# Temporal dilation: the chronostasis illusion and spatial attention

Kielan Yarrow

Have you ever found yourself in a busy train station, looking across from the overhead information board to the station clock to see if you can make the next train? You may recall thinking, just for a moment, that the clock was not working, as it seemed to dwell too long on the current second. Then it ticked on, and you forgot this odd experience as you rushed to get to that train. Or perhaps you have experienced the stopped clock illusion when glancing at your wrist watch, or even when returning your gaze to the blinking cursor of your word-processing display? These anecdotes are familiar to many of us. Brown and Rothwell (1997) reported that the stopped clock illusion is most common when a saccadic eye movement causes us to foveate a counter just after it advances, right at the beginning of a new one-second interval.

It is unlikely that time actually dilates whenever we move our eyes. A more plausible account suggests that it is only our experience of time that has changed, in an illusory fashion. Perceptual illusions can provide insights regarding how the brain draws inferences about the state of the world (e.g. Gregory, 1997). With this in mind, Yarrow and colleagues (2001) developed a protocol to estimate the magnitude of the stopped clock illusion, and labelled the effect 'chronostasis' to reflect the apparent dilation of time.

The experimental task was straightforward. Participants fixated a cross on one side of a computer screen, then made a saccade to a counter presented on the opposite side. The counter initially showed a zero, but eye movements were monitored, with these recordings being used to trigger a change in the display during the saccade. Hence when the eyes arrived at the counter, a new number ('1') was displayed. The display change was assumed to be masked by saccadic suppression (see following section). The new digit (the comparison stimulus) was presented for a variable duration, and followed by a short sequence of reference stimuli (the digits '2', '3', and 'b') displayed for 1 second each. Participants were required to judge whether they had seen the variable-duration comparison stimulus for more or less time than the standard-duration reference stimuli that followed. Their responses were used to determine a point of subjective equality (PSE) at which the comparison stimulus seemed identical to the reference stimuli. In a control condition, participants made the same judgement, but without any saccadic eye movement. They started by fixating the '0', which advanced through the numbers 1–4, all presented at fixation. PSEs were compared between the experimental and control conditions to estimate the chronostasis effect.

The most striking finding came from an experiment in which the size of the saccadic eye movement was varied. Two experimental conditions involving a large (22°) or a very large (55°) saccade were compared with two control conditions in which the counters appeared at matched peripheral positions. To elicit such a large saccade, subjects were seated very close to the monitor in the 55° condition. On average, the smaller saccade took 72ms, and the larger one 139ms, a difference of 67ms. PSEs were lower in the experimental conditions compared with the control



conditions, implying a relative overestimation of the first interval following the saccade. This finding describes the chronostasis effect. Critically, the PSE in the larger saccade condition was 69ms lower than that obtained for the smaller saccade, implying that the size of the chronostasis effect had grown linearly with the duration of the preceding saccade. It was as if the extra time taken to complete the larger saccade had been added on to the estimated duration for the post-saccadic comparison stimulus.

While more recent work has modified and improved this task in a number of ways (see Box 12.1), temporal dilation of the first interval perceived after a saccade has been a consistent finding. In the remainder of this chapter, I will first briefly review some accounts of the

# **Box 12.1 Control conditions for saccadic chronostasis**

The first chronostasis experiments used a counter to allow comparison of the post-saccadic interval with a series of subsequent 1-second reference intervals. Because temporal biases had already been shown to arise when the first of a series of stimuli is compared with subsequent stimuli (Rose and Summers, 1995; see also Eagleman, Chapter 11, this volume) it was important to include a constant-fixation control condition. This allowed the additional effect of a saccade to be determined. While this protocol reproduces the conditions of the stopped clock illusion, it is unnecessarily complicated. Reducing the number of reference intervals from three to one simplifies the procedure (although it does not obviate the need for a control condition, as two-interval comparison tasks can also yield a bias, known as the 'time-order error'; see Hellstroem, 1985, for a review). Furthermore, reducing the reference interval from 1000ms to 500ms (or even less) reduces variance in the data, because time perception appears to follow a generalized version of Weber's law (Wearden and Lejeune, 2008).

In addition to controlling for order effects and related biases, constant fixation conditions should ideally also control for the unusual pattern of visual stimulation experienced in saccadic conditions, as this might itself give rise to changes in temporal perception. Early experiments did so only approximately. For example, in the saccade conditions of Yarrow et al. (2001) and Park et al. (2003), participants foveated a cross, then experienced a brief period of degraded visual motion during the saccade. They then foveated a '1', followed by subsequent reference digits. In control conditions, they foveated a '0', immediately followed by a '1' and subsequent reference digits.

More recent investigations have included improved control conditions, which better match the foveal saccadic experience (e.g. Yarrow et al., 2006a). These conditions match the stimulus that is fixated as the participant prepares to move their eyes, and include a short blank interval to simulate the saccade itself. This still leaves open the possible role of peripheral visual movement experienced during the saccade. However, displacing the saccade target object in a manner that approximates its retinal motion during the saccade does not produce equivalent temporal dilation, as demonstrated in an early control experiment (Yarrow et al., 2001) and subsequently replicated with an improved display (Yarrow et al., 2004a). Furthermore, a chronostasis effect can be obtained relative to such a motion control condition (Georg and Lappe, 2007) which rules out any issues of experimental power for the previously described null effects. As yet, no one has reported a control condition in which the entire visual scene moves with a saccadic time course. This is impossible to achieve using a CRT (cathode ray tube) monitor, but has been accomplished with alternative displays in experiments investigating saccadic suppression (e.g. Diamond et al., 2000).

he saccade. This de condition was the chronostasis if the extra time duration for the

umber of ways cade has been a e accounts of the

e post-saccadic ooral biases had vith subsequent e) it was imporional effect of a e stopped clock intervals from r a control conne-order error'; al from 1000ms ppears to follow

ition conditions erienced in sacon. Early experions of Yarrow erienced a brief '1', followed by diately followed

ıs, which better itions match the include a short e possible role , displacing the the saccade does trol experiment y (Yarrow et al., motion control al power for the ion in which the achieve using a ative displays in

chronostasis effect. Then, in view of the theme of this volume, I will consider the relationship between chronostasis and spatial attention.

## Saccadic suppression and saccadic chronostasis

Saccadic eye movements are a ubiquitous behaviour, yet we are rarely aware of them. A moment's thought illustrates how strange this situation is. When the eye sweeps across a complex visual scene during a saccade, the retina is subjected to a rapidly changing pattern of stimulation. One question that arises is why motion detectors remain quiet in the presence of such a potent motion stimulus?

It now seems likely that an active process of 'saccadic suppression' decreases the responsiveness of visual cells, particularly in the magnocellular division that is most sensitive to motion (Ross et al., 2001; but see Castet et al., 2002). A key finding comes from experiments measuring contrast sensitivity during saccades, which decreases for luminance-modulated stimuli presented at low spatial frequencies, but not for isoluminant colour-modulated stimuli (Burr et al., 1994). Anatomically, saccadic suppression is found in single-cell recordings from extrastriate areas such as middle temporal (MT) and superior middle temporal (MST) (e.g. Thiele et al., 2002) but suppression is greater for phosphenes generated at the eye than those generated in primary visual cortex (Thilo et al., 2004) so the process must start in the lateral geniculate nucleus (LGN)(see also Reppas et al., 2002; Sylvester et al., 2005).

Active suppression is one thing, but for a fuller account of peri-saccadic visual insensitivity we should add the smearing effects of rapid retinal motion on high spatial frequency visual components, and the backwards masking effect of the post-saccadic image (Campbell and Wurtz, 1978). One question that has rarely been asked is why a suppressed or empty period should not register in temporal consciousness. Saccadic chronostasis may offer an explanation, because our experience of time is effectively stitched up to take account of the saccade. The influence of saccade duration on saccadic chronostasis suggests that time is being added on to compensate for the period of degraded vision caused by the saccade (Yarrow et al., 2001). This extra time is presumably tagged on to the beginning of the comparison interval, when the saccade is occurring. This antedating account (see also Spence, Chapter 7, this volume), then, suggests that we see the post-saccadic stimulus earlier in time than the moment of foveation (or indeed the moment the comparison stimulus first appeared physically, during the saccade) and that this illusory impression about the timing of an event subsequently influences our judgement about the interval which that event initiates.

The issue of saccadic suppression is important when explaining saccadic chronostasis, bar also when measuring it, because the interpretation of experimental results requires an assumption about what can be seen during the saccade. The simplest assumption is that the change of stimulus to the variable duration comparison, which occurs during the saccade, is not registered due to saccadic suppression. Hence the duration of the comparison stimulus is often corrected before analysis to reflect the time it was foveated, rather than the time it was present on the screen. This assumption was considered reasonable based on a control experiment showing that the precise time at which the comparison stimulus changed during the saccade did not influence the magnitude of the chronostasis effect (Yarrow et al., 2001).

If the assumption is false, the chronostasis effect will have been overestimated. More critically, the dependency of chronostasis on saccade size might be artefactual, reflecting differences in the size of the corrections applied in the different saccade conditions. For this reason, one recent investigation replicated this important result, but reported effect sizes with and without a correction for saccadic suppression (Yarrow et al., 2006a). This paper demonstrated clearly that a larger saccade vields a larger chronostasis effect in a situation where the correction was carefully equated (or indeed absent). See Yarrow et al. (in press) for a fuller discussion of this issue.

# **Comparing accounts of saccadic chronostasis**

The 'antedating' account is by no means the only explanation that has been offered for saccadic chronostasis. One early alternative posited instead that the act of making a saccade increases physiological arousal (Hodinott-Hill et al., 2002). Arousal is known to prolong subjective time, perhaps by increasing the speed at which a putative internal clock runs (e.g. Penton-Voak et al., 1996). Under this account, the events that border the post-saccadic comparison interval are not shifted, but the intervening time nonetheless dilates.

Another suggestion is that the time at which the sensory consequence of any movement, not just a saccade, is perceived to occur, shifts towards the time of the action (Park et al., 2003). This proposal builds on experimental evidence favouring so-called 'intentional binding' (Haggard et al., 2002; Buehner, Chapter 15, this volume). This is essentially a more general event-shift account. Box 12.2 discusses non-saccadic illusions that have been linked with chronostasis.

### Box 12.2 Chronostasis for non-saccadic movements

Chronostasis-like effects have been reported following manual actions, and even in the absence of any movement at all. Alexander et al. (2005), building on work by Hodinott-Hill et al. (2002), investigated an illusion analogous to the stopped clock illusion, in which the repetitive tone of an engaged telephone may appear delayed when we return our attention to it. Participants heard five tones that marked out four consecutive intervals. The tones were either presented all to one ear (the control condition) or with the first tone in one ear and all subsequent tones in the other ear. The first interval seemed prolonged in comparison to the subsequent intervals when the auditory stimuli that bordered it were presented to different ears, with PSEs reduced by around 160ms compared to the control condition. Presumably, attention was refocused from one ear to the other during the comparison interval of the experimental condition, and this might explain the result. However, increasing the volume of the second tone also yielded somewhat reduced PSEs (an effect of around 50ms) even when all tones were presented to the same ear. These are interesting findings, but temporal dilation can result from a variety of mechanisms. Given the differences in the methods used to elicit auditory and saccadic chronostasis, it is not clear that they are related, or that a common explanation should necessarily be sought.

Chronostasis-like effects have also been sought where a movement is required, but not a saccadic movement. Yarrow and Rothwell (2003) asked participants to make reaching movements towards a vibrating tactile stimulus which marked out target and reference intervals. Participants overestimated the duration of the post-movement interval by 60-120ms compared to a static control condition, but the size of the effect did not change for reaches of different extents/durations. This situation is closely analogous to the saccadic case, because participants only feel the vibrator when they first touch it, leaving its state ambiguous prior to contact. Another closely analogous situation was tested by Jackson et al. (2005) who investigated chronostasis for visual stimuli in a patient with congenital ophthalmoplegia who made rapid head movements in place of saccades. No effect was obtained, although the absence of a matched control group complicates the interpretation.

refully

ıccadic reases e time, c et al., are not

nt, not ). This aggard ıt-shift

et al. titive to it. either ubseubseears. ıttenmen-:cond were from y and

not a novervals. comof difcause ior to vestimade e of a

nould

#### Box 12.2 Chronostasis for non-saccadic movements (continued)

When manual movements trigger the beginning of a visual interval, results have been mixed. Park et al. (2003) initiated a digit sequence either randomly, 500ms after a key press, or immediately after a key press. PSEs for the first interval were reduced by around 70ms when the key press initiated the sequence compared to the random and delayed conditions. These authors also observed a similar effect when a vocal signal initiated the digit sequence. These results contrast with those of Yarrow and Rothwell (2003). They tested conditions in which participants judged visual intervals initiated by reaching to and/or pressing a button. PSEs for the first interval did not differ between movement and control conditions in any of three experiments, with experimental powers ranging from 0.8-0.99. Most recently, Hunt et al. (2008) found a key-press effect of around 70ms in two experiments using a digit sequence, but not in three rather similar subsequent experiments reported in the same paper. It is worth noting that the manual-visual situation, in contrast to the saccadic-visual or manual-tactile cases, introduce no ambiguity about the time at which the critical interval begins. Hence there seems less reason for misperception to occur.

Finally, and most recently, Ibbotson et al. (2007) have suggested that the rapid latency responses recorded from motion-sensitive neurons in MT and MST during a saccade (which contrast with longer latency responses in the post-saccadic epoch) may underlie the chronostasis effect. This hypothesis again has strong similarities with the original antedating account, but emphasizes a relative shift in latencies between the event that initiates the critical comparison interval and the event that terminates it.

What evidence is there to distinguish these possibilities? One class of accounts suggest a shift in the time at which the post-saccadic stimulus is perceived (hereafter referred to as event-shift accounts). A second class suggest an increase in the rate at which time is perceived to pass (hereafter referred to as rate-increase accounts). Behavioural evidence supports the former over the latter. The saccade-length effect found with interval judgements is simple to explain under an event-shift framework by assuming that the initial boundary event is shifted to a position that is constant with respect to saccade initiation. In contrast to this, it is not obvious why a larger saccade should yield a larger increase in the rate of perceived time (although the suggestion that it might is not unreasonable). Furthermore, any rate increase account makes the straightforward prediction that the size of the chronostasis effect should grow in proportion to the duration of the post-saccadic interval that is judged, because perceived time should equal clock rate multiplied by actual time. This prediction has not been verified; for the shortest post-saccadic intervals tested, the chronostasis effect was similar for intervals ranging from 100-300ms (Yarrow et al., 2004a). These data strongly constrain rate-increase accounts, implying that the rate of perceived time would have to rise sharply above baseline following a saccade, then return to baseline within 100ms.

However, the most direct evidence favouring event-shift accounts was obtained in an experiment where the typical interval comparison task was replaced with a temporal order judgement task (Yarrow et al., 2006a). Participants judged whether a brief auditory event occurred before or after they first perceived the post-saccadic target. Relative to control conditions without a saccade, the point of subjective simultaneity (PSS) between these events was shifted substantially. Participants judged the beep to be synchronous with the onset of the post-saccadic visual target when it occurred when they had only just begun to move their eyes, long before the target's physical onset on the screen. This was in direct contrast to an audio-visual PSS of the opposite, sign found in control conditions, which fell in line with the typical observation that sounds must be presented *after* lights to appear simultaneous. This pattern was obtained for both short and long saccades, replicating the saccade-size effect found with interval-comparison tasks.

These behavioural data favour event-shift accounts, but leave open the question of whether the change in event time is implemented as events unfold, or subsequently, based on a retrospective assessment of the preceding saccadic episode. There are two plausible physiological mechanisms for an event shift, and both imply that the illusion reflects neural activity that is available immediately. The first mechanism, proposed by Yarrow et al. (2001), depends upon a class of cells known to shift their receptive fields prior to a saccade. The suggestion is that their neural activity is used to mark the onset of the post-saccadic stimulus. These cells, first described in the lateral intraparietal cortex, but subsequently found in regions such as frontal eye fields and superior colliculus (Duhamel et al., 1992; Walker et al., 1995; Umeno and Goldberg, 1997), respond predictively to a stimulus presented at a position their receptive field should occupy only after the saccade. Across the cell population this predictive response occurs at a range of times, including well before the saccade has even been made. Marking time based on the activity of such a population provides a qualitative fit to behavioural data from chronostasis experiments.

The second mechanism, alluded to earlier and proposed by Ibbotson et al. (2007), is based on their finding that activity in MT or MST arising in response to the mid-saccadic onset of a motion stimulus has a head start compared with activity arising in response to an identical stimulus presented after the saccade. If such activity were used to demarcate the interval of interest in chronostasis experiments, this interval would appear prolonged, because its onset occurs during the saccade whereas its offset occurs after the saccade. This suggestion is intriguing, but it is less easily reconciled with the dependency of the chronostasis illusion on saccade size than an account based on shifting receptive fields.

Of course, the neural events highlighted in each account share some common features. Both must depend upon some saccade-related input such as an efference-copy signal. Because saccadic chronostasis has been observed following express saccades (Yarrow et al., 2004b), and these saccades are commonly considered to arise without a significant contribution from cortical areas involved in saccade generation (Hopp and Fuchs, 2002), it seems likely that the relevant efference copy signal is sent just prior to saccade generation from a subcortical structure such as the superior colliculus. Appropriate pathways exist in the primate brain, including one from the superior colliculus to the frontal eye fields via the dorsal thalamus (Sparks, 1986). This pathway has been shown to carry efference copy information in a double-saccade task (Sommer and Wurtz, 2002).

Although the shift in event time that characterizes chronostasis might typically be implemented in an online fashion, there is also evidence that peri-saccadic perception may be moulded in a surprisingly flexible fashion over a longer time window. In early experiments, the saccade target was made to step to a new position during the saccade (at the same moment that it changed to its new post-saccadic form). The chronostasis illusion was eliminated when the step was perceived, and reduced when it was not (Yarrow et al., 2001). Intuitively, it only makes sense to assume that post-saccadic objects have occupied their current states throughout the saccade (and thus to add on an appropriate amount of time) if things remain much as they were. If not, it is better to make a different assumption. It is as though a veto were available to override the standard mechanism for estimating the peri-saccadic timeline of events.

Even more striking results are obtained when a saccade is made to a moving object. Under these circumstances, we might expect a backwards shift in the perceived position at which a post-saccadic stimulus is first reported to be seen, mirroring the temporal report. There is some evidence for this, at least relative to the forward shift obtained in control conditions (Yarrow et al., 2006b). However, the surprise result is that the position at which the post-saccadic stimulus

is se tho by a way

Ch

Bec shif it is The pre of t init Mo: exp 200 ( (200 or r tion Pari cue inte app trial but was cost effe targ that sacc an i atte

A focument Who Tse, tion descondep-

Τ

tem

oro

WOU

is seen to terminate actually shifts forwards compared to when no saccade is made. It appears as though time added on to the beginning of a period of stimulus motion is compensated partially by an illusory elongation of trajectory at the end of stimulus motion, up to 500ms later. In this way, time, velocity, and position are made to cohere.

#### **Chronostasis and attention**

Because chronostasis occurs in the aftermath of saccades, and saccades are intimately linked with shifts of covert spatial attention (e.g. Deubel and Schneider, 1996; Moore and Armstrong, 2003), it is natural to ask if a relationship exists between chronostasis and processes of selective attention. There are a number of ways in which it is possible to envisage attention playing a role. In the previous section I alluded to physiological events that might operate as time markers for the onset of the post-saccadic stimulus. The shift of attention that is hypothesized to precede saccade initiation is a candidate for this role, although there is little data on its precise time course (but see Montagnini and Castet, 2007). A related suggestion was made by Deubel and colleagues (1999) to explain discrepancies in temporal order judgements for peri-saccadic stimuli (see Yarrow et al., 2006a, for a discussion).

One experiment that bears on this explanation was described by Yarrow and colleagues (2001). Participants began by fixating centrally, then made unspeeded saccades to either the left or right. In addition to a typical saccade condition used to measure chronostasis, a second condition included an additional central arrow cue prior to the saccade, pointing at the saccade target. Participants were required to direct their attention voluntarily in the direction indicated by this cue before beginning their saccade and then completing a duration judgement task as usual. An interleaved reaction-time task, performed every other trial, required speeded saccades to a target appearing randomly to the left or right, without any subsequent duration judgement. Again, some trials included a central arrow cue, this time equally likely to predict the upcoming target or not, but which participants were instructed to obey just as they did in the duration judgement trials. It was concluded that participants were indeed allocating their attention as directed, based on an RT cost at the unattended location in RT trials. In the duration judgement trials, the chronostasis effect was identical regardless of whether attention had been deliberately allocated to the saccade target long in advance of the saccade, or no such instruction had been given. This result suggests that shifting attention is not the critical time marker used to estimate the onset of the postsaccadic object. There are, however, a number of problems which might lead us to question such an interpretation. Most critically, the relationship between an endogenous (instructed) shift of attention and the shift of attention that automatically precedes a saccade is unknown when both processes target the same location. It is far from certain that a pre-saccadic shift of attention would not occur even when attention has already been voluntarily allocated to the saccade target.

Aside from its possible role as a temporal marker, attention will undoubtedly be tightly focused at the position where the post-saccadic stimulus appears in typical chronostasis experiments (Deubel and Schneider, 1996) and might influence judgements about time in other ways. When attention is drawn to an object, it can give rise to temporal dilation (e.g. Tse et al., 2004; Tse, Chapter 10; Brown, Chapter 8, this volume) We can, however, discount attentional modulation of the rate of perceived time as an explanation of chronostasis based on the behavioural data described in the previous section. This is a rate-increase account, and does not fit with either the constant effect size found when post-saccadic stimulus duration was manipulated or the saccadedependent shift in the PSS found using a temporal order judgement task.

Temporal dilation is, however, not the only way in which the focus of attention can influence temporal judgements. 'Prior entry' refers to the advantage found for attended stimuli over

unattended ones when they are compared in a temporal order judgement task (Spence, Chapter 7, this volume). Physiological evidence that attention affects the timing of neural activity has been somewhat mixed (e.g. McDonald et al., 2005; Vibell et al., 2007). Behaviourally, however, this speeding of attended stimuli is robust, although it may be exaggerated in tasks that encourage response biases (Spence et al., 2001). Prior entry might, therefore, be responsible for the shift in the time at which the post-saccadic stimulus is seen in chronostasis experiments.

There are, however, a number of caveats we should bear in mind when attempting to apply prior entry as an explanation of chronostasis. Firstly, chronostasis is obtained with both interval judgements and temporal order judgements, whereas prior entry has been described and explored systematically only for the latter type of task. Secondly, prior entry does not currently explain the saccade-size effect because there is no reason to believe that larger saccades invoke a greater degree of attentional modulation at the saccade target than smaller saccades. Finally, chronostasis experiments require subjects to judge time in both control and saccade conditions. There is currently no evidence that visual attention is concentrated more completely at the target of a saccade prior to the saccade, than it is at a fixed position during steady fixation. All we know is that prior to a saccade, attention is concentrated more completely at the target of a saccade than at other locations assessed at the same time. In summary, we need to make a lot of assumptions in order to explain chronostasis with prior entry.

One recent paper has attempted to move beyond such speculation and explore the relationship between chronostasis and attention directly by investigating how much of the visual scene the illusion applies to. In their first condition, Georg and Lappe (2007) had participants make a saccade to a counter, replicating the original demonstration of chronostasis. They also included a constant fixation control condition, with a moving counter (see Box 12.1). The critical new condition also involved a saccade to a target object (now a cross) but this time the counter was presented mid-way across the screen at a position intermediate between the initial fixation and saccade target positions. This permitted the authors to assess temporal dilation away from the saccade target object. No chronostasis effect was obtained for this intermediate

The result appears to suggest that chronostasis does not occur for the entire visual scene, but only for the object targeted by a saccade, which is known also to be the target of covert attention (e.g. Deubel and Schneider, 1996). It is noteworthy, however, that this result is the exact opposite of that found in an experiment I carried out around the same time, in collaboration with John Rothwell, Patrick Haggard, and Doeschka Ferro. This experiment has not been published, so I present the details here.

Participants were required to saccade towards a letter target that might appear either alone, or accompanied by additional letters arrayed beyond the target letter in a semicircle. There were three possible arrays: target alone, five letters, or nine letters. The five-letter condition is shown in the inset to Figure 12.1, which schematizes the procedure. In saccade conditions, participants pressed a button to reveal the target array in peripheral vision. After 500ms, they had to react to a change of colour at the initial fixation cross by saccading to the middle target letter, then maintaining their fixation at this point. Any one of the letters in the array could change colour during the saccade, signifying that the duration for which that letter was presented in its terminal colour should be judged on an absolute scale. The dependent variable was mean judgement error. A further manipulation varied the degree of advanced knowledge about the letter that would form the basis of the subsequent judgement. On half of all trials, a red outline box cue appeared for 100ms around the letter that would change colour (at the same moment the array appeared) disappearing 400ms before the signal to make a saccade. The same factors were manipulated in control conditions, but subjects fixated a cross while the letter array first appeared in peripheral

Fig. 12. extent c conditio these te random made a the mea Positive schema shown i that its crosses capital | judgem 50% of disappe 10-15% fixation total of CRT colhorizon model 3

vision, visual i: If ch reduce those c

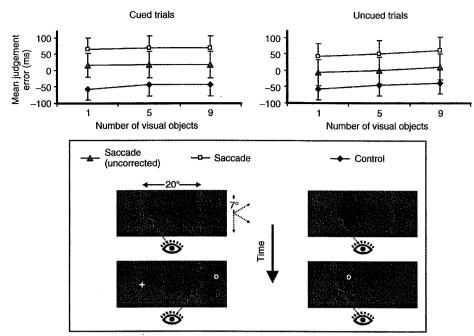


Fig. 12.1 Mean judgement errors in all 12 conditions of an experiment investigating the spatial extent of saccadic chronostasis. Both corrected and uncorrected values are shown for saccade conditions (see section entitled "saccadic suppression and saccadic chronostasis" for explanation of these terms) alongside results from a constant fixation control task. Durations were selected randomly on each trial from a uniform distribution with a range from 250-750 ms, and participants made absolute duration estimates with a range from 0 to 1000 ms. The mean judgement error is the mean difference between subjects' absolute duration estimates and stimulus display times. Positive values denote overestimations. Error bars show standard error of the mean. The inset schematises the experimental task, with the saccade task shown on the left and the control task shown on the right. The schematic shows black letters, with one letter turning white to indicate that its duration should be judged. In the actual experiment, stimuli were black or white fixation crosses (subtending 1° visual angle; cross turned white as an imperative stimulus), blue or red capital letters (approx. 1° visual angle; one letter turned red (here, shown as white) for duration judgement), and a red open square (2° visual angle; used to cue the location of the red letter on 50% of trials). The blue (here, shown as black) letters remained on screen after the red letter had disappeared to ensure that only the red letter could be used when estimating duration. Around 10-15% of trials were rejected and repeated, mainly because of failures to saccade and/or hold fixation according to instructions. Participants completed 45 trials in each of 12 conditions for a total of 540 pseudorandomised trials. Their heads rested in a chin/forehead rest, 41 cm from a 22" CRT colour monitor (refresh rate 120 Hz). Eye movements were recorded from both eyes (left for horizontal, right for vertical) 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).

vision, then disappeared and reappeared around fixation with a time course that approximated visual input in the saccade conditions.

If chronostasis were limited to the saccade target, the effect should have been drastically reduced in the five- and nine-object conditions (because only a small minority of trials in those conditions required a judgement about the saccade target letter, whereas in most trials a

7, en iis ge in olv

*r*al ed he er sis is fа is an

ns цp ıal nts ey he ne nion

ut on ite hn so

ne,

ate

ere in nts o a inng ur or.

ed ed) in ral

ıld

peripheral letter was being judged). Figure 12.1 shows that this was not the case. The data were corrected to reflect saccadic suppression and entered into a three-factor ANOVA. There was a difference between saccade and control conditions, representing the classic chronostasis effect. The presence or absence of the cue also had an effect, and these two factors interacted, indicating that the presence of a cue had no effect in the control conditions, but elevated estimates in saccade conditions. Figure 12.1 also shows the data without any correction for saccadic suppression. The pattern of significance was identical. Critically, the number of objects was not significant in either ANOVA and did not interact with the other factors. Hence the chronostasis effect extended to all the objects in an array of up to nine objects separated by up to 7° visual angle. Visual attention, by contrast, modulates performance at the target of a saccade compared to locations only 1° away (Deubel and Schneider, 1996).

Why the difference in results between this experiment and that of Georg and Lappe (2007)? It is possible that Georg and Lappe's choice of location for the second object represents a special case. Following a saccade, it would have required a shift of attention directly back along the saccade path. This shift of attention might have been unusually slow because of inhibition of return (Posner and Cohen, 1984), an RT effect that is often interpreted as a difficulty in shifting attention back to a location that has recently been visited (Lupiáñez, Chapter 2, this volume). Inhibition of return might affect duration estimates by delaying perception of the mid-trajectory object (i.e. prior entry), counteracting the typical temporal bias caused by a saccade.

Another difference between the two studies is that the study I have described here used a relatively complex semicircular array of objects rather than just two objects. Might such an array have been combined via gestalt grouping, operating like a single object and extending the temporal bias to all component objects in an artificial manner? In other unpublished work, my coworkers and I have used only two objects, with the second object presented at one of three positions 7° beyond the saccade target. We still obtained identical temporal biases when judging either this additional object or the saccade target object. However, these two objects would still be more likely to group than the two objects used by Georg and Lappe (2007) which were separated by 8°. Further research appears necessary to explain the difference in findings, as the outcome is of theoretical importance. For example, an account of chronostasis in terms of the predictive activity of cells with shifting receptive fields implies that the illusion should be obtained at multiple spatial locations (because remapping, which is typically measured in cells with somewhat peripheral receptive fields, can be assumed to occur in numerous cells which combine to form a fairly complete retinotopic map).

#### **Conclusions**

The term saccadic chronostasis describes the temporal overestimation of a stimulus seen immediately following a saccade. The effect can also be observed as a relative misperception of the time at which the post-saccadic stimulus is first seen. It seems likely that both behaviours result from a tendency to time erroneously the uncertain onset of the post-saccadic stimulus using a presaccadic marker. The most plausible physiological marker suggested so far is the activity of a class of cells which shift their receptive fields ahead of a saccade in order to gain a head start when

respondi in terms nisms in dilation : versy reg that prec wins out broken w

#### Refere

Alexander Experi Brown, P. Meetir Burr, D. C durin≨ Campbell, saccad Castet, E., Procee Deubel, H comm Deubel, H saccad Psycho Diamond, of Neu Duhamel, in pari Georg, K. Experi: Gregory, F Press. Haggard, I Neuros Hellstroen Psycho Hodinotttelepho Hopp, J. J. targetii Hunt, A. R **Tourna** fbbotson, l sensitiv

Cortex,

Jackson, S. spatial

<sup>1</sup> This small but reliable effect appears to contrast with the result of Yarrow et al. (2001) described earlier (no effect on temporal estimates for an endogenous cue directing attention to a single target). Because of the many differences between the two studies, it is difficult to draw any strong inferences about the reason for the diverging effects.

responding at their new position. However, the nature of the illusion also suggests explanations in terms of mechanisms of spatial attention. At this point, the exact role played by such mechanisms in generating saccadic chronostasis is unclear. Prior entry and attention-based temporal dilation are not particularly convincing explanations for the illusion, but there is some controversy regarding the spatial extent of chronostasis and its relationship with the shift of attention that precedes a saccade. Further research may help resolve these issues. Whichever explanation wins out, I hope this review will give you pause for thought the next time you glance at your broken watch, or catch the gaze of someone who's been looking at you for a little too long!

#### References

e

a

g

e

e

r II

y

y

Ş

ıl

e

ıf

g

y

a

e

g

e

d

is

re

at

n

SS

เด

ıe

or

- Alexander, I., Thilo, K. V., Cowey, A., and Walsh, V. (2005). Chronostasis without voluntary action. Experimental Brain Research, 161, 125–32.
- Brown, P. and Rothwell, J. C. E. (1997). Illusions of time. Society for Neuroscience Abstracts, 27th Annual Meeting, 23, 1119.
- Burr, D. C., Morrone, M. C., and Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, 371, 511–13.
- Campbell, F. W. and Wurtz, R. H. (1978). Saccadic omission: why we do not see a grey-out during a saccadic eye movement. Vision Research, 18, 1297–303.
- Castet, E., Jeanjean, S., and Masson, G. S. (2002). Motion perception of saccade-induced retinal translation. Proceedings of the National Academy of Science, USA, 99, 15159-63.
- Deubel, H. and Schneider, W. X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Research*, 36, 1827–37.
- Deubel, H., Irwin, D. E., and Schneider, W. X. (1999). The subjective direction of gaze shifts long before the saccade. In W.Becker, H. Deubel, and T. Mergner (Eds.) *Current Oculomotor Research: Physiological and Psychological Aspects*, pp.65–70. New York: Plenum.
- Diamond, M. R., Ross, J., and Morrone, M. C. (2000). Extraretinal control of saccadic suppression. *Journal of Neuroscience*, 20, 3449–55.
- Duhamel, J. R., Colby, C. L., and Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, 255, 90–2.
- Georg, K. and Lappe, M. (2007). Spatio-temporal contingency of saccade-induced chronostasis. Experimental Brain Research, 180, 535–9.
- Gregory, R. L. (1997). Eye and Brain: The Psychology of Seeing, 5th edn. Princeton, NJ: Princeton University Press.
- Haggard, P., Clark, S., and Kalogeras, J. (2002). Voluntary action and conscious awareness. *Nature Neuroscience*, 5, 382–5.
- Hellstroem, A. (1985). The time-order error and its relatives: mirrors of cognitive processes in comparing. *Psychological Bulletin*, **97**, 35–61.
- Hodinott-Hill, I., Thilo, K. V., Cowey, A., and Walsh, V. (2002). Auditory chronostasis: hanging on the telephone. *Current Biology*, 12, 1779–81.
- Hopp, J. J. and Fuchs, A. F. (2002). Investigating the site of human saccadic adaptation with express and targeting saccades. *Experimental Brain Research*, 144, 538–48.
- Hunt, A. R., Chapman, C. S., and Kingstone, A. (2008). Taking a long look at action and time perception. Journal of Experimental Psychology: Human Perception and Performance, 34, 125–36.
- Ibbotson, M. R., Price, N. S., Crowder, N. A., Ono, S., and Mustari, M. J. (2007). Enhanced motion sensitivity follows saccadic suppression in the superior temporal sulcus of the macaque cortex. *Cerebral Cortex*, 17, 1129–38.
- Jackson, S. R., Newport, R., Osborne, F., Wakely, R., Smith, D., and Walsh, V. (2005). Saccade-contingent spatial and temporal errors are absent for saccadic head movements. *Cortex*, **41**, 205–12.

- McDonald, J. J., Teder-Salejarvi, W. A., Di, R. F., and Hillyard, S. A. (2005). Neural basis of auditoryinduced shifts in visual time-order perception. Nature Neuroscience, 8, 1197-202.
- Montagnini, A. and Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: independence and coupling between attention and movement planning. Journal of Vision, 7, 8-16.
- Moore, T. and Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. Nature, 421, 370-3.
- Park, J., Schlag-Rey, M., and Schlag, J. (2003). Voluntary actions expands perceived duration of its sensory consequence. Experimental Brain Research, 149, 527-9.
- Penton-Voak, I. S., Edwards, H., Percival, A., and Wearden, J. H. (1996). Speeding up an internal clock in humans? Effects of click trains on subjective duration. Journal of Experimental Psychology: Animals Behavior Processes, 22, 307-20.
- Posner, M. I. and Cohen, Y. (1984). Components of visual orienting. In H. Bouma and D. Bouwhuis (Eds.) Attention and Performance X: Control of language processes, pp. 531-56. Hove: Erlbaum.
- Reppas, J. B., Usrey, W. M., and Reid, R. C. (2002). Saccadic eye movements modulate visual responses in the lateral geniculate nucleus. Neuron, 35, 961-74.
- Rose, D. and Summers, J. (1995). Duration illusions in a train of visual stimuli. Perception, 24, 1177-87.
- Ross, J., Morrone, M. C., Goldberg, M. E., and Burr, D. C. (2001). Changes in visual perception at the time of saccades. Trends in Neurosciences, 24, 113-21.
- Sommer, M. A. and Wurtz, R. H. (2002). A pathway in primate brain for internal monitoring of movements. Science, 296, 1480-2.
- Sparks, D. L. (1986). Translation of sensory signals into commands for control of saccadic eye movements: role of primate superior colliculus. Physiological Reviews, 66, 118-71.
- Spence, C., Shore, D. I., and Klein, R. M. (2001). Multisensory prior entry. Journal of Experimental Psychology: General, 130, 799-832.
- Sylvester, R., Haynes, J. D., and Rees, G. (2005). Saccades differentially modulate human LGN and V1 responses in the presence and absence of visual stimulation. Current Biology, 15, 37-41.
- Thiele, A., Henning, P., Kubischik, M., and Hoffmann, K. P. (2002). Neural mechanisms of saccadic suppression. Science, 295, 2460-2.
- Thilo, K. V., Santoro, L., Walsh, V., and Blakemore, C. (2004). The site of saccadic suppression. Nature Neuroscience, 7, 13-14.
- Tse, P. U., Intriligator, J., Rivest, J., and Cavanagh, P. (2004). Attention and the subjective expansion of time. Perception and Psychophysics, 66, 1171-89.
- Umeno, M. M. and Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. Journal of Neurophysiology, 78, 1373-83.
- Vibell, J., Klinge, C., Zampini, M., Spence, C., and Nobre, A. C. (2007). Temporal order is coded temporally in the brain: early event-related potential latency shifts underlying prior entry in a crossmodal temporal order judgment task. Journal of Cognitive Neuroscience, 19, 109-20.
- Walker, M. F., Fitzgibbon, E. J., and Goldberg, M. E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. Journal of Neurophysiology, 73, 1988-2003.
- Wearden, J. H. and Lejeune, H. (2008). Scalar properties in human timing: Conformity and violations. Quarterly Journal of Experimental Psychology, 61, 569–87.
- Yarrow, K. and Rothwell, J. C. E. (2003). Manual chronostasis: tactile perception precedes physical contact. Current Biology, 13, 1134-9.
- Yarrow, K., Haggard, P., Heal, R., Brown, P., and Rothwell, J. C. E. (2001). Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. Nature, 414, 302-5.
- Yarrow, K., Haggard, P., and Rothwell, J. C. (2004a). Action, arousal, and subjective time. Consciousness and Cognition, 13, 373-90.

Yarrow, K saccac Yarrow, K perisa Yarrow, K saccad Yarrow, K subjec Time

- Yarrow, K., Johnson, H., Haggard, P., and Rothwell, J. C. E. (2004b). Consistent chronostasis effects across saccade categories imply a subcortical efferent trigger. Journal of Cognitive Neuroscience, 16, 839-47.
- Yarrow, K., Whiteley, L., Haggard, P., and Rothwell, J. C. (2006a). Biases in the perceived timing of perisaccadic visual and motor events. Perception and Psychophysics, 68, 1217-26.
- Yarrow, K., Whiteley, L., Rothwell, J. C., and Haggard, P. (2006b). Spatial consequences of bridging the saccadic gap. Vision Research, 46, 545–55.
- Yarrow, K., Haggard, P., and Rothwell, J. C. (In press). Saccadic chronostasis and the continuity of subjective visual experience across eye movements. In R. Nijhawan and B. Khurana (Eds.) Space and Time in Perception and Action. Cambridge: Cambridge University Press.