrated that post-saccadic moving objects undergo a substantial temporal bias relating to stimulus onset, and that this bias is accompanied by a spatial adjustment at stimulus offset which may be compensatory in nature. These results provide a novel insight into the nature and duration of the window of consciousness (James, 1890). Conscious visual perception appears to be flexible within a time window of around 500 ms when saccades introduce ambiguity into the stream of sensory input. Our data are broadly consistent with accounts that view consciousness as an instantaneous interpretation or best guess based on sensory evidence gathered over a period of a few hundred milliseconds (Dennett et al., 1992). Our results are unusual, however, in that whereas previous findings have shown that a subsequent event can strongly influence perception of an earlier event (e.g. the cutaneous rabbit, Geldard et al., 1986) our results can be interpreted as demonstrating trading between an earlier perceptual interpretation and a later one; the visual system is essentially forced to lie

about space in order to cover an earlier incorrect inference about time. In doing so the brain goes some way towards making the spatial and temporal qualities of stimuli seem coherent. The interaction between representations of temporal and spatial properties suggests complex coding of such properties in the brain. The precise neural loci and time course of the interaction between visual representations remain to be uncovered.

Figure legends

Figure 1. Antedating of saccade targets may modulate spatial perception of moving objects. **(A)** In the chronostasis illusion, the post-saccadic stimulus (here a white circle) need only be presented for a shorter time to seem of equivalent duration to the reference stimulus (red circle). This is achieved by antedating; the onset of the white circle is moved back so that it is perceived to fill the blank period associated with saccadic suppression. The dashed black arrow shows that if a moving stimulus is similarly antedated, its onset might be extrapolated back to occur at an early *spatial* position relative to its true position at foveation. **(B)** Although the brain antedates the percept obtained at the end of the saccade, it may not take account of that percept's static versus dynamic properties. In this panel, a percept of the white circle fills in the saccadic blank, consistent with the temporal illusion, but this percept is stationary. Hence the circle

seems to appear at a position just ahead of the cross it replaces, is momentarily static, then moves forwards with an appropriate velocity. **(C)** Here, the saccade target is seen to move more slowly than the reference stimulus, allowing it to move a shorter distance in the same amount of time. Spatiotemporal coherence is preserved by an illusory change in perceived velocity. **(D)** In this panel the movement path of the post-saccadic object is extrapolated forwards at stimulus offset. The post-saccadic stimulus would then appear to cover a greater distance. This percept would come at the expense of veridical information about the initial movement path of the reference stimulus. The brain might equate the distance covered by the post-saccadic and reference stimuli in line with their equal perceived durations (grey arrow). Alternatively, the post-saccadic stimulus might travel an appropriate distance given the increase in its perceived *absolute* duration (black arrow).

Figure 2. Schematic of the experimental procedure (Experiment 1) for both saccade and control trials. Horizontal eye traces (top) show the position of the eyes during each display epoch (bottom). Screen shots are to scale for a central 36° by 16° (visual angle) section of the monitor. Saccade and control sequences provided near equivalent foveal stimulation.

Figure 3. Results of experiments 1 and 4. **(A)** The top part shows mean post-foveation presentation times for the post-saccadic stimulus judged equivalent to the 500 ms reference stimulus. The bottom part shows the mean constant error of position judgments made about either the onset of the post-saccadic stimulus (Experiment 1) or the color

change marking the change from post-saccadic to reference stimuli (Experiment 4).

Positive values denote forward mislocalizations. Error bars show standard deviations. **(B)**

Schematics showing predicted perception of position for these two experiments, based on

the models presented in Figure 1 parts A and D. Note that only the more extreme

predicted position for the offset judgment made in Experiment 4 is shown (see Figure 1D;

the alternative prediction is a forwards shift that is only half as large). Predictions (black

filled circles) are shown alongside actual percepts inferred using either just the saccade

condition (dark grey rings) or the difference between saccade and control conditions

(light grey rings). The actual positions the target occupied at foveation (Experiment 1) or

when target stimulus color changed from black to red (Experiment 2) are also shown.

Figure 4. **(A)** Schematic of experimental methods for Experiment 3. Subjects attempted

to produce stimulus motion with a constant velocity by making adjustments to an initially

random velocity profile. **(B)** Mean velocity profiles produced by subjects. Grey section

denotes presentation during the period the eyes were in motion. Note that setting the

velocity above its baseline value implies that the stimulus was actually perceived to move

at sub-baseline speeds (see main text).

Figure 5. Results from Experiment 5 (absolute duration estimation). **(A)** Mean bias

(reported duration minus corrected presentation duration) in control and saccade

conditions for presentation durations ranging from 250 to 750 ms. Error bars show

standard deviations. **(B)** Relationship between reported durations and corrected

presentation durations in both control (white) and saccade (black) conditions. Data points

are shown for all eight subjects. Regression lines were calculated individually for each

subject, then slopes and intercepts were averaged to produce the regression equations

plotted in the figure.

Figure 6. Mean constant error of position judgments made about the color change

marking the change from post-saccadic to reference stimuli (Experiment 6; offset

judgments). Error bars show standard deviations.

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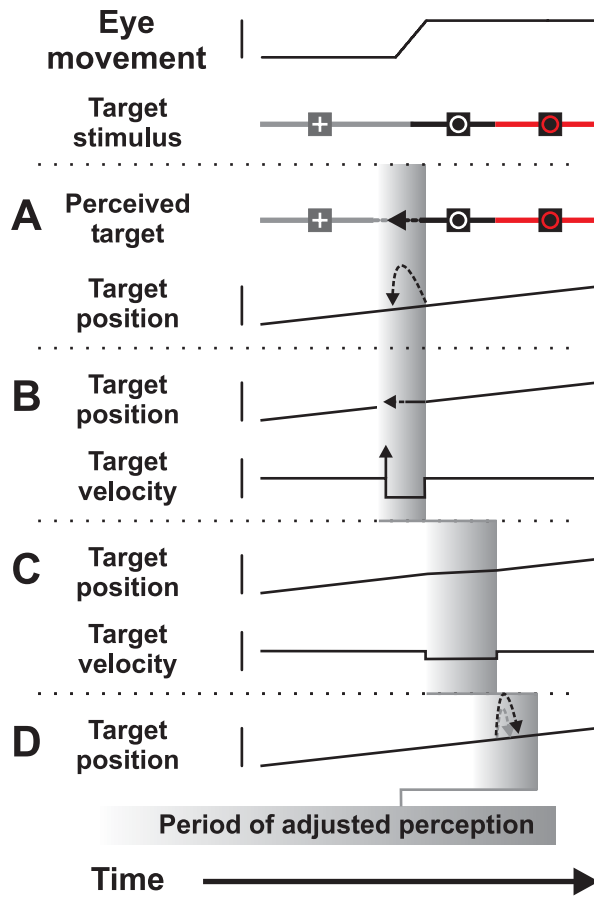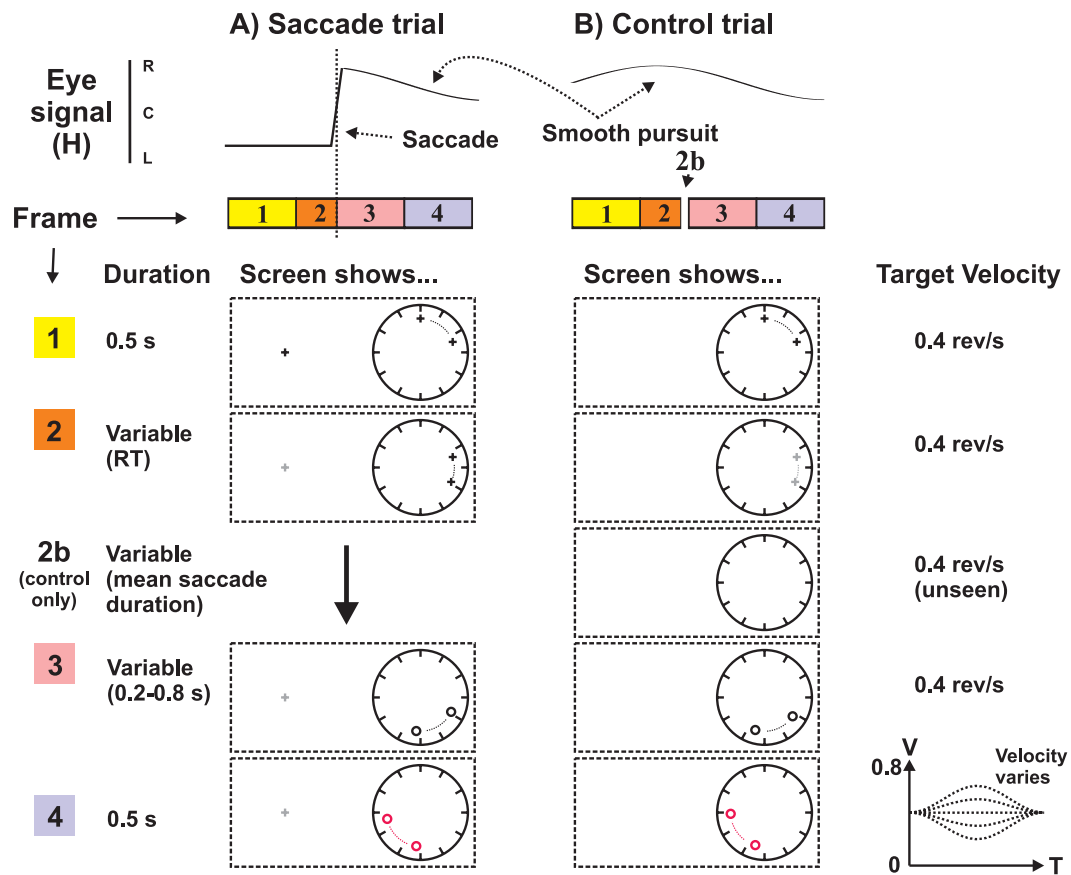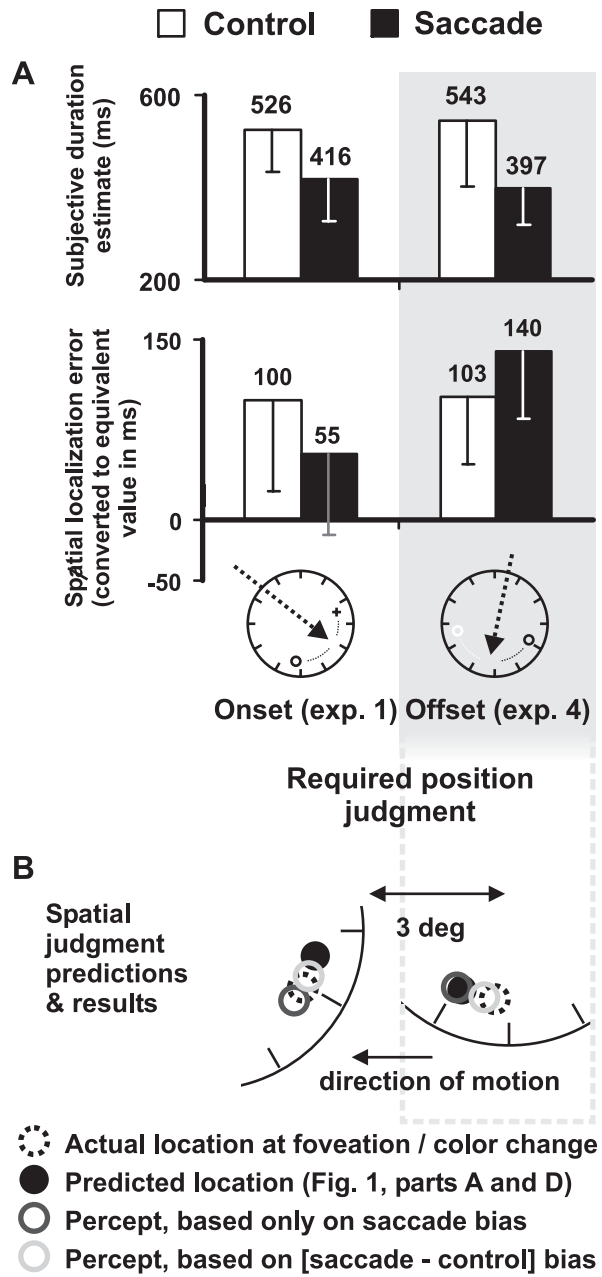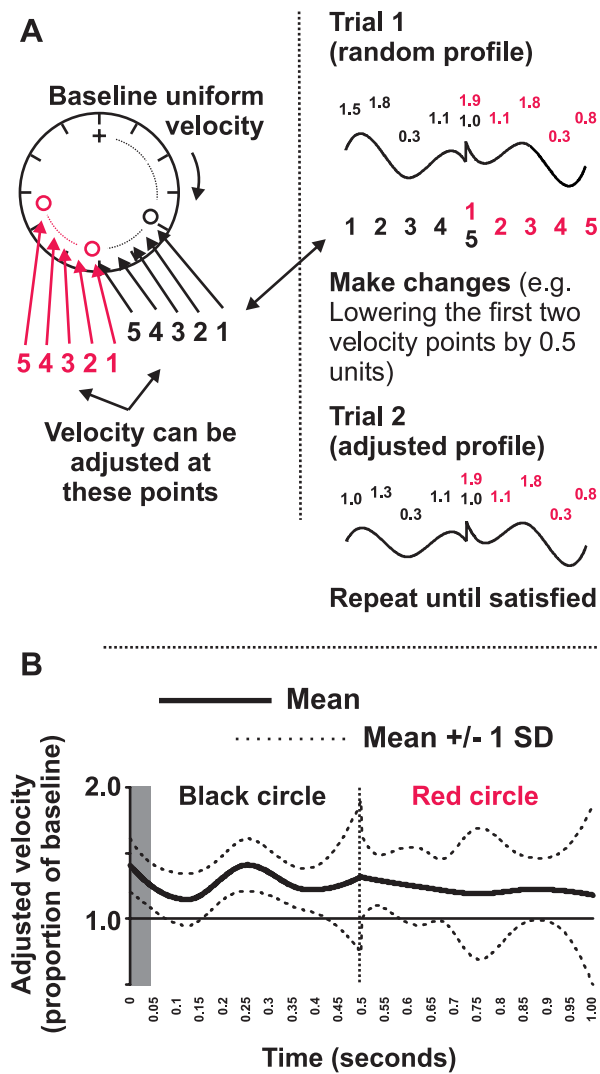
Figure 1

Figure 2

Figure 3

Figure 4

A

Baseline uniform velocity

5 4 3 2 1

5 4 3 2 1

Velocity can be adjusted at these points

Trial 1 (random profile)

1.5 1.8   1.9   1.8
        0.3 1.1 1.0 1.1   0.8
              1.0   0.3

1 2 3 4 **1** **2** **3** **4** **5**
            5

Make changes (e.g. Lowering the first two velocity points by 0.5 units)

Trial 2 (adjusted profile)

1.0 1.3   1.9   1.8
        0.3 1.1 1.0 1.1   0.8
              1.0   0.3

Repeat until satisfied

B

——— **Mean**

·········· **Mean +/- 1 SD**

Black circle   **Red circle**

Adjusted velocity (proportion of baseline)

2.0

1.0

0 0.05 0.1 0.15 0.2 0.25 0.3 0.35 0.4 0.45 0.5 0.55 0.6 0.65 0.7 0.75 0.8 0.85 0.9 0.95 1.00

Time (seconds)

34

Figure 5

Figure 6