Temporal perception in the context of action

Kielan Yarrow [1 *] & Sukhvinder S. Obhi [2]

1. Department of Psychology,
City University London

2. Centre for Cognitive Neuroscience & Department of Psychology,
Wilfrid Laurier University

* Author for correspondence:

Kielan Yarrow,
Social Science Building,
City University,
Northampton Square,
London EC1V 0HB

Tel: +44 (0)20 7040 8530
Fax: +44 (0)20 7040 8580
Email : kielan.yarrow.1@city.ac.uk

We do not usually experience the world as passive recipients of sensory information. Instead, we explore our environment through action. For senses like sight and touch, a framework exists to explain how we can interpret and predict the consequences of our own actions. In order to accurately distinguish sensory events arising in the environment from the sensations we ourselves generate, we make use of an efferent copy of our motor command(s) to generate predictions (Sperry, 1950; Von Holst & Mittelstaedt, 1950). In this chapter, we will offer a selective review of studies investigating how our sense of *time* is affected by our own actions. These studies address how we determine the time of an action (section 1), and also how both the sensory consequences of action (section 2) and externally-generated stimuli occurring around the time of actions (section 3) are processed by the brain in order to determine a subjective temporal narrative of events.

1. The perceived moment of an action

1.1 Actions as complexes of events

Actions unfold over time. For brief motor acts, the physical movement of the body is just the tip of the iceberg. Whereas *movements* can be reflexive, such as the extension of a knee in response to a physician's tap, *actions* comprise both an observable movement component and a series of hidden, mental components. Thus, in action, overt movement is preceded by a sequence of preparatory internal events. These have been inferred from the behavioural assays of cognitive psychologists (e.g. Rosenbaum, 1980;

Sternberg, Monsell, Knoll & Wright, 1978) and also observed directly in neural measurements (e.g. the development of readiness potentials in the electroencephalogram (EEG): Kornhuber & Deecke, 1965; changes in pre-movement motor cortical excitability indexed by motor evoked potentials elicited with TMS: Chen, Yaseen, Cohen & Hallett, 1998).

Indeed, every action generates a *complex* of internal events, reflecting for example the decision to move; the creation of a motor plan; the transmission of that plan to the muscles of the body; the re-afferent feedback that results from the body's movement; and the (iterative) use of this re-afference in correcting the movement. This simple fact implies that any experimental attempt to retrieve a subjective report about the time of an action should be scrutinised very carefully. For one thing, the extent to which a subjective report can accurately separate the internal events that collectively define an action is a matter of debate (although this has certainly not prevented researchers from asking questions of this kind). In the rest of section 1, we describe some attempts to grapple with these kinds of issues and thus determine the subjective time of actions.

1.2 Watching the clock

Although by no means the first attempt to investigate the perceived time of action, a good (and oft-cited) starting point can be found in the classic study of Libet, Gleason, Wright and Pearl (1983). These authors made use of the "complication" experiment (Dunlap, 1910a) in which a visual clock (in Libet et al.'s case, a spot of light rotating around a clock face with a period of 2560 ms) is used to estimate the time of an event.

The relevant events that Libet et al. (1983) investigated were the moment at which an action was 1) intended, and 2) physically initiated (as well as the time of an auditory tone, used as a control). The most famous result from this study relates to the time at which participants reported they first *intended* to act. Naturally enough, this time preceded the moment of action initiation. However, it was itself preceded by the onset of the readiness potential, an event-related potential (ERP) that can be recorded in the EEG in the lead up to an action. This result led the authors to conclude that the conscious decision to move does not in fact initiate action, but rather follows on from unconscious mental activity that is itself causal in nature.

This interpretation has given rise to considerable controversy. We might, for example, question whether the first-deflection method used to estimate the onset of an ERP, which will reflect the left-tail of the distribution of activity across trials, provides a fair comparison with the mean average of clock estimates (Trevena & Miller, 2002). Commentators have also questioned whether equating the readiness potential with the intention to move is reasonable in the first place (with the lateralised readiness potential offered as one preferable alternative, e.g. Haggard & Eimer, 1999). Given the issues outlined above in section 1.1, we should also wonder whether it is even possible to accurately estimate the moment of intention without considering other components of the motor complex. Indeed, recent data suggest that delays applied to the sensory consequences of action generate almost equivalent delays in estimates of the time of intention, suggesting that time of intention is in part estimated based upon the events that are observed subsequently (Banks & Isham, 2009; see also Lau et al., 2007; Strother & Obhi, 2009).

Leaving aside vexing questions about the nature of free will, a second result from the Libet et al. (1983) study was that the time at which the physical action was judged to occur also preceded the moment of action initiation, by around 80 ms (as measured by onset of electromyographic (EMG) activity in the muscles of the wrist). This anticipatory awareness of action suggests that efferent activity relating to the planning and/or execution of action influences the perceived time of action. This interpretation is bolstered by an interesting follow-up study described by Haggard, Newman and Magno (1999), who reported an anticipatory awareness of movement initiation that scaled with the complexity of the movement pattern. They used the Libet clock paradigm, but also made use of a classic result from experimental psychology: The time to initiate a fully-prepared movement sequence increases with the number of sub-movements in that sequence (Henry & Rogers, 1960; Sternberg et al., 1978). This result, which is typically interpreted as evidence that the whole sequence is planned in advance, also suggests that motor planning may begin earlier for longer sequences. The perceptual reports about action onset mirrored this interpretation: Actions were judged to have begun earlier when movement sequences were more complex, as though efferent (or at least "pre-movement") processing components where influencing the percept.

<INSERT FIGURE 1 AROUND HERE>

One recent study has extended this approach further by requiring clock judgements about both active and passive movements made with either the hand or the foot (Obhi, Planetta & Scantlebury, 2009; see also Obhi, 2007). There was a greater anticipatory awareness of active movements, which provide both efferent and re-afferent cues to timing, compared to passive movements, which provided only re-afferent cues. This again implies a role for efferent cues in judgements about the time of an action. However, anticipatory awareness was less pronounced for foot movements, where the motor command would be expected to come *earlier* relative to the time of physical movement (due to the longer neural pathway to the foot) than for hand movements (see Figure 1). This finding suggests that re-afferent cues (which would be expected to reach the brain *later* for foot movements) also influence the perceived time of action. Hence, awareness of action appears to be based on a combination of predictive and re-afferent cues.

Results emphasizing the role of re-afference in action awareness also bring up other interesting issues. For example, if judgments of action really are anticipatory, and don't just appear anticipatory due to problems with the measurement of subjective time (see below), then how does sensory re-afference, which arises after movement onset, inform the judgment? The mechanism by which "after the fact" information is used to construct a "before the fact" judgment remains to be elucidated (although see Libet, 2004, for discussion of a backward referral mechanism that might have some explanatory power).

1.3 The order of events

The clock method brings with it a range of problems. Firstly, interpreting clock estimates in any absolute sense is complicated by the unknown time taken to register clock position by the visual system. Relative differences in clock estimates between conditions are therefore preferable, and have generally been employed. Secondly, the requirement to monitor the clock alongside an action is problematic, because the degree to which an event is being attended influences judgements about its time of occurrence ("prior entry", e.g. Spence et al., 2001). There are no easy fixes for these kinds of problem.

Temporal order judgements (TOJs) provide one alternative means of estimating the time of an action. Here, the clock is replaced by a brief sensory event such as a tap or a beep, and observers judge whether this event preceded or followed the movement. Plotting a psychometric function reveals the point of subjective simultaneity (PSS), where "before" and "after" judgements are equally likely. Of course these judgements too suffer from problems akin to the clock method. One could argue, though, that the motion of the clock exacerbates the problems of interpreting instantaneous time from a perceptual judgement (c.f. Nijhawan, 1994) and that a tactile event *may* be less problematic when divisions of attention are considered.

One example of the TOJ approach, which parallels the work of Libet et al. (1983), comes from McCloskey, Colebatch, Potter & Burke (1983). They used brief tactile electrical stimulation to the ankle presented around the time subjects made a voluntary movement. Individual participants made contractions primarily involving a single muscle, but a range of movements were studied across subjects, including those of the foot and jaw. Participants judged the onset of a movement to be synchronous with the shock when EMG activity actually preceded the shock by 40-320 ms. They were, however, capable of differentially judging the moment of their internal instruction to begin movement (their conscious intention). This was judged to precede the onset of EMG by up to 100 ms. While the finding that a conscious decision to move is judged to have arisen before actual movement concurs approximately with studies using the clock method (e.g. Haggard & Eimer, 1999) the movement onset result is essentially opposite.

Another example, this time using a ternary (“before”, “during”, “after”) TOJ approach is provided by Dassonville (1995) who required subjects to judge when a tactile stimulus delivered to the index finger occurred relative to a horizontal (left to right) arm movement. Here, anticipatory awareness was reported, at least for the time of movement onset. Hence there is no simple division between the TOJ and clock approaches in terms of whether an anticipatory/delayed awareness of action results.

Aside from discrete and continuous movements of the limbs, a number of early studies also investigated observers’ temporal perception of visual stimuli around the time of saccades. For example, when subjects were asked to judge whether a test grating was presented before, during or after an eye movement, a complex pattern of results emerged (Volkmann & Moore, 1978). For stimuli presented after the onset of the saccade, observers showed a strong bias towards judging the stimulus to have arrived during the saccade (i.e. delayed awareness of action; see also Dassonville, 1995). For the single observer tested with stimuli also occurring prior to the saccade (and additionally given the “before” response option) these stimuli where also judged to have occurred during the saccade more often than would be expected (i.e. anticipatory awareness of action). Stimuli that arrived during the saccade where typically judged to have arrived before it, so times of occurrence for all stimuli were not simply drawn inwards towards the saccadic event.

However, more recent work has demonstrated that brief visual events undergo temporal distortions in the peri-saccadic interval even when judged without reference to the saccade itself (Morrone, Ross & Burr, 2005, reviewed below in section 3). This may help to explain the inconsistencies in Volkmann and Moore's (1978) results, because their visual reference was itself subject to distortion. When an auditory marker was used instead, and observers reported whether the tone came before or after the *end* of a saccade, a bias consistent with anticipatory awareness was obtained (Yarrow, Whiteley, Haggard & Rothwell, 2006a). Of course it seems likely that estimating the beginning or end of a saccadic eye movement will spontaneously evoke strategies that make use of correlated visual information (i.e. the offset and onset of fixations). These sensory cues are subject to their own substantial biases, discussed in section 2.2 below.

1.4 Tapping to the beat

Another approach to determine the perceived time of a sensory event is to use synchronisation tapping tasks (e.g. Dunlap, 1910b). Participants listen to a sequence of regular beats (like a metronome) and tap along. The time of their button presses relative to the time of each stimulus provides a measure of the perceived time of action, because participants are presumably trying to align their actions with the stimuli.

In fact, it seems that participants behave as though they were aligning the sensory consequences of their actions with the external beat, i.e. a delayed awareness of action (if considered relative to the onset of EMG). For example, taps consistently precede an auditory beat (at least when the taps do not make a distinct noise at contact) which is consistent with a shorter sensory latency for auditory compared to somatosensory events. Furthermore, this anticipatory tendency grows larger when tapping with the foot compared to tapping with the hand, in line with a longer neural pathway (Fraisse, 1980; Paillard, 1949). Hence in this task, re-afferent feedback appears to be the dominant cue used to determine the time of action, with little heed paid to efferent internal events. Of course, synchronisation tapping brings its own interpretational difficulties, but is a valuable complement to purely sensory judgements. For a more nuanced and complete review of work using this task, see Aschersleben (2002).

1.5 Adapting to delays

One of the most intriguing results in recent years regarding the perceived time of action comes from Stetson, Cui, Montague and Eagleman (2006). These experiments built upon earlier work suggesting that participants can adapt to the timing relations experienced during repetitive sequences of paired visual and auditory stimuli. If visual stimuli are consistently presented after auditory stimuli, or vice versa, small audiovisual asynchronies in the same direction (which were previously judged asynchronous) now begin to seem synchronous (Fujisaki, Shimojo, Kashino & Nishida, 2004; Vroomen. Keetels, de Gelder & Bertelson, 2004). Stetson et al. (2006) applied this notion to actions by varying the interval between a key press and the flash of light that the key press evoked (i.e. a source of artificial sensory feedback; see also Cunningham, Billock & Tsou, 2001; Pesavento & Schlag, 2006). In their first experiment, delays were fixed on 60% of trials and varied randomly on the remaining 40%. Participants judged whether the flash came before or after their key press on every trial (a TOJ). Comparing two different contexts where the typical delay was either small (35 ms) or large (135 ms), the point of subject equality between action and flash shifted forwards by around 40 ms, such that large delays seemed more synchronous in the context of other regular large delays.

This result has now been replicated and extended in other labs. Both Heron, Hanson and Whitaker (2009) and Sugano, Keetels & Vroomen (2010) have demonstrated shifts in the PSS following delayed sensory feedback (but see Winter, Harrar, Gozdzik & Harris, 2008, for an exception). Both groups also extended another finding from Stetson et al.'s (2006) experiments. Stetson et al. had found that adapting to LED flashes of three different colours generalised so as to cause PSS shifts in test trials using a fourth LED colour. Heron et al. (2009) and Sugano et al. (2010) showed that generalisation also occurred when test TOJs were made in a different sensory modality (e.g. adapt to delayed flashes, test with beeps). Although it is possible that delayed feedback in one modality brings about a realignment of event time across all sensory modalities, the most straightforward interpretation of this result would be that the perceived time of the action is shifting forwards towards its delayed sensory consequence. This would explain why testing with any sensory event yields an equivalent shift.

Considering sections 1.1-1.5 together, what can we conclude from this brief overview relating to the perceived time of action? Different experimenters have come to quite different conclusions regarding the anticipatory versus delayed awareness of action. Undoubtedly, the following factors are important in contributing to these differences: The various kinds of questions that have been asked; the uneven (and generally unknown) allocation of attention to different streams of events; the definition of action onset (e.g.

key depression versus EMG); the history of recent action-dependent feedback; and the sensory delays inherent in the clocks and markers used for comparison with motor acts. However, it seems most reasonable to conclude that all of the internal events that constitute the "movement complex" can probably influence judgements about the time of an action, and that the particular blend of cues taking precedence varies in a context-dependent manner. Such an account might suggest that the recalibration found by Stetson et al. (2006) represents a shift from early towards late cues brought about by motor-sensory delays, but this hypothesis is currently untested.

2. Timing actions and their sensory consequences

2.1 Intentional binding

Actions yield results: That is generally why we act in the first place. Are the consequences of action perceived as temporally veridical, and does the outcome of an action affect when the action is perceived to occur? In a series of experiments only one step removed from the complication experiment described in section 1.2, Haggard, Clark and Kalogeras (2002) asked participants to judge a clock's position at the moment when they made an action (either voluntary or involuntary) or heard a brief tone. The innovation in these experiments was that the authors varied systematically the context in which these events occurred. The actions were a voluntary key press, or an involuntary muscular contraction of the hand (evoked by applying a transcranial magnetic pulse to the primary motor cortex). In baseline blocks, either one of the actions or the brief tone were presented in isolation. In operant blocks, an action (be it voluntary or involuntary) was followed consistently after 250 ms by the tone, and participants judged when one or other of these events had occurred (in separate blocks).

The main finding, termed "intentional binding", was that when an intended action caused the tone, the action was perceived to occur later, and the tone was perceived to occur earlier, than when these events were presented in isolation. What's more, when an involuntary action caused the tone, the reverse pattern emerged, with the action seeming earlier compared to baseline and the tone appearing to come later. It seems as though actions cause their delayed sensory consequences to appear earlier in time, while the perceived time of the action is also drawn towards the contingent sensory event. This result may suggest a binding process that can help support conscious inferences of causality (although such an account seems a little tautological, given that the brain must register causality to implement binding in the first place). Many have begun to think of intentional binding as an implicit measure of agency for self-produced action (but see below).

Taken alone, the experimental findings presented so far might suggest partial explanations in terms of other mechanisms. For example, the apparent backwards shift of the tone towards its generative action might represent a case of attentional prior entry, given that the voluntary-causal condition permitted better temporal prediction about the time of the tone compared to the tone-alone baseline condition. A quite comparable situation arises in recent demonstrations of the flash-lag illusion (the tendency of a moving object to appear ahead of a co-incident flashed object; Nijhawan, 1994): The perception of the forward shift for the moving object (c.f. Haggard et al.'s clock) is strongly modulated (reduced) when the flash is caused by an action (Lopez-Moliner & Linares, 2006). The other component of intentional binding, the forwards shift in the perceived time of the action, might have resulted from the motor-sensory temporal adaptation described in section 1.5 (which was discovered only subsequently, and thus not discussed in Haggard et al.'s 2002 paper). This possibility might be discernable by analyzing later trials in operant conditions, versus early trials. Presumably, adaptation is more likely at the later stage of blocks, compared to earlier stages. To our knowledge, such an analysis has not been carried out.

However, other details of the original result, and other experiments reported in the same and subsequent papers, support the proposed mechanism. For example, a second experiment from Haggard et al. (2002) varied the interval between the action and the tone (250, 450, 650 ms) and found that the magnitude of the shift of the tone fell off very dramatically across this range. The precision of temporal expectation would deteriorate to some extent across this range (Weber’s law for time; e.g. Wearden & Lejeune, 2008) but it is doubtful whether this could explain such a rapid decay of effect size.

Of the various papers that have followed on from the original demonstration of intentional binding, we will describe only a few intriguing results. Firstly, the effect appears to consist of two components, one predictive and one postdictive (i.e. resulting from interpretation of the episode after the event). Moore and Haggard (2008) investigated blocks of trials in which an action produced a tone with varying consistency. When actions often produced tones, the perceived time of action shifted forwards, even when the tone never actually materialised. This suggests the involvement of a predictive process that operates even when the tone never arrives. The predictive effect disappeared when the contingency (and thus the prediction) weakened. However, even with a weak contingency, a forwards shift occurred on trials when the tone did arrive, suggesting an additional postdictive mechanism.

To avoid conceptual confusion, it is important to separate “predictive” effects into those based on the processing of efference copy by an internal forward model (i.e., those that operate immediately before an action is produced) and those that arise out of a longer history of experienced contingencies, such at those in the experiment just described. These types of predictive effects may be more accurately described as top-down expectation effects. The key point emerging from a range of experiments, however, is that both types of predictive signal seem to be important in producing our temporal perception of various events in an action-effect sequence.

A second intriguing result from recent temporal binding experiments is that the overall effect is enhanced in schizophrenic patients (Haggard et al., 2003), consistent with their abnormalities in assigning causal relationships between agents and actions (i.e. delusions of control). Moreover, referring back to the study by Moore and Haggard (2008), the predictive component of the binding effect is actually reduced in schizophrenia, while the postdictive component is exaggerated (Voss et al., 2010). Some authors have argued that intentional binding may arise for causal relationships in general, rather than depending specifically on intentional action, and thus relating mostly to the sense of agency (Buehner & Humphreys, 2009). It is interesting to note that the effect is reduced by repetitive transcranial magnetic stimulation to the pre-supplementary motor area, a site known to be important in the generation of voluntary actions (Moore et al., 2010).

A very new line of work, which certainly falls in to the intriguing category, considers intentional binding in scenarios where multiple individuals act together. This work also attempts to determine the relationship, if any, between intentional binding and subjective feelings of agency. Strother, House and Obhi (2010) required participants to sit together with right index fingers on a single long button. Both were instructed to intend to press the button at a time of their own choosing, but not to press actively if the other person initiated the action. As in the original experiment, participants judged the position of a rotating clock hand at the onset of various (action and sensory) events. Participants were also required to indicate after every trial whether they felt responsible for the key press or not (subjective agency rating). When temporal compression of an interval was used as a measure of intentional binding, both participants showed significant binding, even when one of them felt *no subjective agency*. If intentional binding was defined not as an interval, but as perceived shifts of action and effect times, then neither participant showed binding, despite one person feeling subjectively responsible for the key press and resultant tone. Hence, no matter how intentional binding is calculated, it appears not to be tied to subjective feelings of agency. This however, does not preclude the possibility that it is an implicit measure of agency, as has been suggested by Moore, Wegner and Haggard (2009).

A potentially fruitful area for future research is also to add an affective component to the sensory effect produced by an action, as previous studies have included affectively neutral effects only. Most real-life actions are associated with some type of positive or negative outcome, and it is plausible that this might alter the perceived time of actions and effects. Experiments examining this issue are underway, but final data is not available at this time (Obhi et al, in preparation). The take home is that, despite the impressive results gathered thus far, the full nature of the intentional binding effect remains to be clarified, as does the full nature of the mechanisms that underlie it.

Finally, it is noteworthy that, whilst intentional binding has generally been demonstrated using the clock-comparison approach outlined at the beginning of this section, recent reports have changed emphasis, making use of time estimation / reproduction tasks which assess the interval between the action and the tone (e.g. Humphreys & Buehner, 2009; Humphreys & Buehner, 2010). The duration that is perceived to accrue between the action and its delayed sensory consequence is measured directly in this approach, and is found to be shorter than in control conditions. However, in contrast to the original finding, the effect is found to remain strong (and even grow) for sensory delays exceeding a second in duration. This leads us neatly on to what some have considered a related phenomenon: Chronostasis.

2.2 Chronostasis

If you have ever owned a watch with a silently advancing second counter, you may have experienced chronostasis (although you probably didn’t realise it had such a catchy name). Sometimes, when glancing down at your watch, you may have had the momentary impression that the watch had stopped. The watch soon ticked on of course, and you probably forgot all about it. What is strange about this phenomenon is that it occurs exclusively when we make a saccadic eye movement towards the counter just as the counter advances (Brown & Rothwell, 1997). It is as though a little bit of time were being added on to the duration of the newly fixated image, so that a saccade right at the beginning of a new one-second interval gives the impression of an interval that exceeds one second in duration.

To test and develop this idea, we can employ the following method (first described by Yarrow et al., 2001, and developed in subsequent publications; for a fuller review, see Yarrow, Haggard & Rothwell, 2010). In saccade conditions, the participant fixates at one location, and then makes a saccade to a target at a different location. The target changes form or colour during the saccade, so that it is first visible in its new state at the end of the saccade. It is presented for a short (usually variable) time, and then replaced by a sequence of one or more reference stimuli. When more than one reference is presented, (a rather superfluous feature of earlier experiments) they are all identical in duration. The task is to decide whether the post-saccadic target stimulus was present for more or less time than the reference stimulus. This permits the calculation of a point of subjective equality (PSE), i.e. the duration for which we must present the post-saccadic stimulus for it to appear equal to a given reference stimulus.

The PSE for a post-saccadic target compared to a reference of 1000 ms is in the region of 800-900 ms (Yarrow et al., 2001). However, this piece of information is not very informative, because when two intervals of time are compared it is common to have a bias which leads to a non-veridical PSE (known as the time-order error, e.g. Hellstroem, 1985). Hence it is essential to include a control condition, where a similar judgement is made but without any saccade having been made. The simplest control conditions match only post-saccadic stimulation precisely; better ones match pre and post-saccadic stimulation; and the best yet employed match pre, post and peri-saccadic stimulation, at least for the fovea (e.g. by initially displaying a peripheral stimulus which jumps to fixation with a saccadic timecourse; Georg & Lappe, 2007; Yarrow, Haggard & Rothwell, 2004a; Yarrow et al., 2001). However, the fine details of the control conditions don't actually seem to matter all that much (Yarrow et al., 2004a). Nor do technical issues regarding when the post-saccadic stimulus is assumed to become objectively visible (i.e. whether it is timed from the moment it appears on screen, or, as is more typical, from the moment it is first fixated; Yarrow et al., 2006a; Yarrow, 2010). The key point is that the PSE is substantially and significantly reduced in saccade conditions *compared to control conditions*, suggesting that a newly fixated object/scene has a subjectively expanded duration.

An expanded duration might imply changes at the onset or offset of an image, or indeed an altered rate of time accrual between these events. In fact, it seems very much as if the point in time at which the newly fixated object/scene is first perceived gets moved backwards, or *antedated*, to reflect the moment when the eyes first left the previous fixation point. The evidence is as follows. Firstly, in experiments where participants make either a small or a large saccade, the size of the saccadic chronostasis effect changes: It grows larger following a large saccade, and the amount by which it grows conforms quite well to the additional time taken to complete the saccade (Yarrow et al., 2006a; Yarrow et al., 2001). This suggests that the post-saccadic image is being antedated to a moment that remains constant with respect to saccade initiation.

Secondly, the exact duration of the post-saccadic interval doesn't affect the magnitude of saccadic chronostasis (Yarrow et al., 2004a). This suggests that time is being distorted by a shift in an event marker, rather than a change in the rate of some putative internal clock (which might be caused by mechanisms such as arousal or attention). Rate change accounts predict that experimental effects should scale with duration (because subjective time equals objective time multiplied by clock rate), but no scaling is evident in chronostasis experiments. Indeed, saccadic chronostasis is clearly evident when the post-saccadic target is presented for only 100 ms.

The third (and most direct) line of evidence for the antedating account comes from experiments where the interval comparison task is replaced by a temporal order judgement task (Yarrow et al., 2006a). Here, participants must compare the time of onset of the post-saccadic image with the time of a brief tone. In control conditions, the tone must be presented after the visual onset to yield perceived simultaneity, but in saccadic conditions the PSS occurs when the tone is presented much earlier, near the time of saccade onset. The difference between saccade and control conditions for this task once again grows for larger saccades, emphasising antedating towards a pre-saccadic reference.

Taken collectively, the data from saccadic chronostasis experiments seem to provide the missing link in a broader story relating to our peri-saccadic perception. Think about a bad home video, where the camera leaps from person to person. Pretty unsettling, right? But a situation like this arises whenever we move our own personal cameras, our eyes. However, when we make a saccade, vision, specifically magnocellular vision, is actively suppressed (and masked), presumably in order to prevent activation of low-level motion sensors that would otherwise signal movement of the entire visual scene (Burr & Morrone, 1996; Ross, Morrone, Goldberg, & Burr, 2001; Campbell & Wurtz, 1978). This process operates alongside other mechanisms designed to maintain the perceived stability of the visual world (Bridgeman, Van der Hejiden & Velichkovsky, 1994). Why, then, is our vision not interrupted with a brief period of nothingness every time we move our eyes, rather like someone flicking the lights off and on around three times every second? Saccadic chronostasis may reflect the process that stitches individual fixations together in order to generate the illusion of continuous vision (Yarrow et al., 2001).

This story is supplemented by the existence of a plausible physiological mechanism to support saccadic chronostasis. As traditionally defined, the receptive field of neurones in the visual system reflects the position at which a stimulus will modulate the cell's response, measured with respect to fixation (i.e. in a retinotopic frame of reference). However, it is now clear that many cells in the brain have receptive fields that are best defined with respect to the position of the head or body, regardless of eye position. Most critically, some cells (originally described in the lateral intraparietal area, but now found quite widely) have receptive fields that shift suddenly before an eye movement, so that they will respond predictively to stimuli presented at a location their retinotopic receptive fields would usually incorporate only after the saccade (Duhamel, Colby & Goldberg, 1992; Umeno & Goldberg, 1997; Walker, Fitzgibbon & Goldberg, 1995). This predictive response, occurring around the time of saccade onset, might be the signal that is used to begin timing of the post-saccadic scene.

<INSERT FIGURE 2 AROUND HERE>

A few other interesting results from saccadic chronostasis experiments are outlined in Figure 2. They are generally in accordance with the antedating account outlined above. As noted above, one of the reasons that the antedating account is tempting is that it fits elegantly into the broader story of peri-saccadic vision. Unfortunately, this neat and tidy picture is undermined somewhat by the existence of potentially analogous effects for movements of other parts of the body.

The most directly analogous experiments have been described by Yarrow and Rothwell (2003) and Jackson et al. (2005). When observers reach to touch a vibrating tactile target, that target undergoes subjective temporal dilation, just as in the saccadic case. This effect does not scale with reach extent, which implies some differences from the saccadic situation (Yarrow & Rothwell, 2003). The observation does, however, suggest that a more general account than the one outlined above (involving receptive field shifts in visual neurones) should be considered. A slightly different situation was explored by Jackson et al. (2005), who failed to detect a significant chronostasis effect in a patient who makes saccadic head movements in place of saccadic eye movements. In this case, an explanation of saccadic chronostasis in terms of saccade-specific mechanisms garners some support.

These experiments are directly analogous to the saccadic situations described above because the judged stimulus is the natural sensory consequence of the action, and its state is unclear until the action has been completed. These features differentiate the chronostasis situation from typical intentional binding experiments, which ask a question about an artificial and delayed sensory re-afferent. Other experiments have blurred this distinction, with mixed results.

Yarrow and Rothwell (2003) describe two experiments in which participants pressed a button to initiate a visually-defined interval. No temporal dilation was detected, despite good experimental power. However, Park, Schlag-Rey & Schlag (2003) have reported experiments in which temporal dilation of a visually-defined interval *was* observed, following either a button press or a verbal utterance. Some time later, Hunt, Chapman and Kingstone (2008) presented a series of experiments using button presses and judgements about visual intervals, and obtained temporal dilation in some, but not all, cases. Meanwhile, Verstynen, Oliver and Ivry (2010) describe a study in which a right-hand button press initiated a vibrotactile interval applied to the left hand. They found a small but reliable temporal expansion. Interestingly, the size of their effect grew when the onset of the vibrotactile interval was delayed slightly (by 50 ms), consistent with antedating towards an efferent signal. Finally, the observant reader will note that we segued to this section with a discussion of some intentional binding experiments which used an interval duration estimate about the time between a button press and a subsequent beep. In these experiments, the significant effects were actually in the opposite direction to the scenarios described above, i.e. the interval was perceived as shorter in action-initiated conditions. Of course there are some potentially important differences for this final example, as the judgement was about empty rather than filled intervals, and the markers were auditory, not visual. Overall, then, it appears that more work is necessary to reconcile the confusing pattern or results regarding the perceived time of visual, tactile and auditory intervals following a button press.

3. Contextual effects of action on sensation

To complete our survey of experiments investigating how temporal perception changes in the context of movement, we will consider briefly the situation where ex-afferent sensory events which have no causal relationship to a movement are nonetheless presented around the time of movement, and judged without reference to the movement itself. These experiments have generally been conducted using saccades.

An experiment that falls midway between the experiments we described in section 1 (judging the time of an action relative to a sensory referent) and the situation we wish to focus upon in this section (judging sensory events relative to one another) was conducted by Deubel, Irwin and Schneider (1999). Participants made saccades from a central position to a peripheral target. An open circle appeared on screen for 20 ms, at a time ranging from 450 ms before the saccade to 250 ms after it. The circle was located at one of three locations: the initial fixation point, the saccade target point, or the opposite point (i.e. the alternative saccade target). Participants judged whether their gaze had been on the central fixation point or the saccade target point when the circle appeared. They often incorrectly felt that they were already looking at the saccade target even when the circle appeared well before their saccade. The effect was less marked when the circle appeared opposite the target, and nearly absent when it appeared at the initial fixation point. An important issue here is what exactly the subjects were attempting to do in these experiments. The question about the direction of gaze might be answered with reference to the perceived time of the movement (c.f. section 1.3), the perceived time of onset of the post-saccadic image (c.f. section 2.2) or the perceived time of offset of the pre-saccadic image (a judgement that has not yet been investigated in detail).

Subsequent attempts to look at the timing of visual events around the time of saccadic eye movements have used questions that are rather less ambiguous. This approach is exemplified by results from two high-profile papers from the same group (Binda, Cicchini, Burr & Morrone, 2009; Morrone, Ross & Burr, 2005). The key findings are as follows:

1) When participants are asked to judge the duration between two peri-saccadic visual events (flashed lines) the time between them can appear compressed. This effect is strongest when the two lines are flashed around 75 ms before and 25 ms after saccade onset.
2) When time is compressed in this manner, the precision of time perception actually improves, in line with Weber's law.
3) Compression does not occur between two auditory events presented with a similar time course, suggesting that auditory time remains veridical.
4) Judging two visual events can also result in an apparent reversal of order. When the lines are flashed specifically so that the later one arrives around 50 ms before the saccade onset, they are perceived in the wrong order.
5) Finally, when a single visual event is presented for peri-saccadic temporal comparison with an auditory event (TOJ) or two successive auditory events (bisection), the relative time to perception for the visual event changes depending on exactly when it flashed. Flashed lines are perceived faster if presented around 50 ms before the saccade, and slower if presented slightly later (i.e. immediately before or during the saccade). The speeding observed at around -50 ms is substantial enough to explain the order reversals described in

point 4. The slowing from around the time of saccade onset may explain the compression noted in point 1.

These data provide a reasonably consistent story about the timing of transient visual events around the time of a saccade, one that like the account of saccadic chronostasis outlined in section 2.2 appeals to the receptive field shifts described in neurophysiological experiments (e.g. Duhamel et al., 1992). However, some puzzles and outstanding issues remain. For example, if the changes observed in the timing of brief intervals are driven by changes in event times, why is only compression found? Expansions should also be evident, for example when the first stimulus is presented 50 ms before the saccade and the second comes around 50 ms after saccade onset. Furthermore, while neural recordings do show changes in the latency of response for a population of dorsal medial superior temporal neurones when stimuli are presented either near to the time of a saccade or during steady fixation, sensory acceleration is evident just *after* a saccade, not before it (Ibbotson et al., 2008). Terao, Watanabe, Yagi and Nishida (2008) have also complicated the interpretation of the initial interval timing experiments by showing that similar effects arise when stimuli are reduced in contrast. Such contrast reductions would be expected to occur in the saccadic conditions of Morrone et al. (2005), in line with known properties of saccadic suppression, suggesting a rather simpler explanation of the observed temporal compression.

In concluding this section (and the chapter as a whole) we can briefly consider the relationship between biases in the timing of peri-saccadic visual transients, and biases in the timing of the post-saccadic visual information revealed by the saccade. There is a clear overlap in the physiological mechanisms that have been used to explain both situations. Both Yarrow et al. (2001) and Morrone et al. (2005) have invoked shifting receptive fields found in lateral intraparietal cortex and other regions known to be involved in saccadic control, and Binda et al. (2009) have presented a detailed quantitative model based on the available physiological data which explains many of their temporal distortions (and indeed some related spatial ones). However, at this point it is not quite clear whether a single mechanism can explain all the current results pertaining to the shifts in visual timing that occur for both ex-afferent stimuli presented near a saccade and the natural (post-saccadic / re-afferent) stimulus that is revealed by a saccade. What *is* clear, however, when considering this chapter as a whole, is that representing time in the context of action is an extremely complex mental activity. The oddities of temporal perception that occur before, during and after an action will certainly need to be taken into account in order to generate a complete account of human temporal perception.

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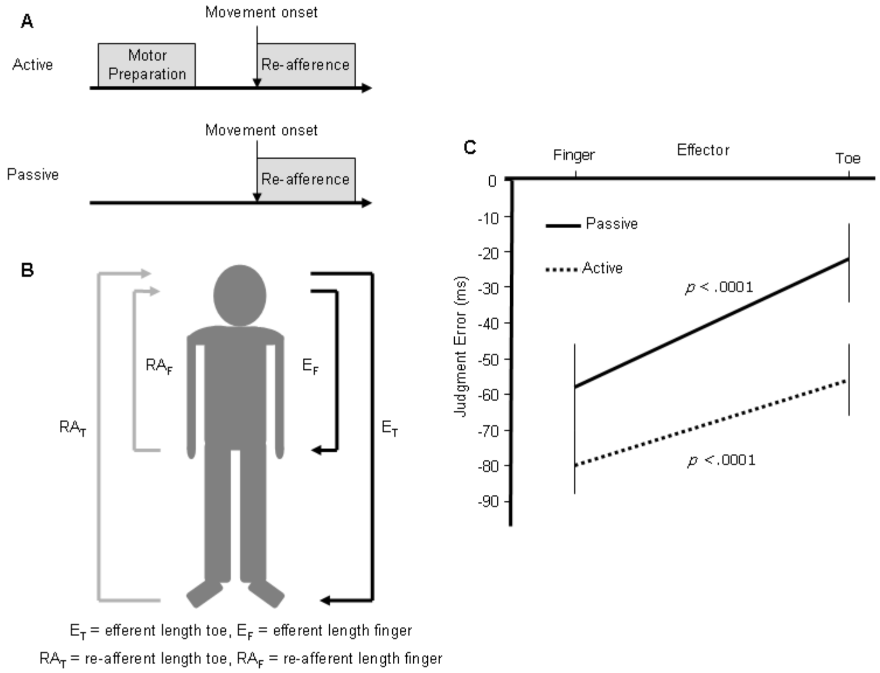
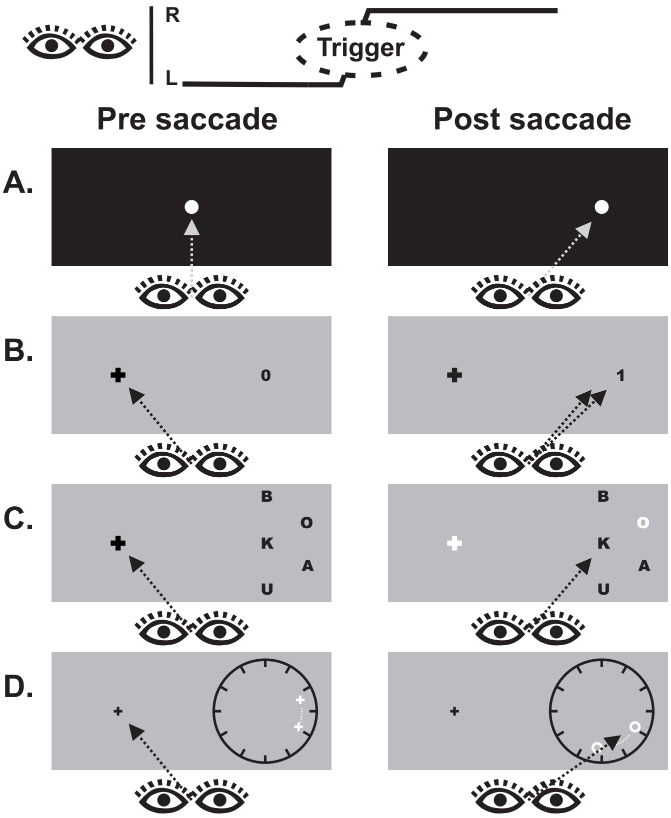
Figure 1



Legend to Figure 1

A. Signals available in active and passive movements respectively. The perceived time of action could be based on efferent information, re-afferent information, or both for active movements, but only on re-afferent information for passive movements. **B.** If awareness of action is based on efferent information, this predicts that toe movements should be judged as occurring earlier than finger movements because $E_T > E_F$. If awareness of action is instead based on re-afferent information, the prediction is that toe movements will be judged to occur later than finger movements because $RA_T > RA_F$. **C.** Judgment errors (difference between actual action onset and judged onset). Active movements produce earlier judgments than passive movements, which supports a role for efferent information. However, toe movements are judged later than finger movements, which supports role for re-afferent information. Hence, both efferent and re-afferent signals contribute to judgments of action onset.

Figure 2



Legend to Figure 2

Some additional saccadic chronostasis results not described in the main text. **A.** Saccadic chronostasis is found for extremely rapid and highly automatic classes of saccade, such as express saccades elicited in complete darkness (Yarrow, Johnson, Haggard & Rothwell, 2004b). This suggests that a subcortical efferent trigger may be important. **B.** Saccadic chronostasis is reduced when the saccade target shifts suddenly but imperceptibly during the saccade, and eliminated when this shift is actually perceived (Yarrow et al., 2001). This suggests that expectations about cross-saccadic continuity must be fulfilled before the illusion is implemented. **C.** When objects other than the saccade target are judged, the chronostasis effect is still found (Yarrow, 2010), suggesting that the illusion extends to large parts of the visual scene (but see Georg & Lappe, 2007, for an opposite result). **D.** Saccades made towards a moving object give rise to chronostasis, and also to spatial misperceptions that suggest spatiotemporal coherence is maintained in the brain, but in a highly postdictive manner (Yarrow, Whiteley, Rothwell & Haggard, 2006b; see also Hunt & Cavanagh, 2009).