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Action, arousal and subjective time

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Running head: Action, arousal and subjective time

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Abstract

Saccadic chronostasis refers to the subjective temporal lengthening of the first visual stimulus perceived after an eye movement. It has been quantified using a duration discrimination task. Most models of human duration discrimination hypothesise an internal clock. These models could explain chronostasis as a transient increase in internal clock speed due to arousal following a saccade, leading to temporal overestimation. Two experiments are described which addressed this hypothesis by parametrically varying the duration of the stimuli that are being judged. Changes in internal clock speed predict chronostasis effects proportional to stimulus duration. No evidence for proportionality was found. Two further experiments assessed the appropriateness of the control conditions employed. Results indicated that the chronostasis effect is constant across a wide range of stimulus durations and does not reflect the pattern of visual stimulation experienced during a saccade, suggesting that arousal is not critical. Instead, alternative processes, such as one affecting the onset of timing (i.e. the time of internal clock switch closure) are implicated. Further research is required to select between these alternatives.

Introduction

The term *saccadic chronostasis* refers to the subjective temporal lengthening of a post-saccadic visual stimulus (Yarrow, Haggard, Heal,

Brown, & Rothwell, 2001; Yarrow, Johnson, Haggard, & Rothwell, in press). In a typical experiment, observers judge the duration of a stimulus that changes form or colour mid-saccade, such that it can only be perceived in its new state at refixation. A comparison is made with subsequent reference stimuli, allowing a matched estimate to be derived (the point of subjective equality). Participants reliably overestimate the time for which they have seen the saccadic target compared to constant fixation conditions, usually by an amount that exceeds the duration of the saccade.

The size of the illusion has been shown to increase approximately linearly with the duration of a saccade (Yarrow et al., 2001). It can be disrupted by some but not all changes in the visual scene occurring mid saccade. Specifically, when the counter is noticeably displaced during the saccade the illusion disappears. These data prompted the following explanation of the effect (hereafter termed the *shifted perceptual onset* account). During a saccade, retinal blur and mechanisms of active suppression degrade visual input (Ross, Morrone, Goldberg, & Burr, 2001) leaving a “gap” in perception, yet we feel that we have continuous awareness of the state of objects in the world. The brain may simply assume that the information in the post-saccadic image has remained constant throughout the saccade, providing the continuity we experience. Hence, post-saccadic events are antedated to just before saccadic onset. The initial response of neurones with receptive fields that shift in the temporal vicinity of a movement (Duhamel, Colby, & Goldberg, 1992; Walker, Fitzgibbon, & Goldberg, 1995; Umeno & Goldberg, 1997) may underlie our conscious

visual experience with regard to the onset of perceptual properties that are only established later.

Given that saccadic chronostasis is measured by having subjects assess the duration of stimuli, we wished to relate the illusion to the sizeable literature on temporal interval estimation. The most popular template for models of time perception is the pacemaker-accumulator internal clock (Treisman, 1963). A timer sends out pulses that, when a switch is closed, amass in a temporary store and can subsequently be compared with values stored in long-term memory. The basic architecture of the model deals well with data showing a linear relationship between perceived time and real time (reviewed in Allan, 1979) and specific instantiations can handle scalar variability (the positive relationship between variability in time judgements and the time being judged, e.g. Gibbon & Church, 1990). One such instantiation is the temporal information-processing model developed in scalar expectancy theory (SET; Gibbon, 1981).

The SET model posits a number of specialised components, with temporal information passing between them. It has been extensively investigated and widely employed in timing research, and has gained considerable support from both animal and human timing studies (Allan, 1998). Although the model remains contentious and has a number of competitors that claim greater neural plausibility (e.g. Matell & Meck, 2000; Rosenbaum, 2002) most of the components evident in SET (e.g. the memory stores, comparator, and switch or related interval marker) appear

logically necessary in almost any conceivable timing model (Matell et al., 2000). A schematic is presented in Figure 1.

FIGURE 1 ABOUT HERE

The model can accommodate a shift in the perceived duration of a stimulus by adjusting the function of any one of a number of its components. Various studies have attempted to relate specific effects found in duration discrimination tasks to the function of these clock components (Burle & Casini, 2001; Franssen & Vandierendonck, 2002; Wearden & Culpin, 2002). The broad aim of the experiments described here was to characterise saccadic chronostasis in a similar manner, i.e. to determine which clock model components might be responsible for the illusion.

A theoretically important point is that influences on some of these components are characterised by a mean duration shift effect that scales with the duration that is being judged, while some imply a shift that is constant across durations. For example, a number of manipulations are thought to affect the speed of the pacemaker by influencing an individual's level of arousal (Penton-Voak, Edwards, Percival, & Wearden, 1996). Examples include accompanying or preceding a temporal stimulus with a train of clicks (Treisman, Faulkner, Naish, & Brogan, 1990), changing reinforcement rate for animals (Fetterman & Killeen, 1995), inducing boredom in human subjects via prolonged testing (Wearden, Pilkington, & Carter, 1999), creating stressful environments or administering

stimulant/depressant drugs (Boltz, 1994), and changing body temperature (Wearden & Penton-Voak, 1995). Such manipulations would be expected to produce a larger effect for longer duration stimuli because the number of pulses accumulated by an internal clock is equal to rate multiplied by time, a prediction that has been verified in the case of arousing trains of clicks and flashes (Penton-Voak et al., 1996; Wearden, Edwards, Fakhri, & Percival, 1998). It has recently been suggested that saccadic chronostasis may also be a result of arousal operating on the pacemaker of the internal clock (Hodinott-Hill, Thilo, Cowey, & Walsh, 2002). These authors introduce this possibility only briefly, so what follows represents our own interpretation of such a position rather than a clear exposition of their views (to be developed more fully in later publications; V. Walsh, personal communication). The saccade might be responsible for a transient increase in arousal. This might come about in one of two ways. Either some aspect of the movement or its preparation might itself be arousing, or the perceptual blank that the saccade creates might cause the post-saccadic stimulus to be effectively perceived anew, with such a stimulus onset giving rise to arousal. Hodinott-Hill et al. (2002) explicitly linked saccadic chronostasis with two other temporal illusions. They presented data demonstrating that a period demarcated by a key press (start) and a brief tone (end) was overestimated when it contained a shift of auditory spatial attention. They also discussed an earlier finding that the first and last stimuli in a train of four identical squares of light are perceived to have an extended duration relative to the middle two (Rose & Summers, 1995). Arousal was proposed to account for all three illusions. It

might also account for more recent demonstrations of chronostasis-like effects following key presses and reaching movements (Park, Schlag-Rey, & Schlag, 2003; Yarrow & Rothwell, 2003).

An arousal explanation contrasts with the shifted perceptual onset account presented earlier. The shifted perceptual onset account has obvious similarities with the idea of “subjective referral” proposed by Libet, Wright, Feinstein, & Pearl (1979) to explain why trains of direct electrical stimulation of a duration just long enough to elicit tactile sensation (approx. 200 ms) appear delayed relative to stimulation of the skin if applied to somatosensory cortex, but not when applied to the medial lemniscus (see Pockett, 2002, and other articles in the same journal issue for extensive critiques). When chronostasis occurs following a saccade, conscious visual awareness (those aspects of our visual experience that we are able to report or make judgements about) appears to reflect a reconstruction or reinterpretation of prior events by the brain (Dennett & Kinsbourne, 1992). At the level of the internal clock, which presumably interacts with systems giving rise to conscious awareness, we can envisage the switch that allows pulses to accumulate being closed well before a stimulus is actually fixated, at the time the motor system is calculating movement parameters, rather than at the point that the post-saccadic stimulus is perceptually resolved.

The specific aim of the current study was to compare the arousal and shifted perceptual onset accounts of saccadic chronostasis. To this end we considered a simple experimental manipulation in Experiment 1: varying stimulus duration. If the duration of the target stimulus is changed, the

arousal account predicts a proportional variation in effect size (recall that perceived time equals arousal-dependent pacemaker rate multiplied by real time). By contrast, the shifted perceptual onset account predicts a constant effect, because the event that is being used to mark the onset of subsequent perception, be it a receptive field shift, efferent command, shift of spatial attention, or some alternative process, remains constant across alterations in stimulus duration.

Materials and methods

Participants. 20 subjects (12 male, mean age 31.8, SD 8.4) completed the experiment.

Apparatus. Subjects sat before a 22" CRT colour monitor refreshing at 60 Hz (first 10 subjects) or 120 Hz (final 10 subjects). Eye to screen distance was maintained at 41 cm using an adjustable chin rest. Horizontal eye movements were recorded from the left eye using an infra-red eye tracker (Microguide 1000 spectacles, low-pass filtered at 40 Hz) and sampled at 200 Hz. Stimuli were black or red on a white background, subtending 1.2° of visual angle. They consisted of crosses and open circles. The experiment was controlled by a PC interfaced with a 12 bit A/D card (National Instruments DAQ 1200).

Design. A two factor (2 x 4) repeated-measures design was employed. The first factor *eye status* compared a voluntary saccade of 20° to constant

fixation at matched eccentricity ($\pm 10^\circ$). The second factor *stimulus duration* varied the length of the reference stimulus across the following values: 333 ms, 667 ms, 1000 ms, 1333 ms. Trials from each of the eight conditions were presented in separate blocks. Four constant fixation blocks and four saccade blocks were completed at each level of stimulus duration for a total of 32 blocks. Each subject received these blocks in a random order.

FIGURE 2 ABOUT HERE

Procedure. A schematic of the experimental procedure for the 1000 ms saccade condition is shown in Figure 2. In saccade blocks, subjects fixated a red cross on one side of the screen, initiated the trial with a mouse key press then made a saccade towards a black cross on the far side of the screen (within two seconds of their key press). Eye movement triggered the black cross to be replaced with a circle when the saccade had travelled one fifth of the distance to target. The circle remained on screen for a variable duration, within limits determined by the current reference stimulus duration. The lower limit was set equal to 20% of stimulus duration (e.g. 67 ms for the 333 ms conditions). The upper limit was set to 180% of stimulus duration. The circle then disappeared, to be replaced by an identical circle (the reference stimulus) after a 500 ms blank period. Subjects indicated whether the time they saw the first circle was longer or shorter than that for which the reference circle was displayed. The duration of the first circle was controlled by a modified binary search (MOBS; Tyrrell & Owens, 1988)

procedure that homed in on a single matched estimate (five reversals to terminate, initial presentation random in the range 0.8-1.2 x stimulus duration). Blocks finished when the MOBS had terminated, typically after 6-20 trials.

Subjective duration estimates were obtained by taking the average of the four MOBS termination values in each condition. In the saccade conditions, each estimate was corrected post hoc to match the time the first circle was on screen *following target foveation* by subtracting the average time the eye was in motion following the triggered change to a circle (averaged across all four blocks). Saccade start/end points were calculated automatically using a velocity criterion. Trials where the first saccade recorded did not exceed 90% of the total distance recorded (summed across all detected saccades) were excluded on line and repeated immediately.

In control (constant fixation) trials, subjects initially fixated a cross at equivalent eccentricity. It was blanked 400ms after the subject's mouse key press, then replaced 100 ms later by the to-be-judged circle, with subsequent stimulus presentation and subject responses as per saccade trials. Direction of saccade (saccade conditions: left to right and vice versa) or position of the fixation cross (control conditions: left or right) alternated every trial.

Statistical analyses. For all statistical tests, alpha was set at 0.05 (Bonferroni corrected for multiple comparisons). ANOVA sphericity violations were corrected using the Greenhouse-Geisser correction when ϵ was below 0.7

and the Huynh-Feldt correction when Greenhouse-Geisser ϵ was above 0.7 (Howell, 1997).

Results

Saccade characteristics. Primary saccades had an average duration of 57 ms across subjects and conditions. Their duration did not differ significantly for different stimulus durations.

Variability in time judgements. Estimates of timing variability were obtained by calculating for each subject/condition the standard deviation of the four MOBS-derived values. Mean variability increased monotonically with reference stimulus duration from 333 to 1333 ms (constant fixation control: 48, 71, 134, 142; saccade: 49, 97, 150, 179; main effect: $f = 28.571$, adjusted $df = 2, 33$, $p < 0.001$; linear trend test: $f = 53.7$, $df = 1, 19$, $p < 0.001$). Timing variability was significantly greater in saccade than control conditions ($f = 9.037$, $df = 1, 19$, $p = 0.007$). The two factors did not interact significantly.

FIGURE 3 ABOUT HERE

Subjective duration estimates. Figure 3 shows mean subjective duration estimates across subjects in all eight conditions. Saccadic chronostasis was clearly evident at all four levels of stimulus duration, with saccade

conditions yielding reduced subjective duration estimates relative to constant fixation control conditions. Hence subjects overestimated the time for which they had seen the target of a saccade. A two-factor ANOVA was carried out (following square-root transformation of the data to reduce heterogeneity of variance) and supported this conclusion, showing a main effect of eye status ($f = 22.267$, $df = 1, 19$, $p < 0.001$). The main effect of stimulus duration ($f = 582.697$, corrected $df = 2, 36$, $p < 0.001$) represented a predictable linear trend from shortest to longest stimulus duration (trend test, $f = 858.474$, $df = 1, 19$, $p < 0.001$). There was no significant interaction between eye status and stimulus duration ($f = 1.254$, corrected $df = 3, 57$, $p = 0.299$). Visual inspection, however, suggested that there might be some small proportional trend (compare the 87 ms effect at 333 ms with the 119 ms effect at 1333 ms).

Discussion

The data provide strong support for the presence of a large constant component in saccadic chronostasis. At first glance, these data might seem contrary to an arousal account of chronostasis. However, the predictions drawn from an arousal account depend upon how arousal varies over time. In order to generate a directly proportional effect, arousal would need to increase rapidly during a saccade and then drop back instantaneously at the offset of the post-saccadic stimulus (Figure 4(A)). In the SET model, perceived time is equal to real time multiplied by clock rate. In Figure 4, the

perceived time for each stimulus is given by the area under the curve in the appropriate temporal interval. The model in Figure 4(A) predicts proportional effect sizes (36, 71, 107 and 143 ms) which are a poor match for the present data (87, 95, 126 and 119 ms respectively).

FIGURE 4 ABOUT HERE

Figure 4(B) shows a more physiologically plausible timecourse of arousal. Arousal decays exponentially after a saccade. Hence arousal decay is not related to the offset of the target stimulus, but only to its onset (the end of the saccade). The arousal function is consequently identical in the left and right sections of Figure 4(B). Given that the delay between the target and reference stimuli was constant in the current experiment, arousal will vary between stimulus duration conditions not just for the target stimulus but also for the reference stimulus. This makes it particularly difficult to make simple predictions. The example pictured in Figure 4(B) was produced by least-squares fitting the mean data from Experiment 1 to this simple exponential decay model with a constrained search. It predicts effect sizes of 82, 111, 116 and 117 ms for the four levels of stimulus duration employed here.

In fact, the arousal account could have predicted an entirely constant effect in the current experiment if we assume that arousal increases transiently and has already returned to baseline within about 200 ms (the average time for which the post-saccadic stimulus needed to be presented to

yield an illusion in the briefest condition tested). In the absence of independent evidence about the shape of the arousal function, an arousal explanation of saccadic chronostasis is essentially an exercise in curve fitting. The shape of any arousal function capable of explaining these data is further constrained later in Experiment 4, and its plausibility considered in relation to what is known about human physiological responses.

Firstly, however, the issue of the appropriateness of the control condition employed is addressed. Several potentially arousing visual events occur around the time of a saccade, so estimating the contribution of the movement itself to chronostasis is problematic. In Experiment 1, the constant fixation control condition involved fixation of a cross which disappeared for 100 ms before the target stimulus was displayed. This procedure was employed to roughly compensate for the period of suppressed and degraded vision produced by a saccade, which might have introduced a difference between the control and saccade conditions in earlier experiments (Yarrow et al., 2001). A saccade-induced stimulus offset/onset might, for example, have produced transient arousal (Hodinott-Hill et al., 2002). Another possibility is that low-level perceptual or attentional factors affected the perceived onset time of the target stimulus (Bachmann, 1999; Scharlau, 2002). Such effects would complicate the interpretation of data, which is based on differences between fixation and saccade conditions. In Experiment 2 a comparison was made between four possible control conditions that differed in the temporal relationship between fixation cross offset and first stimulus onset. This manipulation was intended to assess the

degree to which the sequence of visual stimuli experienced during a saccade might contribute to the experience of saccadic chronostasis.

Materials and methods

Participants. 8 subjects (5 male, mean age 32.1, SD 7.7) completed the experiment.

Apparatus. The set-up from Experiment 1 was used, except that eye position was not monitored. Monitor refresh rate was 120 Hz.

Design. Four constant fixation conditions were tested in a repeated-measures design. The time between the offset of the fixation cross and the onset of the first stimulus could take one of the following values: 0 ms (no gap), 50 ms, 100 ms or 500 ms. Trials from each condition were presented in separate blocks. Four blocks were completed per condition for a total of 16 blocks. Each subject received these blocks in a random order.

Procedure. The procedure was identical to the constant fixation control conditions employed in Experiment 1, with the following exceptions. The reference stimulus was now presented *first*, and the judged (variable duration) stimulus *second*. This change was made to facilitate the comparison with an additional chronostasis experiment using very short stimulus durations (see Experiment 4) but also lends generality to the

results. Hence subjects judged whether the second (variable) stimulus was of longer or shorter duration than the first (the reference). Reference stimulus duration was always 300 ms. Lower and upper limits for the MOBS controlling second stimulus duration were set to 10 ms and 600 ms respectively. The first (reference) stimulus always appeared 500 ms after the mouse key press initiating the trial, but the visual display varied during this period in different conditions. The fixation cross remained visible for 0, 400, 450 or 500 ms after the key press, resulting in an blank period between cross and first stimulus of 500, 100, 50 or 0 ms respectively.

Results

Subjective duration estimates. Figure 5(A) shows the mean subjective duration estimates across subjects for all four conditions. Note that because of the reversal in stimulus presentation order, a subjective duration estimate above the reference stimulus duration (here 300 ms) now indicates that the first stimulus appeared of subjectively longer duration than the second (i.e. this result is equivalent to a value below the reference stimulus duration in Experiment 1). Hence the direction of bias is the same for the 100 ms offset condition in this experiment and the identical control condition employed in Experiment 1. This bias is in fact evident for all four offset values tested here, but only as a non-significant trend. The four conditions did not differ from one another reliably by ANOVA ($f = 0.479$, corrected $df = 1, 9$, $p > 0.05$).

FIGURE 5 ABOUT HERE

Discussion

The precise temporal relationship between the offset of the fixation cross and the onset of the first stimulus appears unimportant for saccadic chronostasis effects. Any bias towards perceiving the first stimulus as persisting longer than the second probably represents a time order error (Hellstroem, 1985) although this has not been tested explicitly here. Such a bias is controlled for in the saccadic chronostasis procedure by the inclusion of a constant fixation condition and cannot be responsible for the illusion. If arousal plays a role in saccadic chronostasis, it does not seem to arise from the onset properties of the first stimulus, but must instead depend upon some internal feature of the saccadic motor act.

The constant fixation conditions tested thus far mimic the pattern of visual stimulation experienced during a saccade under the assumption of complete saccadic suppression; the first circle appeared at fixation following a blank period. In the interests of completeness, Experiment 3 went on to test a constant fixation condition in which the critical stimuli were displaced horizontally with a timecourse roughly equivalent to that experienced during a saccade. Hence, for task-relevant visual stimuli, the pattern of stimulation was roughly equivalent to that falling on the retina in saccade conditions. For comparability, this condition was tested alongside a 100 ms offset

condition like that employed in Experiments 1 and 2. A similar 100 ms offset condition in which the initial fixation cross was reduced in size and contrast was also included.

Materials and methods

Participants. 8 subjects (5 male, mean age 32.1, SD 7.7) completed the experiment.

Apparatus. The set-up from Experiment 1 was used, with eye position monitored in the simulated saccade condition. Monitor refresh rate was 120 Hz.

Design. Three conditions were tested in a repeated-measures design. In the first two, the time between the offset of the fixation cross and the onset of the first stimulus was 100 ms. The size and contrast of the fixation cross was varied. The third condition involved a simulated saccade. Trials from each condition were presented in separate blocks. Four blocks were completed per condition for a total of 12 blocks. Each subject received these blocks in a random order.

Procedure. The procedure for the two offset conditions was identical to that employed in Experiment 2, except that in the small/dim offset condition the initial fixation cross was presented in grey (rather than black) and subtended

only 0.24° of visual angle. In the simulated saccade condition, eye position was monitored and trials rejected when the eyes wandered by $> 2^\circ$ horizontally. Each trial began with the presentation of a fixation cross (10° to the left or right) and a target cross (20° away across the subject's midline). 400 ms after a mouse key press the target cross was reduced in contrast (black to grey) and began to move towards the point of fixation at a rate of $200^\circ/\text{second}$. It traversed 10° in 50 ms (6 screen refreshes) then changed to become a grey open circle (the reference stimulus) which proceeded to traverse the second 10° in 50 ms. The original fixation cross was reduced in contrast and displaced by 20° at this time, consistent with the movement of the target cross. Apparent motion was convincing with these presentation materials. Following movement, the reference stimulus was displayed in black and remained visible at fixation for 300 ms; subjects were told to judge its duration at this time and discount the period of cross/circle movement. Following a pause of 500 ms, the second (variable length) circle stimulus was presented at fixation. The initial position of fixation and target crosses alternated on each trial.

Results

Subjective duration estimates. Figure 5(B) shows the mean subjective duration estimates across subjects for the three conditions. Consistent with Experiments 1 and 2 there was a trend for subjects to overestimate the duration of the first stimulus, although only the simulated saccade condition

differed from 300 ms reliably. The three conditions did not differ significantly from one another by ANOVA ($f = 0.583$, corrected $df = 2, 14$, $p > 0.05$).

Discussion

As in Experiment 2, manipulations of the stimuli presented during constant fixation had no detectable effect on subjective duration estimates. Visual factors alone do not make a substantial contribution to the illusion of chronostasis. Having ruled out arousal of visual origin as an explanation of chronostasis, we now return to the transient motor arousal explanation of Figure 4(B). In Experiment 4, a saccade/constant fixation comparison was reintroduced using the 100 ms offset control condition employed in Experiment 1. Three extremely brief reference stimulus durations (100, 200 and 300 ms) were tested. An additional change was to hold constant the period from saccade termination to the onset of the second (variable-length) stimulus at 800 ms, such that arousal would be expected to be similar for this stimulus in all conditions. This simplifies the process of conceptualising how arousal might affect subjective duration estimates, because the position of the second stimulus no longer shifts along the arousal function. Finally, a second constant fixation control condition (the 0 ms offset condition from Experiment 2) was included to ensure that stimulus effects did not emerge at very low reference stimulus durations.

Materials and methods

Participants. 8 subjects (5 male, mean age 31.5, SD 8.8) completed the experiment.

Apparatus. Apparatus and stimuli were identical to those used in Experiment 1, with monitor refresh rate set at 120 Hz.

Design. A two factor (3 x 3) repeated-measures design was employed. The first factor *eye status* compared a voluntary saccade of 20° to two variations of constant fixation at matched eccentricity ($\pm 10^\circ$): 100 ms offset and 0 ms offset. The second factor *stimulus duration* varied the length of the reference stimulus across the following values: 100 ms, 200 ms and 300 ms. Trials from each of the nine conditions were presented in separate blocks. There were four blocks per condition for a total of 36 blocks. Each subject received these blocks in a random order.

Procedure. The two control conditions were similar to those employed in Experiment 2. The reference stimulus was presented first and was of constant duration for a given level of stimulus duration. By contrast, the pause between the end of the reference stimulus and the beginning of the second variable-length stimulus varied across levels of stimulus duration (700, 600 or 500 ms) such that its onset always occurred 800 ms after that of the first (reference) stimulus. MOBS boundaries were set at 10 ms (low

boundary in all conditions) and *reference stimulus duration* + 300 ms (high boundary). The saccade condition was similar to that employed in Experiment 1. Procedural changes were necessary because the reference stimulus now appeared first (a change introduced to prevent ceiling effects). The mid-saccadic change from cross to circle was now triggered when the saccade had travelled 70% of the distance to target. On each trial, the time between this trigger and saccade termination was calculated, and used to update an average (set at 25 ms for the first trial of the experiment). The first stimulus was displayed for the appropriate stimulus duration (100, 200 or 300 ms, depending on condition) plus this value, with a correction made for presentation delays introduced by screen refresh rate. In this manner, the duration for which the reference stimulus was displayed following saccade termination was, on average, maintained at the correct value. The target (variable length) stimulus was always presented 800 ms after saccade termination.

Results

Saccade characteristics. Primary saccades had an average duration of 57 ms across subjects and conditions. Although this value varied significantly across different stimulus durations ($f = 3.757$, corrected $df = 2, 14$, $p = 0.049$) the greatest mean difference between conditions amounted to only 2 ms.

Variability in time judgements. Estimates of timing variability increased monotonically as reference stimulus increased from 100 to 300 ms (100 ms offset control: 15, 19, 46; zero ms offset control: 15, 24, 40; saccade: 24, 45, 46; main effect: $f = 16.233$, $df = 2, 14$, $p < 0.001$; linear trend: $f = 5.808$, $df = 1, 7$, $p = 0.047$). The trend towards increased variability in timing judgements in saccade conditions compared to control conditions narrowly missed significance ($f = 4.536$, corrected $df = 1, 8$, $p = 0.062$). The two factors did not reliably interact.

Subjective duration estimates. Figure 6 shows mean subjective duration estimates across subjects in all nine conditions. Estimates in both control conditions at all levels of stimulus duration once again displayed a trend suggesting that the first of the two stimuli was overestimated relative to the second, but no individual comparison reached significance. Saccadic chronostasis was evident for all levels of stimulus duration, with saccade conditions yielding enhanced subjective duration estimates relative to constant fixation control conditions (note that the opposite pattern of means from Experiment 1 implies an identical illusion because here the reference stimulus is presented first). Subjects therefore overestimated the time for which they had seen the first stimulus following a saccade relative to both of the constant fixation control conditions. A two-factor ANOVA was carried out (following square-root transformation of the data to reduce heterogeneity of variance) and supported this conclusion. There was a main effect of eye status ($f = 19.724$, $df = 2, 14$, $p < 0.001$). Follow up testing

showed that both controls differed significantly from the saccade condition, but not from one another. As in Experiment 1, the main effect of stimulus duration ($f = 132.486$, corrected $df = 2, 13$, $p < 0.001$) represented a predictable linear trend from shortest to longest stimulus duration across all levels of eye status (trend test, $f = 176.214$, $df = 1, 7$, $p < 0.001$). There was no significant interaction between eye status and stimulus duration suggesting a constant effect size across reference stimulus durations ($f = 1.734$, corrected $df = 2, 15$, $p = 0.21$).

Discussion

The mean subjective duration estimate data from Experiment 4 were clear, showing a similar illusory effect of around 60 ms at all three levels of stimulus duration. If anything, the trend was for slightly larger effect sizes at shorter reference stimulus durations. The magnitude of the illusion is a little lower than that obtained in Experiment 1 (and previous studies) but fluctuations across subjects are common when saccadic chronostasis is assessed. The critical comparison is between conditions within a single repeated-measures study.

Once again, the data can easily be explained by the notion that the subjective duration of the post-saccadic stimulus is effectively extended by a constant duration. As noted in the discussion to Experiment 1, it is difficult to entirely reject the arousal account with this kind of design. However, if we return to a consideration of what any putative arousal

function would have to look like to explain the current data, the arousal account becomes increasingly implausible. The only viable timecourse of arousal for a constant effect across the stimulus durations used here is one in which arousal has decayed entirely by 100 ms after saccade termination. It must also be of a magnitude capable of increasing the rate of the internal clock to 60% above baseline *on average* over this 100 ms period. Given that it is unlikely to decay instantaneously, this means that clock rate must actually increase well above this level.

There is of course no gold standard for the measurement of fluctuations in arousal, but some consideration of previous literature examining physiological responses in the context of movement is useful. Measurements of a range of variables including skin resistance, heart rate, skin temperature, respiratory frequency and pupil dilation all show marked modulation in response to movement preparation, production and inhibition, but such changes tend to persist for a period of seconds, not milliseconds (Astor-Jack & Haggard, 2003; Collet, Dittmar, & Vernet-Maury, 1999; Richer & Beatty, 1985; van der Veen, van der Molen, & Jennings, 2000). The mapping between these physiological changes and arousal as used in the internal clock literature is unclear. Nonetheless, when arousal has been invoked to explain experimental effects on time perception (e.g. following a train of clicks) effect size increases in a roughly linear manner out to stimulus durations of at least a second (Burle et al., 2001; Wearden et al., 1998). Hence any increase in arousal would have to be maintained for a similar interval. These same studies also suggest an increase in clock rate of

only 10-30% (see Penton-Voak et al., 1996, for a discussion). Trains of clicks are likely to generate a different degree of arousal from saccades, but it is not clear why decay rate should vary so dramatically for the two kinds of resultant arousal functions.

General discussion

In the introduction, two explanations of saccadic chronostasis were discussed and shown to differ regarding their predictions when stimulus duration is manipulated. The arousal account predicts an increase in effect size with stimulus duration; the linearity and magnitude of this increase depends on the underlying arousal function. The shifted perceptual onset account predicts a constant effect size across stimulus durations. Experiment 1 showed a primarily constant effect for stimuli varying in duration from 333 to 1333 ms. Experiments 2 and 3 showed that purely visual factors do not make a substantial contribution to saccadic chronostasis effects. Experiment 4 showed an entirely constant effect size for stimuli varying in duration from 100 to 300 ms.

All of these results are straightforwardly compatible with the shifted perceptual onset account. Some pre-saccadic event is preferentially used to mark the moment at which a post-saccadic stimulus is perceived, at least as long as certain assumptions about the visual world are not noticeably violated. Our conscious visual experience reflects this process. By contrast, the arousal account is tightly constrained by the current results. Arousal

cannot be the result of the pattern of stimulus offsets and onsets (Experiments 2 & 3) so must arise entirely as the result of a saccade. The saccade would need to increase arousal rapidly, for a period of 100 ms or less, before it dropped away suddenly. During this time, the internal clock would need to be profoundly accelerated.

If these data were the only reason to doubt the arousal account, we might still wish to consider it. However, there are other reasons for concern. Yarrow et al. (2001) showed that saccadic chronostasis differs for saccades of differing extents. This would require the additional assumption that arousal is greater following larger eye movements. More critically, they also demonstrated that saccadic chronostasis largely disappears when a stimulus is noticeably displaced during a saccade. Such an event would seem likely to increase, rather than dampen, arousal. Saccadic chronostasis is also equivalent following pro and anti saccades (Yarrow et al., in press). The anti-saccade task is cognitively challenging and involves the suppression of a prepotent response, factors that increase arousal as indexed by pupil dilation (Astor-Jack et al., 2003).

Arousal has been proposed as a parsimonious explanation for saccadic chronostasis and a range of other temporal illusions (Hodinott-Hill et al., 2002). Arousal contributes to prospective duration estimation in general, and some specific biases (Penton-Voak et al., 1996; Wearden et al., 1998). It cannot, however, easily explain saccadic chronostasis. Neither is it a particularly good explanation of other temporal illusions that have recently been considered alongside saccadic chronostasis. The first and last stimuli in

a train of four squares of light undergo a very large temporal bias, but manipulations that would be predicted to modulate arousal (e.g. stimulus intensity) do not affect this illusion (Rose et al., 1995). The duration of a vibrating stimulus touched following an arm movement is overestimated relative to subsequent reference stimuli, but this effect does not (always) extend to judgements about visual stimuli (Yarrow et al., 2003). Arousal ought to affect both modalities. It therefore seems wise to exercise caution when extending arousal explanations to new temporal illusions.

In rejecting an arousal account of the current data, we can also conclude that any other clock component predicted to yield a proportional effect across changes in stimulus duration cannot be responsible for saccadic chronostasis. Divided attention, for example, typically investigated in a dual-task paradigm (e.g. Burle et al., 2001) now seems an unlikely explanation. Both “attentional gate” and “flickering switch” accounts of attentional effects (Lejeune, 1998; Lejeune, 2000; Zakay, 2000) predict a proportional effect, unless we once again assume that the effect is very brief. Instead, our data shows a constant effect. We have already considered the operation of the switch in relation to our favoured shifted perceptual onset account. Other possibilities include a process that affects the representation of pulse counts in the accumulator or short term memory store. In effect, a constant would be being added in at one of these levels before a comparison is made. Another possibility is that the comparator itself is affected, for example by employing a decision rule with a constant

bias. Further research may help to exclude some of these components from consideration.

In conclusion, saccadic chronostasis arises regardless of the duration of the post-saccadic stimulus, at least down to a duration of 100 ms. It also arises regardless of the kind of saccade that precedes it (Yarrow et al., submitted). In all these situations, observers feel that they have seen a post-saccadic stimulus for considerably longer than is actually the case, with this experience reflecting temporal qualities of the saccade and the brain's implicit assumptions about the stability of external visual objects (Yarrow et al., 2001). Exactly how clock processes come to influence the contents of consciousness is an interesting and under-researched question which will no doubt yield different answers in different contexts. Our eye movements provide us with critical new perceptual data but disrupt ongoing processing of visual information. They create a context in which conscious attributions about stimuli must depend on prior assumptions, and are therefore particularly liable to distortion (Schlag & Schlag-Rey, 2002). Future research on saccadic chronostasis may help us understand this process, particularly in addressing how information from multiple sources is combined to yield a coherent perception of both the order and temporal extent of perceptual events.

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Figure legends

Figure 1. Schematic of SET internal clock. When timing a given interval, the switch closes to allow pulses to accumulate. These pulses can be compared with a value retrieved from reference memory for a target interval, the reference memory representations having themselves been built up via the prior functioning of the clock.

Figure 2. Schematic of procedure for Experiment 1. A trial from a 1000 ms reference duration saccade block is shown (saccade made from left to right). Eye movement triggered the appearance of a circle (frame 2) and subjects were required to compare its duration with that of a reference stimulus (frame 4). Stimuli shown in grey were actually displayed in red.

Figure 3. Mean time matched to a reference stimulus in saccade and constant fixation conditions for four levels of reference stimulus duration. Error bars show standard deviations.

Figure 4. Schematic contrasting two arousal-based accounts of saccadic chronostasis. Subjective durations can be found by integration. Dotted lines outline the period for which the post-saccadic stimulus must be displayed to equal the reference stimulus (solid lines) in perceived duration. The two most extreme stimulus durations tested in Experiment 1 are shown: 333 ms (left) and 1333 ms (right). **A.** Arousal increases rapidly during a saccade, then decreases as a step function when the post-saccadic stimulus disappears. Based on an a priori prediction of a 12% increase in clock rate. **B.** Arousal increases rapidly during a saccade, then decays back to baseline following the function $y = sa^t + 1.0$ (y = clock rate as a proportion of baseline, s and a are free parameters). Based on a least-squares fit to mean data across all stimulus duration conditions: $a = 0.0061$, $s = 0.6$ (equivalent to an initial 60% increase in clock rate).

Figure 5. Error bars show standard deviations. **A.** Mean time matched to a 300 ms reference stimulus (presented first) in four constant fixation conditions varying the temporal relationship between cross offset and circle onset. **B.** Three further constant fixation conditions tested in Experiment 3. Both offset conditions involved a 100 ms offset, but varied the nature of the fixation cross. In the simulated saccade condition, a peripheral cross travelled 20° towards fixation in 100 ms (12 refreshes), changing to become the first (reference) circle stimulus at the midpoint of its motion.

Figure 6. Mean time matched to a reference stimulus following a saccade and in two types of constant fixation control conditions for three levels of reference stimulus duration. Values in the 0 ms offset control condition have been shifted slightly to the left to improve clarity. Error bars show standard deviations.

Figure 1 (Yarrow, Haggard and Rothwell)

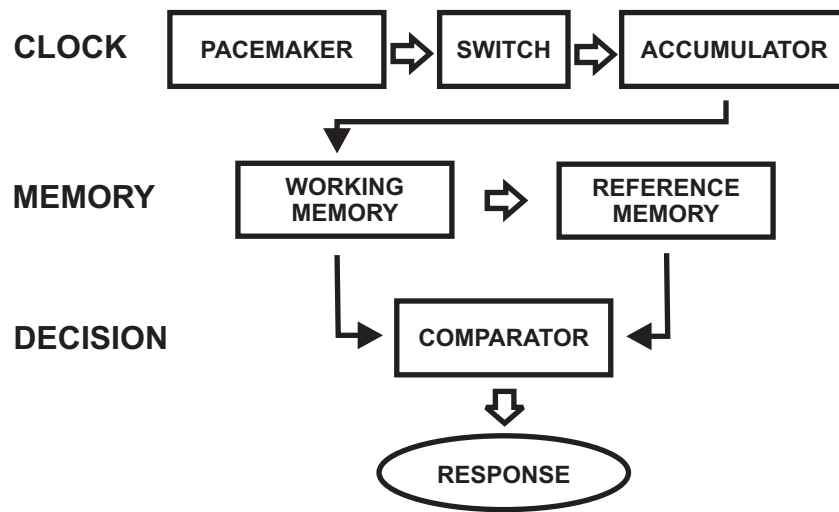


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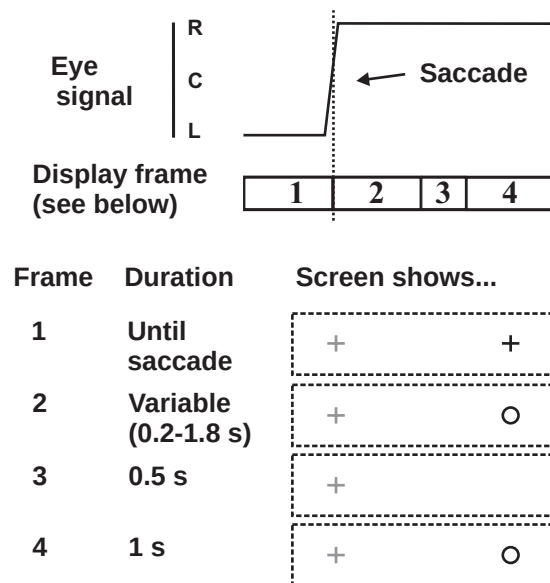


Figure 3 (Yarrow, Haggard and Rothwell)

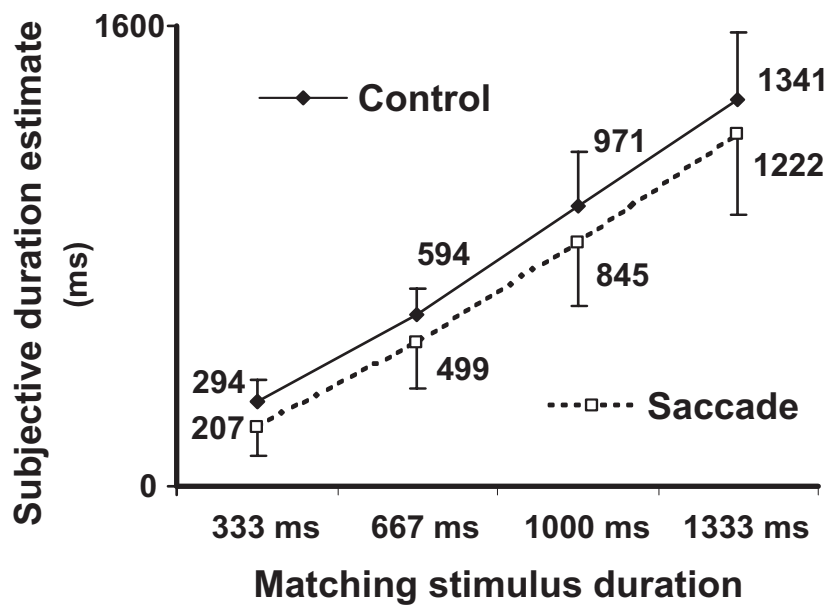


Figure 4 (Yarrow, Haggard and Rothwell)

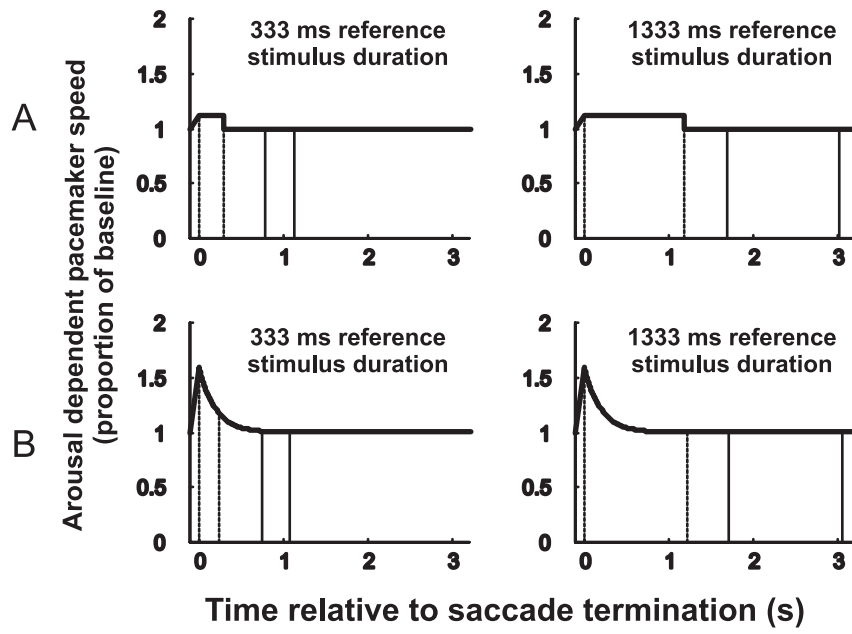


Figure 5 (Yarrow, Haggard and Rothwell)

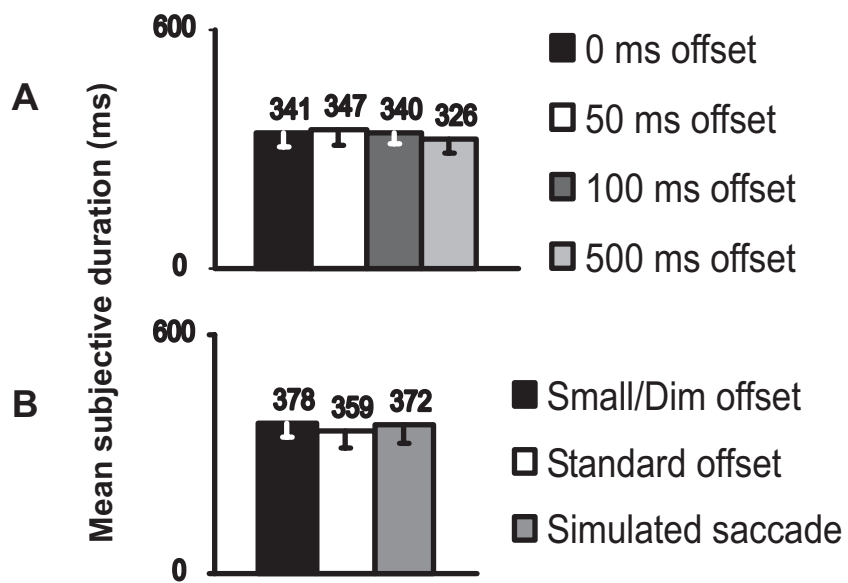


Figure 6 (Yarrow, Haggard and Rothwell)

