Royal Holloway, University of London

How vision influences perceived duration: An empirical and computational investigation

Thesis submitted in fulfilment of the degree
of Doctor of Philosophy

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DECLARATION OF AUTHORSHIP

I, Edward Charles Peter Rowland hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated.

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ABSTRACT

Time perception is often thought of as arising from a centralised mechanism. Recently, there has been a shift away from this perspective, with evidence showing that adaptation to particular visual properties at specific locations and stimulus predictability affects perceived event duration, implying that sensory systems carry out duration processing. This thesis investigates the following three questions: (1) Does adaptation induced duration compression affect other visual processes? (2) Can sensory systems encode duration using their basic response properties? (3) What is the relationship between predictability, perceived duration and neural response to a visual stimulus? The first question was investigated using a visual illusion called Flash-Lag, commonly thought to possess a fixed time component. After pilot investigations comparing psychophysical techniques, results from a behavioural experiment show that adapting to a high temporal frequency stimulus reduces the time component of the Flash-Lag illusion, implying a role for duration in positional and/or motion computations. We demonstrate that a model using labelled lines and the varying temporal responses of neurons can encode the duration of a temporally normalised input. The model exhibits effects similar to those observed in the literature, including adaptation induced duration compression, central tendency and perceived duration scaling with the magnitude of various stimulus properties. Finally, a new paradigm is developed to test if stimulus duration decreases with stimulus predictability. Although behavioural results show no effect of predictability, event related fMRI shows significant differences in BOLD signal. Area MST demonstrates reduced response to expected events in a duration judgement task, but not an orientation judgement task, suggesting response is reduced by predictability, dependent on the task. These results show that duration may be encoded in sensory systems and is used in perceptual tasks. Furthermore, it is proposed that duration is estimated using ramping or climbing activity within neural populations in the dorsal visual pathway.

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1. CHAPTER ONE - BACKGROUND

1.1. INTRODUCTION

Time perception and its basis in the brain is a broad and complex topic and the timescales humans and other animals operate on are extremely variable. From the precise millisecond timing of spikes fired from individual neurons, through to circadian rhythms controlling the wake-sleep cycle over the course of a day and onto the ability to conceive of events many months and years into the past or imagine ourselves along similar timescales in the future. The ability to operate on such wide timescales requires a range of different brain functions. Circadian rhythms are driven by autonomous cellular and molecular mechanisms (Dunlap, 1999). While the timing of spikes is crucial in audition for the detection of interaural time differences (Wagner & Takahashi, 1992), these time differences are perceived 'indirectly' as auditory locations rather than differences in timing. Structures such as the hippocampus have been identified as important in the storage and retrieval of long-term memory (Corkin, 2002), but again this can be considered a less directly perceived quantity of time.

The material covered here will concentrate upon the timescale of sub-second to second duration required for perception, cognition and action, where, arguably durations are a sensory property of a stimulus, as opposed to being indirectly coded from other attributes or more cognitively/semantically encoded. Informed by studies on both human and animal behaviour this area has historically been the domain of 'central clock' models. Such models provide the first focus for discussion before concentrating on the experimental results concerning the visual perception of time on these shorter (not more than a couple of seconds) timescales. Discussing this work will lead onto identifying the research questions that will form the motivation behind the experimental and theoretical work carried out in the rest of this thesis.

1.2. CENTRALISED MODELS OF TIMING

1.2.1. INTERNAL CLOCK

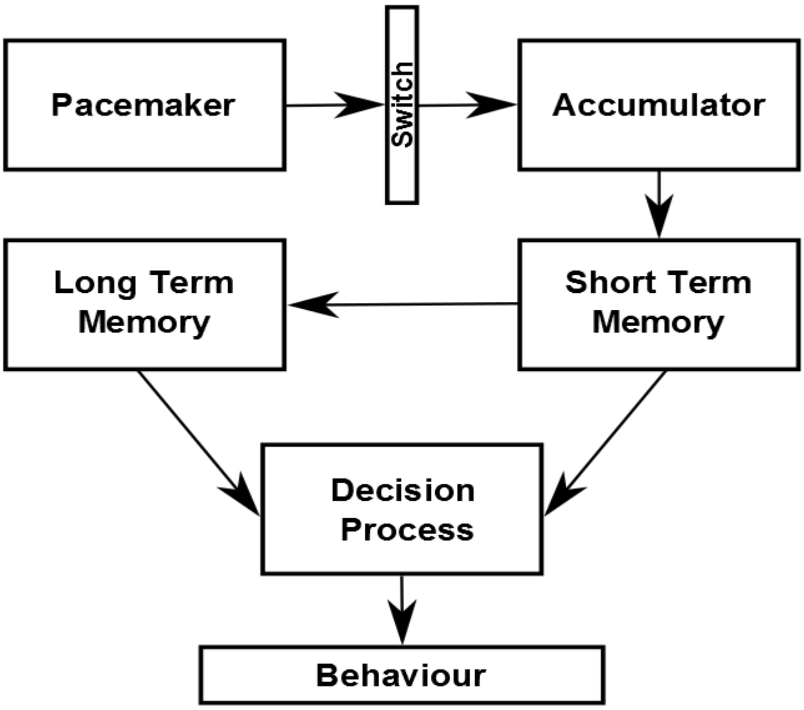


Figure 1-1: A block diagram showing the clock model typically used to explain time perception in humans.

A mechanism commonly proposed to account for the perception of time is the internal clock (Gibbon, Church, & Meck, 1984; Treisman, 1963). The internal clock consists of a central pacemaker emitting pulses typically according to a Poisson distribution so over a given time period the same amount of pulses occur, although not equally spaced), which transmits to an accumulator counting the pulses to give a measure of time. When learning a task where an explicit measure of duration is behaviourally relevant the learnt duration is stored in long-term memory for future reference. By comparing this learnt duration to the current or a more recently acquired duration from the accumulator stored in short-term memory, a decision can be made to guide behaviour appropriately (Figure 1-1). While originally used to explain animal behaviour (Church & Gibbon, 1982) pacemaker-accumulator model also have been applied to human timing (Wearden, 1991), though human judgments appear more variable, possibly due to effects of attention and arousal.

The internal clock model was extended by Treisman, Faulkner, Naish, and Brogan (1990) to include effects of attention and arousal. This model is made up of a central pacemaker with multiple, task-specific control units that receive input from the central pacemaker, which transforms the input from the pacemaker to an output - a timing signal tuned to a particular task or sensory domain. As each control unit’s output is task specific, the timing signal can change in response to the requirements of the task or directed attention, whilst overall arousal levels can speed up or slow down the internal clock depending on the prevailing environmental and organism states. It has been used to explain various experimental findings in human sensory time perception, showing that perceived duration is affected by attention (Seifried & Ulrich, 2011), arousal (Stetson, Fiesta, & Eagleman, 2007) and body temperature (Wearden & Penton-Voak, 1995). Some have used attention to explain why the first event in a sequence appears to last longer than subsequent events that are of the same length (Rose & Summers, 1995) or, why an unexpected or ‘oddball’ stimulus appears to last longer than a non-oddball stimulus (Tse, Intriligator, Rivest, & Cavanagh, 2004). These results are interpreted using internal clock models as a change in control unit tick speed or a speeding up of the central clock. There is also evidence showing that faster moving stimuli appear to last longer (Brown, 1995), suggesting stimulus properties could also speed up the internal clock. This claim was backed-up by Kanai, Paffen, Hogendoorn and Verstraten (2006), who control for spatial frequency, pinning the velocity temporal expansion effect onto the temporal frequency of the stimulus and propose an event related timing mechanism, so that stimulus duration is estimated by the rate of change of the stimulus. Clock models affect perceived duration by tuning their tick rate to the environment so that an environment where events are occurring rapidly requires a faster clock rate to discern when events happen. This leads to more ‘ticks’ from the timing mechanism over the same actual duration causing the temporal expansion effects observed and an increase in perceived duration. Other stimulus properties such as size (Xuan, Zhang, He, & Chen, 2007), brightness (Bowen, Pola, & Matin, 1974; Brigner, 1986) and magnitude in general (Alards-Tomalin, Leboe-McGowan, Shaw, & Leboe-McGowan, 2014) have also been shown to change perceived duration. While these phenomena cannot be attributed to the event related mechanisms, attention can be drawn to differences in stimulus properties (Bernardino, Cavallet, Sousa, & Galera, 2013; Camgoz, Yener, & Guvenc, 2004; Proulx, 2010), so they may be explained in terms of attentionally driven increases in internal clock speed.

1.2.2. SCALAR EXPECTANCY AND WEBER'S LAW

One of the more dominant theories arising from the central clock approach is Scalar Expectancy Theory (SET) proposed by Gibbon (1977). SET is a model of time perception stating that time across all modalities is measured against a centralised clock that uses a pacemaker with a variable tick rate changing on a trial-to-trial basis (Church & Gibbon, 1982). This explains why time perception appears to be unified across senses and that, on average, accurate measures of duration can be made, with the variability of such estimates scaling with the estimates' mean duration. This feature of timing is termed, the scalar property, which is an example of Weber's Law. Weber's law is a long established property of sensory perception whereby the sensitivity of the sensory system to differences in stimulus properties is inversely proportional to the magnitude of the stimulus property. As sensory systems are noisy processes (Faisal, Selen, & Wolpert, 2008), sensory judgements are variable across different presentations of the same stimulus. The variability can be computed by taking the standard deviation of a number of judgements and dividing by the mean judgement, giving the Weber fraction: the ratio between the stimulus property magnitude and the variability. If Weber's law holds then this ratio should be approximately constant across a range of stimuli with differing magnitudes as when the magnitude increases, sensitivity decreases in proportion and more variability in judgements is observed. SET was originally informed by studies on non-human primates, performing a task where they learn they have to respond a particular amount of time after stimulus onset to receive a reward rather than immediately afterwards. The distribution of the delay of these responses for this task follows Weber's law, i.e. the scalar property (Figure 1-2). Gibbon (1977) posits the animals in these experiments have an internal representation of time provided by the internal clock mechanism to explain the animal’s ability to perform the task.

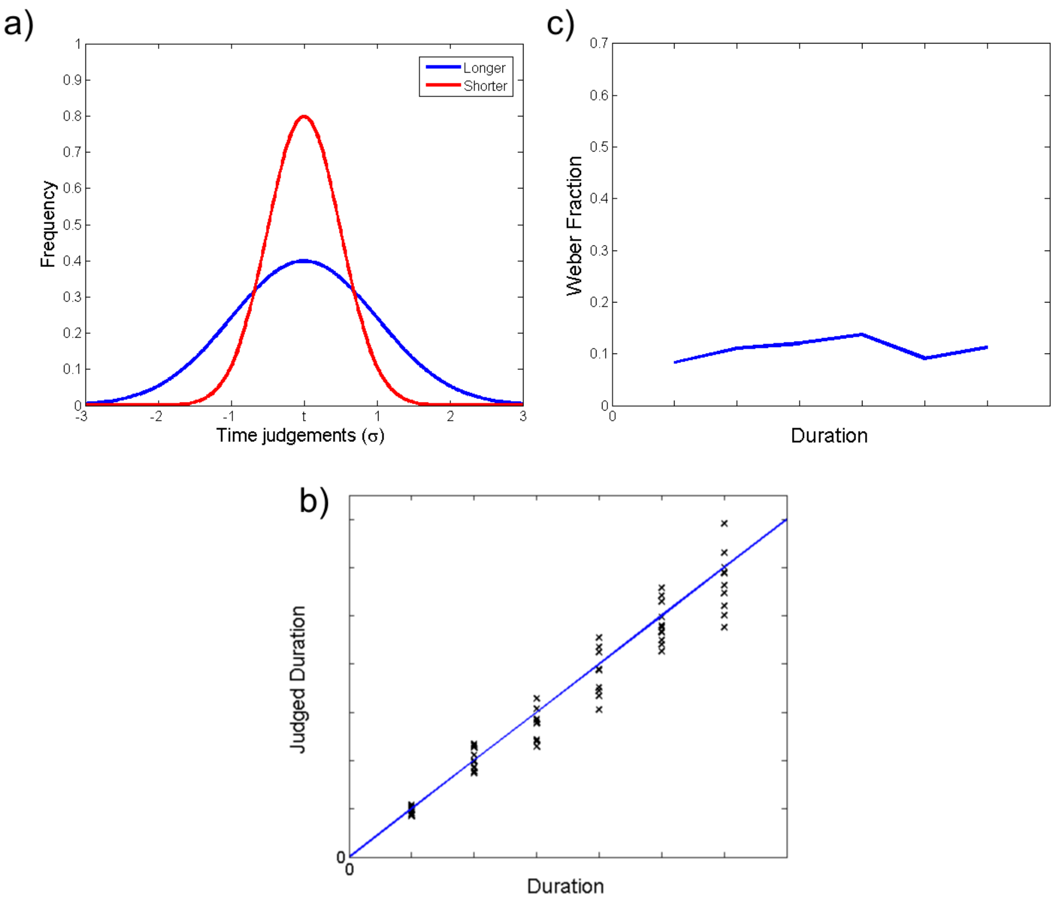


Figure 1-2: Graphs showing Weber’s law in Scalar Expectancy Theory expressing the scalar property labelled anticlockwise. a) Shows the distribution of timing judgements for a shorter duration (red) and a duration twice as long (blue), where the distribution of longer duration judgements is twice that of the shorter duration as according to Scalar Expectancy Theory. b) Shows a computationally generated example set of duration judgements (judgement: black cross) following Weber’s law, as the duration increases so does the variance in the judged durations, the blue line shows equality. c) Gives the Weber fractions (σ/μ) for the example data shown in b) demonstrating that the Weber fraction is approximately constant (~0.1) across all the durations.

1.2.3. IS SCALAR EXPECTANCY A FUNDAMENTAL PROPERTY OF TIME PERCEPTION?

Gibbon (1977) also proposed the existence of multiple timing mechanisms over different timescales, claiming that behavioural data shows an abrupt change in Weber fractions across shorter (<1.5s) and longer (>1.5s) durations, implying two different mechanisms i.e. different clocks with different variability for the two different timescales. However, the data presented to underpin this claim are from a meta-analysis across experiments using different animal species with different methodologies, so this could be an artefact of various experimental factors. Lewis and Miall (2009) performed experiments collecting duration judgements from human participants across a similar range of durations to Gibbon (1977), finding some suggestion of a difference in Weber fractions between durations of less than and greater than 3s. However, fitting the data at above and below 3s with two different regression models and comparing this to a single model for the whole data set did not produce a significantly better fit, indicating that this difference is not necessarily due to separate mechanisms. While there may be separate mechanisms for different durations, they do not show differences in Weber fractions.

One other result of Lewis and Miall (2009) is that Weber fractions are not constant but instead are inversely proportional to perceived event duration. Other studies find that the scalar property does not hold for shorter durations of less than 0.3s (Wearden, Edwards, Fakhri, & Percival, 1998) or that Weber fractions decrease initially, then increase with duration (Bizo, Chu, Sanabria, & Killeen, 2006) or increase with duration (Grondin, 2010b). As Weber’s law traditionally provides the basis for SET and internal clock models these findings poses significant theoretical challenges. It is possible to accommodate some of these results without modifications, for example Bizo et al., (2006) and Wearden et al., (1998) could be interpreted to show a breakdown of Weber's law at extremes where the internal clock mechanisms are not capable of consistent measurement. The Lewis and Miall (2009) claim is more difficult to explain, especially given their result is a conceptual replication of Gibbon (1977) in humans as opposed to animals with a cleaner, less variable dataset, though they may simply show a difference between human and other animals' perception of time. This is a problem for those who support SET as common, cross species timing mechanism. Staddon and Higa (1999) argue this has long been a problem for the internal clock model, as its use of a Poisson pacemaker, where there is variation in the exact time each clock 'tick' occurs, does not explain the scalar property of time. Over increasing durations, the noise would cancel out, leading to a decrease in the Weber fraction with duration, which is observed by Lewis and Miall (2009). Church (1999) states the Poisson pacemaker's noise is not responsible for the scalar property and suggests it is a strength of the model, as it does not require a pacemaker with a specific tick output distribution. The subject of pacemaker noise and the scalar property is noted in Church and Gibbon (1982), who instead explain the scalar property as resulting from drift in the mean clock rate, creating trial-by-trial variability. While originally used as a fundamental property of time perception and clock models, there is considerable evidence suggesting that SET does not always hold. Instead, it depends on various aspects of the environment and experimental task, which casts doubt on the claim that the scalar property of timing is fundamental aspect of time perception, thus undermines one of the original foundations of central clock models (Gibbon, 1977). This was addressed by Church and Gibbon (1982) with the use of a Poisson timer with the presence or absence of clock-rate drift, which means the pacemaker-accumulator model can be made to follow or not follow the scalar property depending on the particular variables used, so does account for occasions where the scalar property is not observed in behaviour. Therefore, it is not possible to falsify this model based upon the scalar property of timing so the lack of consistency in measuring the scalar property is not fatal for clock models in itself but cannot be used to support them either.

1.2.4. NEUROPHYSIOLOGICAL EVIDENCE FOR CENTRALISED TIMING

One clear prediction from internal clock models is that timing is a centralised process and therefore it should be possible to localise brain areas responsible for time perception. Initial work suggests the cerebellum as a key structure in temporal perception (Ivry, Spencer, Zelaznik, & Diedrichsen, 2002) as patients with cerebellar lesions or other cerebellar atrophy have difficulty in timing actions with short (<1s) (Ivry, 1996; Ivry & Keele, 1989) and longer (400ms to 4s) delays (Mangels, Ivry, & Shimizu, 1998). Neuroimaging experiments also show cerebellar activation in an interval comparison task (Jueptner et al., 1995; Mathiak, Hertrich, Grodd, & Ackermann, 2004). The extent to which timing is associated centrally with the cerebellum has been debated (Harrington, Lee, Boyd, Rapcsak, & Knight, 2004; Ivry & Spencer, 2004) and numerous studies show that multiple areas are associated with interval timing.

Single cell electrophysiology shows an increase in spike rate in anticipation of an event in macaque LIP (Janssen & Shadlen, 2005), cells in motor and premotor areas show estimation of temporal intervals before performing an action (Lebedev, O'Doherty & Nicolelis, 2008). Cells in prefrontal cortex also show temporal properties, with time interval related activity (Constantinidis, Williams, & Goldman-Rakic, 2002). There is also evidence from neuroimaging; Coull, Vidal, Nazarian, and Macar (2004) and Macar, Coull, and Vidal (2006) show BOLD increases in a number of areas with increasing attention to time, including pre-supplementary motor and right frontal areas, making up a corticostriatal network. Frontal areas also show activity related to timing, as does the striatum and thalamus (Hinton & Meck, 2004).

With this literature, there appears to be a shift away from the proposal that timing is solely a function of the cerebellum. However, one issue, particularly with neuroimaging studies showing large networks as being involved in timing is that it is difficult to separate brain areas that are involved in other processes such as attention, decision making and memory, which are required in time perception tasks, from those that may be involved in pure time perception. During a time perception task in a study

Rao, Mayer and Harrington (2001) examine the BOLD time course to separate out the roles of different brain areas in interval timing. Early onset of BOLD activation in basal ganglia, right inferior parietal cortex and bilateral premotor cortex is claimed to indicate these regions are active in time perception, while later activation of the cerebellum during interval timing tasks implies its involvement in non-timing tasks such as movement planning and execution. Late activity in right dorsolateral prefrontal cortex in a duration comparison task and not a pitch comparison task suggests its involvement in time interval comparisons. Another fMRI study (Livesey, Wall, & Smith, 2007) aims to isolate areas purely responsible for timing. This is performed by comparing BOLD response between a hard and easy timing task to remove those areas more involved with other processes such as attention and memory as the harder task places greater demands on such functions. Results show small areas of the supramarginal gyrus, the confluence of the inferior frontal gyrus and anterior insula as well as the putamen in the basal ganglia to have significant BOLD response in both tasks. So, a much smaller number of areas are revealed as responsible for pure timing than in some of the previous studies. However, the role of the anterior insular may be acting as a decision maker rather than directly involved in timing (Kosillo & Smith, 2010).

Of particular interest in Livesey et al., (2007) and Rao et al., (2001) is the inclusion of activations in basal ganglia, which is theorised as having a crucial role in timing tasks (Nenadic et al., 2003). Parkinson's patients have also been identified as a special population that show deficits in time perception (Harrington, Haaland, & Hermanowitz, 1998). The pathology of Parkinson's disease involves reduction in the production of dopamine in areas of the midbrain including the basal ganglia (Bernheimer, Birkmayer, Hornykiewicz, Jellinger, & Seitelberger, 1973). It has been proposed that the dopamergic system has a role in time perception (Rammsayer, 1999). GABA is another neurotransmitter that may influence timing (Meck, 1996) as GABAergic neurons influence timing and pattern of cell firing in the neostratium (Tepper & Bolam, 2004), which includes the putamen. Other research has identified correlations with increased GABA in visual cortex and underestimation of duration in sub-second interval time perception

(Terhune, Russo, Near, Stagg, & Cohen Kadosh, 2014). This evidence may seem to suggest that the basal ganglia performs central timing functions. However, one proposed role of the basal ganglia is its involvement in executive function and decision-making (Hazy, Frank, & O'Reilly, 2007; Packard & Knowlton, 2002). Therefore, a non-centralised view of timing is that the basal ganglia integrates information from multiple systems that are involved in a timing task as part of the decision making process. The fact that areas within the basal ganglia often appear to be activated in time perception task and not other areas can be explained as, depending on factors such as the task and modality, different information from different brain areas and networks is used to make decisions and guide behaviour. For example for longer durations (several seconds and longer), frontal and prefrontal areas involved in working memory are activated (Hinton & Meck, 2004) and tasks that require orientation of attention in time show activity in parietal and pre-motor areas (Coull, 2004; Coull et al., 2004; Macar et al., 2006).

While there has been considerable progress in identifying areas and neurotransmitters involved in time perception and data showing individual neurons responding to elapsed time in different areas, the consensus of this research is that there are multiple areas and systems involved in time perception. The underlying theme of these results suggests the use of multiple functions including attention, working memory, motor planning and perceptual systems in timing, implying that duration perception is not processed by a single, centralised mechanism but involves functions that are performed across networks in the brain. Thus, this research shows a shift away from centralised explanations of timing. Though there are some caveats to this argued by Ivry and Schlerf (2008) who claim non-centralised models have difficulty explaining cross-modal transfer, for which there is some evidence. For example, participants show improvements in timing action when trained using a perceptual timing task that lack a time critical motor component (Meegan, Aslin, & Jacobs, 2000). Central clock models have proven to be a powerful tool in conceptualisation of results, particularly in behavioural measures, of time perception but there is little evidence supporting a single, central area acting as a timer that one would expect in a strict interpretation of the internal clock models previously discussed.

1.2.5. CONCEPTUAL ISSUES IN INVESTIGATING THE PERCEPTION OF TIME

An implicit assumption of centralised timing mechanisms, whether an internal clock or other model, is that they take a Cartesian approach to the problem of conscious perception. This can be understood using the Cartesian theatre analogy. All sensory information is projected on a screen in a theatre where there sits a homunculus observing the screen and perception is considered to be what the homunculus sees. This does not solve the problem of perception, it just shifts the question to how does the homunculus perceive? Thus, this explanation creates an infinite regress. The central clock implies that there is a central reference point for the perception of time so acts as the homunculus in the theatre. It may be argued that the central clock does not imply an infinite regress as it attempts to describe the mechanism, thus provides some explanation of the perception of time, taking a weaker Cartesian stance, but does not remove the concept of a perceptual ‘end’.

However, another problem remains; in sensory systems, there is a divergence in processing. Different sensory properties are processed in increasingly separate areas and it is not clear where these converge, which is a problem for centralised models of timing that would require such a convergence. It might be tempting to think that a distributed view of timing would automatically avoid some of the pitfalls here. While not referring directly to time perception, one example of an explanation that attempts to explain sensory perception using a distributed sensory system is provided by Zeki (2003) and Zeki and Bartels (1999). They use the concept of micro-conciousness, where each property is encoded separately in a distinct area and each area produces its own independent conscious awareness of the property being encoded. Each individual micro-conscious area is distributed in time as well as space so some visual properties are processed faster and perceived sooner than others are. This means visual properties are not represented according to a centralised process. While this argument can make a convincing case without automatically assuming that there is a single, unified conscious 'process' within the brain, in attempting to explain consciousness, it makes the same pitfalls as centralised explanations. It does not explain what consciousness is, just that it is made up of smaller, localised micro-consciousnesses, which begs the question, what makes these, micro-conscious? Is each micro-conscious made up of yet smaller nano-consciousnesses, and so on? Clearly, this does not get around the problem of infinite regression. That different micro-consciousness process properties which reach awareness at different times is also a problem, it implies a final end-point for perception, similar to the homunculus in the Cartesian theatre. It is clear these problems are not exclusive to central clock models or other centralised timing mechanisms. Therefore, it is not safe to assume that proposing a distributed scheme can get around the conceptual issues apparent in centralised timing explanations. Therefore, this needs to be a consideration when formulating alternatives to centralised mechanisms. The next section of this review will focus on results from experiments investigating the visual perception of time, which a central clock cannot explain.

1.3. PERCEPTION OF SHORT DURATIONS IN THE VISUAL SYSTEM

1.3.1. EFFECTS OF ADAPTATION ON VISUAL DURATION

In the previous sections an event related clock model of visual timing, proposed to account for results in visual experiments showing faster moving objects are perceived to last longer (Brown, 1995), was described. Kanai et al., (2006) show that this duration expansion effect is due to increased temporal frequency of the stimulus. An event related clock accounts for these findings as the tick rate increases in response to a more rapidly changing stimulus, effectively increasing temporal resolution of the visual system allowing for more precise temporal precepts. However, results from Johnston, Arnold, and Nishida (2006) demonstrate a decoupling of temporal frequency adaptation and perceived duration. They show 20Hz adaptation reduces the perceived duration and temporal frequency (TF) of a grating stimulus but 5Hz adaptation increases perceived temporal frequency, but does not cause an increase in perceived duration, which the event related model would predict if the tick rate were dependent on perceived temporal frequency. The fact that the adaptor may attract attention cannot explain the effect either, as attending to a stimulus generally results in it being perceived as longer (Brown, 1995; Mattes & Ulrich, 1998). Further work adapting to contrast (Bruno & Johnston, 2010) and luminance (Ayhan, Bruno, Nishida, & Johnston, 2011) also suggests that the visual system does not use an event related (TF dependent) timing signal to measure duration.

The magnocellular layer in the lateral geniculate nucleus (LGN) is an area of the thalamus that makes up part of the pre-cortical visual pathway and receives input from the retina. It is sensitive to high temporal frequency and low contrast stimuli, saturating at higher contrast levels (Xu et al., 2001). Therefore, it is likely adaptation to stimuli with these properties reflects changes in the response of M-cells that make up the magnocellular layer. It is claimed (Bruno & Johnston, 2010; Johnston et al., 2006) these results provide evidence that contrast gain control in M-cells (Solomon, Peirce, Dhruv, & Lennie, 2004) plays a role in visual time perception. This is a process where adaptation to a high temporal frequency or a high contrast, transient stimulus, causes a subsequent reduction in M-cell contrast response. This results in these cells becoming more sensitive to fine changes in high contrast stimuli. As adaptation to both high temporal frequency and high contrast stimuli affects perceived duration, this implies duration is encoded in the Magnocellular layer in LGN, so duration or processes that influence duration perception are represented in the early visual system.

Further evidence shows a compression of time with stimuli presented immediately preceding or early into a long horizontal saccade (Morrone, Ross, & Burr, 2005). Saccades also elicit a suppression of the magnocellular pathway (Ross, Burr, & Morrone, 1996), which implicates a similar mechanism to that used to explain the visual adaptation findings. One other aspect of saccades is the remapping of receptive fields in LIP around saccades (Colby & Goldberg, 1999) and, as already discussed the finding that LIP neurons also appear to encode duration (Janssen & Shadlen, 2005; Leon & Shadlen, 2003). Overall, this research implicates LIP and the Magnocellular pathway in visual duration perception.

There is debate regarding the use of contrast gain in LGN M-cells as an explanation. Burr, Tozzi, and Morrone, (2007) have replicated the result of Johnston et al., (2006) but claim that when changes in perceived speed due to adaptation are factored out, there is no retinotopic, only spatiotopic adaptation. They propose that duration adaptation occurs in MT and MST, citing fMRI evidence from their own lab of spatiotopic maps in these areas (d'Avossa et al., 2007) however this finding is contentious and attempts to replicate this have not found such maps (Gardner, Merriam, Movshon, & Heeger, 2008). A counter claim from the same lab as the original fMRI study (Crespi et al., 2011) argues that visual attention is necessary for the spatial coding of visual stimuli, hence the difference in results between d'Avossa et al., (2007) and Gardner et al., (2008). The behavioural findings of spatiotopic specificity of duration adaptation in Burr et al., (2007) have also been subject to debate. Bruno, Ayhan, and Johnston, (2010) dispute the existence of a spatiotopic duration mechanism, arguing that the speed matching of stimuli in Burr et al., (2007) to show duration affects factor out in retinotopic co-ordinates does not hold up. In a reply Burr, Cicchini, Arrighi, and Morrone (2011) state that Bruno et al., (2010) do measure a spatiotopic duration compression but of a smaller magnitude than they did previously, which they put down to fewer participants and different instructions given to them. Other work previously mentioned, shows contrast adaptation (Bruno et al., 2010) and luminance (Ayhan et al., 2011) affecting duration, which both implicate retinotopic, lower level mechanisms, contrary to Burr et al., (2007). While it is possible that as parietal areas appear to encode position egocentrically/spatiotopically as lesions lead to hemispatial neglect (Driver & Mattingley, 1998) and these maps are attentionally selective, it is odd why the retinotopic effects should disappear.

A contribution of Burr et al., (2007) is to suggest that visual duration is computed across multiple stages in the hierarchy of the visual system including cortical areas which is expanded upon in further work (Morrone, Cicchini, & Burr, 2010). Experimental evidence for this view comes from Curran and Benton (2012), who use moving random dot and plaid stimuli to activate motion sensitive cells in the cortex, particularly in MT+ (Dubner & Zeki, 1971), which are directionally selective when adapting to motion (Kohn & Movshon, 2004; Krekelberg, Boynton, & van Wezel, 2006). The findings show duration adaptation only when the adaptor moves in the same direction to the adapted stimulus, demonstrating that duration perception is processed cortically as well as pre-cortically and appears to be retinotopic (Latimer, Curran & Benton, 2014). No matter, which view, retinotopic, spatiotopic/egocentric or perhaps both, depending on attention, is correct, the fact that duration perception is affected by sensory adaptation in the particular area of the visual field where the adaptor is positioned suggests that duration is encoded locally in a similar manner to other visual properties. Evidence also suggests both pre-cortical and cortical areas are involved in duration perception demonstrating that visual duration is not computed by an event-based clock at a single processing level but is instead computed across the visual hierarchy with contributions at multiple levels. The implication that the Magnocellular pathway and/or medial temporal areas are involved may broadly localise time perception to the dorsal stream (Goodale & Milner, 1992).

1.3.2. THE EFFECT OF TOP DOWN PROCESSES ON DURATION

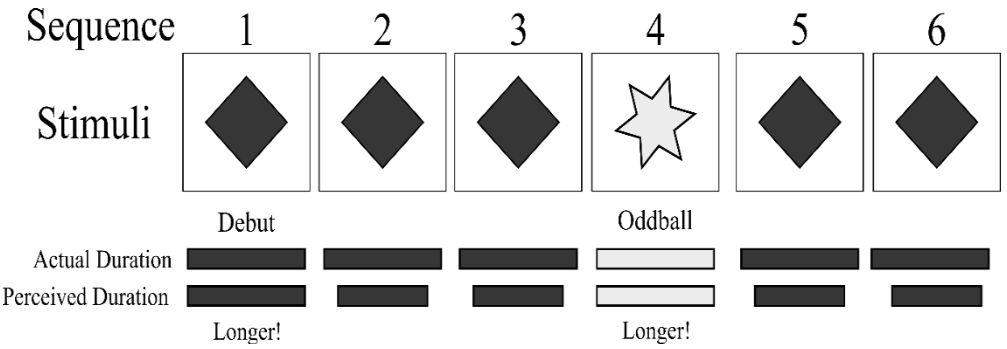


Figure 1-3: Oddball paradigm showing oddball and debut relative temporal expansion effects. All stimuli are displayed for the same amount of time, but the debut and oddball stimuli are perceived to last longer relative to the other stimuli in the sequence.

Sensory adaptation is not the only process that can influence perceived time. Other factors can play a part, for instance, highly emotional/arousing events such as falling from a tower (Stetson et al., 2007), are reported to last longer. Increases in body temperature also result in increases in perceived time (Wearden & Penton-Voak, 1995). As mentioned previously, time is reported to change with attention so that increased attention results in increases in perceived duration (Thomas & Weaver, 1975). Splitting attention between temporal and non-temporal tasks results in a decrease in perceived duration (Grondin & Macar, 1992).

One behavioural paradigm that has been shown to affect perceived duration is the oddball paradigm and is explained using cognitive mechanisms such as the effects of attention and expectation as opposed to bottom up sensory adaptation. The oddball paradigm is where the participant is presented with a succession of stimuli where one stimulus or more within the stream are unexpected, termed the ‘oddball’. One example of the oddball paradigm in vision is where a low probability ‘oddball’ stimulus appears unexpectedly in a stream of high probability stimuli. Upon each trial, a series of stimuli are presented, all of which are the same stimulus except one different or ‘oddball’ stimulus, inserted at a random position toward the middle of the series. This experimental design has a duration effect where the oddball is perceived to persist longer in vision as first reported by Rose and Summers (1995). This oddball duration effect is illustrated in Figure 1-3 along with the debut effect, where the first stimulus in a series is perceived to last for a longer duration (Pariyadath & Eagleman, 2012).

Tse et al., (2004) show that the oddball stimulus appears to persist in vision for approximately 10% longer than the expected stimulus, where the actual stimulus duration is greater than 120ms. This effect is consistent for oddballs defined by different visual properties such as colour, shape and velocity and holds for auditory tones. Tse et al., (2004) explain the effect in terms of a central clock in that attention increases the tick rate of an internal clock, resulting in a perceived increase in subjective time (Treisman et al., 1990). Tse et al., (2004) also claim that the lag between offset and attentional orientation explains why this effect does not apply to stimuli of durations shorter than 120ms as this is not enough time to direct attention to the stimulus. Pariyadath and Eagleman, (2007) expand upon this finding, showing that time does not expand during stimulus presentation of an oddball in all aspects. When an auditory tone is played at the same time as the oddball, participants do not report the tone to have a lower frequency. The same result was found when the visual stimulus was made to flicker at 10Hz, there was no change in the temporal frequency of the perceived flicker, meaning the temporal expansion effect is one of duration alone and does not carry over to rate-of-change judgements. As the effect does not carry across different judgements, this suggests the internal clock mechanism can only be used for duration judgements, not rate-of-change. Another test of the internal clock model carried out by Pariyadath and Eagleman (2007) uses oddball stimuli with increased emotional salience, comparing these to emotionally neutral stimuli. Treisman et al., (1990) claim the internal clock rate increases with arousal and attention, predicting a difference in oddball temporal expansion effects between stimuli of differing emotional salience as these would increase either arousal, attention or both. No effect is found by Pariyadath and Eagleman (2007). Thus they suggest instead that the effect is driven by stimulus unpredictability; hypothesising that perceived duration is inversely proportional to the predictability of the stimulus.

Pariyadath and Eagleman (2007) reinforce this idea by showing that the first stimulus in a sequence of identical images also shows an oddball effect and by showing one of three different numerical sequences; where the same number is repeated (e.g. 1,1,1,1,1), an incremental sequence (e.g. 1,2,3,4,5) and a scrambled sequence (e.g. 1,4,2,5,3). They find an oddball effect with both the sequential and repeated presentations but not the scrambled, demonstrating that a sequence of visually dissimilar stimuli related by only abstract properties exhibits temporal expansion when expectations are violated. This result is backed up by a further study (Schindel, Rowlands & Arnold, 2011)that uses Troxler fading; a gradual reduction in perceived brightness of a persistent visual stimulus caused by low-level neural adaptation (Martinez-Conde, Macknik, & Hubel, 2004). It shows that the oddball is always perceived as brighter than the standard, no matter which eye it is presented to and the effect is stronger when shown in different eyes for both repeated and persistent initial presentations of the standard. If temporal expansion is caused by low-level adaptation, the same underlying mechanism that causes Troxler fading, then the oddball temporal expansion effect should exhibit a similar pattern to perceived brightness. However, it does not. Temporal expansion only occurs with flickering (i.e. a stimulus repeated over time), not persistent initial presentation of the standard and there is no significant difference depending on eye of presentation. This provides clear behavioural evidence disassociating oddball temporal expansion effects from low-level adaptation mechanisms, clearly showing that the oddball temporal expansion effect is separate to the effects of adaptation described in section 1.3.1. Pariyadath and Eagleman (2012) show that the temporal expansion of the oddball is influenced by the number of repetitions and the difference in orientation between the standard and oddball that scales in a way that was consistent with a predication error signal.

The consensus is that the subjective temporal expansion observed in the oddball effect is not a result of sensory adaptation but one of top down cognitive processes of attention (Tse et al., 2004) or expectation (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012; Schindel et al., 2011).

It is also argued (Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012) that the duration expansion of unexpected events is directly related to neural suppression. This is observed as a decrease in ERP magnitude in EEG experiments (Pazo-Alvarez, Cadaveira, & Amenedo, 2003) and when using fMRI as a reduction in BOLD signal (Grill-Spector, Henson, & Martin, 2006; Larsson & Smith. 2012) on subsequent presentations of a stimulus relative to the initial presentation. This may provide a way of linking duration perception directly to neurophysiology, which in turn could provide insight into the neural mechanism behind duration perception. This work is of particular relevance as predictability takes a central role in some recent theories of brain function (e.g. Friston, 2010), which claim that the brain optimises encoding based upon an internal model so that events predicted by the internal model beforehand are encoded more efficiently. This avenue of research may then provide a way to link duration effects, neural suppression and more general theories of brain function.

1.4. DOES DURATION PERCEPTION HAVE OTHER FUNCTIONS?

The previous sections cover a range of literature on time perception representing the current ‘state-of-the-art’ on the topic. An influential model of time perception is the central clock model with its foundations in the scalar property of timing. However, the scalar property does not appear to be as hard a rule as first thought and there is little neurophysiological evidence for a centralised timing mechanism. Instead, there appears to be a wider distributed network of timing. Focusing more on visual perception of time over shorter (generally sub-second) durations, clock models do not appear to account for low-level adaptation effects nor higher-level expectation effects. This leaves a significant gap in knowledge on time perception in explaining why the sensory perception of time is altered by adaptation to particular visual properties and expectation, what mechanisms are behind the time sense and what the neurophysiological correlates of time perception are. The focus will now shift to examine the research questions that arise from this body of research and the specific literature surrounding them, as they will make the focus of this thesis.

We have seen that sub-second durations are susceptible to distortions, so a question arising from this is why do these distortions exist? A good starting point for any such question is to examine the possible evolutionary advantages of such distortions. So how does the inclusion of a mechanism coding duration in the perceptual system assist an organism's survival? When an organism perceives an object in the world, the information the perceptual system gathers needs to be useful in inferring its effect on the organism's survival. So such questions as, 'Is the object a threat?', 'A food source?', 'A potential mate?', 'Another organism I can co-operate with?' and so on are the type that the organism needs answering. It is important for the perceptual system to provide answers to these questions. So how does time perception fit into this? While implicit time in motion is useful, motion perception does not rely on explicit measures of space or time. Two flashes, separated in space and time but at too small a distance or timing difference to be distinguished, are perceived as a single moving object (Exner, 1875). The key conclusion from adaptation studies on duration perception (Section 1.3.1) is there are separate mechanisms for temporal frequency, which involves an implicit, not an explicit measure of duration, and time. What the explicit measure does is inform how long an object has been present in the visual field and it is not immediately clear how this would be of benefit behaviourally.

Therefore, from a purely perceptual view an explicit measure of time is not obviously critical to survival. One hypothesis is that the duration mechanism has 'piggy backed' onto other mechanisms to give a crude estimate on the few occasions where it is required. The estimates produced by such a mechanism distort easily when neurons that have a primary purpose other than encoding duration are adapted. Another possibility is that other processes require a measure of duration for more survival critical features of the environment such as in the timing of action and that duration changes caused by adaptation may serve useful functions. One such possibility is that visual duration is used in timing of actions, which is explored in the following section.

1.4.1. DURATION ADAPTATION AND ANTICIPATORY ACTION TIMING

A possibility investigated by Marinovic and Arnold (2012) is that visual time perception influences precise timings required for anticipatory action. They measured the effects of fast (68.4 rpm) and slow (5.7rpm) rotating motion adaptation over five rotation circles on perceived speed and duration of a single rotation circle (34.2 rpm). They found these match the results of Johnston et al., (2006), where the faster speed shows duration and speed compression, analogous to 20Hz temporal frequency adaptation and the slower only shows speed adaptation, analogous to 5Hz temporal frequency adaptation. Further experiments show adaptation to cause mismatches between actual and perceived onset of a round object moving along a circular path. Fast speed adaptation causes the object to appear earlier in time in a position behind the actual starting point, while after slow speed adaptation, the object appears ahead of the starting position. The moving object is perceived forward or backward in time at onset after slow and fast motion adaptation respectively by approximately 50ms in both instances. Johnston et al., (2006) measure stimulus onset to be earlier after both 5 and 20Hz adaptation but this is not reported as significant. This is smaller (<20ms) than that reported by Marinovic and Arnold (2012) and the slower speed adaptation (equivalent to 5Hz adaptation) in Marinovic and Arnold (2012) has the opposite effect to the fast speed (20Hz equivalent), so the changes in onset time reported in Johnston et al., (2006) are not the same as the effect here.

To test if changes in duration map onto changes in timing of actions, a final experiment requires participants to view either a fast or slow adapting stimulus as before, then they are asked to indicate when a round object moving in a circular path, in the same area as the adapting stimulus, passes between two markers. A fast moving adapting stimulus in the same direction as the test stimulus sped anticipatory actions, whilst slow moving adaptation in the same direction slowed anticipatory action. This result is down to changes in perceived motion after adaptation but not duration, as the fast adapting stimulus causes the round object to slow down and the slower adaptor causes it to speed up. Marinovic and Arnold (2012) conclude that anticipatory action time and perceived visual duration have separate mechanisms to compute temporal measures as action timing changes in line with an increase in perceived speed but not perceived duration, showing that adaptation based duration compression is not carried over to timing of action.

Another study (Tomassini, Gori, Burr, Sandini & Morrone, 2012), claims to show that duration compression of a tactile stimulus caused by adaptation to tactile motion disappears when participants make voluntary movements, suggesting that actions reset temporal biases induced by adaptation, which might be applicable to Marinovic and Arnold, (2012). This does not provide evidence that duration adaptation does not affect other mechanisms beyond the perception of duration itself, thus does not provide any insight into why adaptation to particular visual properties changes perceived duration. However, it does add further evidence against central clock models, as with a central, multimodal timer, distortions should be common across different modalities.

1.5. MIGHT DURATION COMPRESSION CAUSED BY ADAPTATION AFFECT VISUAL PROCESSES?

If there is no effect on action timing, perhaps duration is used in mechanisms processing visual properties. This might also explain why adaptation to particular visual properties changes perceived duration as these changes might prove advantageous in creating a more informative percept of the environment. Such a process must be reasonably robust and have a temporal dependence. The Flash-Lag illusion, discovered by Mackay (1958), later rediscovered and quantified by Nijhawan (1994) is characterized by an erroneous perception of a moving object's spatial position at the time of a brief visual event such as a flash. As such, it gives insight into mechanisms responsible for the perception of space and motion and their interactions. This erroneously perceived displacement increases with the moving object's speed linearly within a certain range (Nijhawan, 1994; Wojtach, Sung, Truong, & Purves, 2008). Dividing distance by speed gives a measurement of time, in the Flash-Lag illusion this temporal component is consistently measured at around 80ms and is fairly robust

(Durant & Johnston, 2004). So why does this effect exist? In the visual system, there is a delay of about 100ms between photons hitting the retina and perceptual awareness of the object reflecting the photons. Encoding and transmitting information about the object causes this delay (Nijhawan, 2002). This presents the visual system with a problem if the object in question is moving as it moved to a new location in the world by the time the brain perceives it. This error is significant; for an object that is moving at a velocity of 20mph (~ $9ms^{-1}$) the error will be 90cm. As this is plainly not the case otherwise, actions like catching a ball would be impossible, the visual system must then have mechanisms to compensate for these perceptual errors. The Flash-Lag illusion can be interpreted in terms of such mechanisms and as it appears to be an illusion with a temporal component, it gives insight as to how estimates of time might be used in visual system.

1.5.1. WHAT CAUSES THE FLASH-LAG ILLUSION?

There are a number of explanations for the Flash-Lag illusion, Nijhawan (1994) hypothesized that the erroneous offset in the Flash-Lag illusion is caused by motion extrapolation in the visual system. At the time of the flash the position of the moving object is extrapolated ahead in space, so what is perceived is a prediction of where the object is, not its physical position. Later, it was observed that motion after the flash, not before, generates the Flash-Lag illusion (Whitney & Murakami, 1998; Brenner & Smeets, 2000), debunking this, though alternative extrapolation models have been proposed (Khoei, Perrinet, & Masson, 2014) that account for this.

Whitney and Murakami (1998) argue that each visual property (motion, colour etc.) has its own, largely autonomous and independent process for perception (Zeki & Bartels, 1998) in a ‘race to awareness’. So the percept that arrives first is perceived to happen the earliest, in the case of Flash-Lag motion is processed faster than the flash. This latency difference explanation hinges upon a regress to a point of awareness at the process’ end-point, where the exact mechanism of racing to consciousness is left unexplained as discussed in Section 1.2.5.

Krekelberg and Lappe (2000a) explain the Flash-Lag illusion as a positional averaging error, where the moving object’s position at the time of the flash is computed by integrating position over a temporal window after the time of the flash. So the moving object's perceived position is shifted along its motion trajectory.

Eagleman and Sejnowski (2000) argue for a postdictive explanation of Flash-Lag whereby, the unexpected appearance of the flash causes the visual system to reset its predictions about visual objects. The perceived relative position of the moving object compared to the flash is computed using information about the moving object after the event, the appearance of a flash, to calculate what happened in the immediate past. This causes a shift in perceived position of the moving object, in a similar manner to the integration explanation.

Each explanation uses time in some manner to explain the Flash-Lag effect, with either a temporal window (motion integration and postdiction), difference in processing time (latency delay), or predicting forward in time (extrapolation).

1.6. USING FLASH-LAG TO FIND A FUNCTIONAL ROLE FOR EXPLICIT DURATION

There is little consensus as to the mechanism behind the Flash-Lag illusion (e.g. Eagleman & Sejnowski, 2007; Krekelberg & Lappe, 2000b; Patel, Ogmen, Bedell, & Sampath, 2000). However, one thing is clear. Each explanation (extrapolation, attentional shift, latency delay, integration) all agree that there is a temporal component of Flash-Lag. This is either the amount of time the bar is predicted forward in time, the amount of time taken to shift attention from one object to another, a difference in processing time of the two objects or a temporal window after the flash where the position is averaged in extrapolation, attentional shift, latency delay, integration respectively. This means if an adaptor, known to compress duration (e.g. 20Hz flicker), is presented before showing the Flash-Lag stimulus, this might have an effect on the time component of the Flash-Lag illusion.

The obvious prediction from the literature would be that the Flash-Lag time component would shrink in line with the duration compression effects (Bruno & Johnston, 2010; Burr et al., 2007; Curran & Benton, 2012b;

Johnston et al., 2006). However, the position of a moving object has been reported to shift along its trajectory after 20Hz adaptation (Hogendoorn, Verstraten, & Johnston, 2010) so any effect of duration on Flash-Lag is not clear-cut. Evidence showing that a measure of duration is responsible for changing the Flash-Lag illusion would implicate explicit duration coding in motion and position computations within the visual system. This would show explicit duration estimation has a functional role outside of pure duration perception measures and must be encoded explicitly in the visual system. The next step would be to investigate how duration might be encoded in the visual system.

1.7. FURTHER MODELS OF DURATION PERCEPTION

As the previous sections describe, there is a general trend in time perception research that indicates event duration is not computed by centralised clock mechanisms but is instead computed using a wide network of brain areas and represented in sensory systems alongside other visual properties across multiple stages in the their hierarchy. As such duration as computed in sensory systems is influenced by the stimulus properties (Alards-Tomalin et al., 2014) and functions such as adaptation (Johnston et al., 2006), attention (Mattes & Ulrich, 1998) and expectation (Pariyadath & Eagleman, 2007). Other models of duration perception have been proposed based upon this idea that duration is encoded as an emergent property of processing in sensory systems. Two of the more influential are the neural energy hypothesis (Eagleman & Pariyadath, 2009), whereby subjective time is encoded within one or more components of neural activity that correlate with perceived duration of an event and the use of state dependent networks to encode duration (Buonomano & Maass, 2009; Karmarkar & Buonomano, 2007). Each of which shall now be discussed in more detail.

1.7.1. NEURAL ENERGY

Arising from research on oddball durations (section 1.3.2), where an unexpected stimulus is perceived to last longer, and evidence showing a reduction in neurophysiological activity associated with expected versus unexpected events influenced the proposal made by (Eagleman & Pariyadath, 2009) that duration is encoded by the amount of neural activity associated with an particular event. Time, encoded in this way can be represented at any point in the visual system where a representation of a stimulus exists thus is encoded at multiple stages in the processing hierarchy. Such a framework aims to explain changes in perceived time caused by adaptation, as perceptual adaptation can broadly be considered to cause reductions in the firing rates of neural populations encoding a particular stimulus property.

The neural energy hypothesis can also explain other effects of time perception, such as the shortest duration required between two flashes to perceived them as separate is larger than flicker fusion threshold in a stream of flashes (Herrick, 1974). This can be considered a manifestation of the oddball duration effect. As each individual flash in a stream is predictable, the duration of the flash in a sequence is reduced, leaving a larger perceived gap between them to make the separate flashes in a stream more easily discernible. The first flash in a pair of flashes does not exhibit a perceived reduction in each flash's duration, as no expectation is created, so no reduction in perceived flash duration occurs.

Other effects are explained in a similar manner to flicker fusion. These include the time shrinking effect, where a second stimulus is perceived to be shorter in duration than the first (Nakajima, Ten Hoopen, Hilkhuysen, & Sasaki, 1992), where the appearance of the first stimulus creates an expectation so the perceived duration of the second stimulus is reduced, similar to the debut effect in Pariyadath and Eagleman, (2007). The stopped clock illusion; where a second hand of a clock is perceived to linger longer than subsequent ticks (Yarrow, Haggard, Heal, Brown, & Rothwell, 2001), is also suggested as similar as the first 'tick' is perceived to last longer. Increases in magnitude of perceptual properties such as size, brightness and numerosity are claimed by Eagleman and Pariyadath (2009) to correlate positively with perceived duration and result in increased neural activity.

It has also been proposed that the properties of time, space and number are encoded using a common magnitude mechanism (Walsh, 2003) where magnitude is represented in the parietal cortex (Bueti & Walsh, 2009). This would help explain why properties such as time, size, brightness etc. would influence perception of each other. As Eagleman and Pariyadath, (2009) state, currently neural energy hypothesis has not yet been expressed as a formal model nor has a specific foundation in neurophysiology and as such needs further work to develop the hypothesis.

1.7.2. STATE DEPENDENT NETWORKS

It has been proposed that temporal information can be encoded intrinsically in recurrent neural networks that exist everywhere in the brain, where the interconnectivity between the neurons in such a network means the response of the network to a particular input evolves over time (Buonomano & Merzenich, 1995). In such a network properties that change in response to the stimulus (e.g. spike rate), provide variables to encode information. Each variable is represented as a single dimension that combine to make up a multidimensional space where a single point within this space represents the combined state of each variable within the network. This network state is used to encode information. For example, there is one point in the network space that encodes input X and another for input Y so the network is able to discriminate between two types of input. The importance of the theory described in Buonomano and Merzenich (1995) is that they show a neural network made up of integrate and fire model neurons can discriminate between different durations separating two inputs i.e. there is a network state that encodes input X followed by input X 100ms later and another where input X happens 200ms after the original. State dependent networks have been proposed as a general timing mechanism (Buonomano & Maass, 2009; Karmarkar & Buonomano, 2007).

An important property of these state dependent networks is the inability for the network to switch instantly to its default resting state as, by their nature, they rely on the temporal dynamics of the network to encode duration. This dependence on the initial state of the network prior to any input to code duration places limitations on this method of encoding time. Buonomano and Maass (2009) and Karmarkar and Buonomano (2007) show that this property is reflected in behaviour by demonstrating that the presence of a distractor appearing at unpredictable times increases variability in interval discrimination which does not occur when the distractor appears at a predictable time. This is predicted by state dependent network models as a distractor acts as additional input into the network and would therefore change the network state. In cases where the distractor appears at the same time, the state of the network changes in the same way every time, therefore the duration encoded is internally consistent. With an unpredictable distractor the network state alters differently upon each trial, therefore duration comparisons are less consistent. This property may also explain adaptation effects described in Section 1.3.1. The adapting stimulus changes the way a population of neurons responds to subsequent stimuli, affecting the state of the network and thus, perceived duration. In fact, any mechanism that changes how neurons respond to stimuli, such as attention, expectation and even the exact properties of the stimuli themselves could potentially affect perceived duration, so it is plausible that state dependent networks could be used to explain duration effects discussed in Section 1.3.

State dependent models are a computationally efficient way of encoding duration within local networks of neurons responding to the same stimulus property in sensory systems and provide an intriguing alternative to central clock models. One problem is that computationally, they are almost too good. It may be possible, with sufficient training and optimisation of network parameters for state dependent networks to extract information about almost any property of the stimulus. Therefore, it may be difficult to falsify them, beyond the lack of an instant reset previously discussed. The fact that an unpredictable distractor increases variability in interval discrimination highlights a vulnerability in this type of encoding scheme as it demonstrates state dependent networks are sensitive to variations in input i.e. noise. Since noise exists at every level in sensory systems (Faisal et al., 2008), this presents a serious limitation in these models, though this may be overcome with future modifications to the model.

1.7.3. A PREDICT AND COMPARE CLOCK

Internal clocks (Gibbon, 1977; Gibbon et al., 1984; Treisman et al., 1990; Wearden, 1991) and event related clocks (Kanai et al., 2006) cannot explain the adaptation effects on perceived time described in Section 1.3.1. These adaptation effects implicate early visual mechanisms in the magnocellular pathway (Solomon et al., 2004). Johnston (2010) proposed a content dependent clock based upon the temporal filter properties of early visual neurons (Hess & Snowden, 1992; Johnston & Clifford, 1995) which contains at least two, possibly three temporal filter channels, one low pass and one or two band pass filters. Johnston (2010) describes how these filters can be used to predict the luminance of the current stimulus either backward or forward in time. A clock can be built by storing a forward prediction in time then cross correlating the stored component with the current visual input. When the cross correlation output peaks, this produces a 'tick', the ticks are counted by an accumulator to get a measure of duration. Adapting the band pass filter which peaks at around 15-20Hz using a 20Hz flickering adaptor Johnston et al., (2006) induces a phase shift in the output of the band-pass filter, equivalent in the model to magnocellular output (Benardete & Kaplan, 1999). This has the effect of shifting the forward prediction further along in time meaning it takes longer for the cross correlation between the predicted and current visual input to peak, leading a longer duration between each tick. Fewer ticks mean a shorter perceived duration, thus demonstrating how selectively adapting the magnocellular pathway might affect perceived duration.

There are some unresolved stages in this model, such has how the forward prediction is stored, how the cross correlation peak is detected and where in the visual system these processes might be performed. This model does show how a clock mechanism can be built on top of other mechanisms and how adapting these mechanisms might change the functioning of a clock. Johnston (2010) also states that this type of predict and compare clock mechanism can exist outside the early visual system using other mechanisms, so forms the basis for a distributed view of timing throughout the brain. As this makes use of predictive mechanisms, this means that prediction/expectation and time may be inseparably linked in the brain.

1.8. A POSSIBLE NEUROPHYSIOLOGICAL SIGNATURE OF DURATION IN VISION

Pariyadath and Eagleman (2012) argue that the temporal expansion of unpredictable events is related to the repetition suppression of BOLD signal, thus supporting the neural energy hypothesis - where subjective event time is represented in the brain by the amount of neural activity associated with a particular event. There are several proposed causes of repetition suppression. Fatigue: where neurons responsive to a stimulus monotonically reduce their response upon repeated presentations of the stimulus. Sharpening: where the neurons most responsive to a stimulus retain their response on repeated presentations but those moderately responsive become less so. Facilitation: neurons respond faster to stimulus repetitions initially producing a strong response that quickly reduces compared to the initial stimulus presentation. BOLD response has a temporal resolution of seconds, so it gives an average of neural response that, over time, is reduced for repeated stimuli. Both fatigue and sharpening are bottom-up processes that facilitate metabolically and computationally efficient processing, while facilitation is often framed in terms of predictive coding with the neuronal firing rate representing an error signal: the difference between bottom-up sensory input and top-down expectations. As repeated stimuli are expected, top down signals effectively cancel bottom up input (Grill-Spector et al., 2006).

The hierarchical organisation of sensory systems with recurrent top-down feedback to lower levels lends itself well to processes like facilitation listed here. Bottom up sensory signal from sense organs provide a driving input. At various stages in the hierarchy, the sensory signal is subject to processing so various properties of the environment can be explicitly represented within the system. These representations can be used to make predictions about future sensory input, which are fed back to lower levels in the hierarchy. One role of these lower stages is to compute the error between the prediction from higher levels and the sensory input, which is fed forward to the higher levels. This error signal is used to update the representation of the world, so increasingly accurate predictions can be made in future.

This process is formalised using empirical Bayes (Friston, 2005) and has been referred to as the free energy principle. The central claim regarding this is that one important, if not the most important role of neural systems is to construct accurate representations of the environment that minimise the amount of ‘free energy’, defined as the upper bound for the surprise (negative log probability), and so free energy can be considered the prediction error within the system (Friston, 2009, 2010). In summary, there are multiple viable theoretical explanations for repetition suppression positing both top-down and bottom-up mechanisms.

Summerfield et al., (2008) investigate the nature of repetition suppression in an fMRI experiment, finding evidence for repetition suppression as an encoding of error signal. They present trials where two faces are shown. These faces are either two different images of the same person for (repeated trial) or images of two different people (different trial). These were shown in two separate blocks with different frequencies so that in one block repeated trials appeared more and the other different trials appeared more often. Additionally, depending on the block, the participant is cued to expect two of the same or two different faces. The BOLD signal, averaged across the fusiform face area (FFA) shows that repeated trials invoked a smaller response than different trials. In comparing BOLD response for the two trial types across blocks shows a decrease in BOLD when the trial type was expected relative to blocks where it was unexpected, showing evidence of an error signal.

Larsson and Smith (2012) conducted a follow up fMRI study inducing suppression of BOLD by fMRI adaptation as well as repetition suppression through expectation, by repeatedly showing stimuli over four seconds to act as an adaptor. Furthermore, the experiment manipulates attention using a distractor. This study shows significant suppression across multiple visual areas in both conditions where attention is manipulated but shows significantly more suppression where attention is focused compared to when attention is distracted. This implies that when attention is diverted the observed repetition suppression is a bottom-up effect, not the effect of repetition on expectation, and when participants attend to the task the repetition suppression is due to both bottom up adaptation and top down expectations, so multiple mechanisms contribute toward repetition suppression of BOLD in fMRI. This is an important finding as it shows the effect of expectation is task dependant and separable from low-level mechanisms. As the effects of stimulus specific adaptation and probability rule based expectation are separable it implies that there are at least two mechanisms that contribute to BOLD suppression, so it is possible that more than one, if not all of the mechanisms discussed by Grill-Spector et al., (2006) contribute to BOLD suppression. This has implications for the hypothesised link between repetition suppression and perceived duration: is the temporal expansion effect observed using the oddball paradigm due to bottom-up, top-down repetition suppression or both?

The research already discussed in Section 1.3.2 indicates that top down suppression created by expectations is responsible for the temporal expansion effect in oddball. If the temporal expansion effect is associated with repetition suppression it must be repetition suppression induced by perceptual expectation, not adaptation. This provides a potential link between the effects of repetition suppression induced by expectation and perceived duration which if confirmed would show a neurophysiological signature of duration. The proposed mechanism for this is facilitation, where the reduction in BOLD for repeated stimuli is a reduced error signal which is the result of perceptual expectations being met.

If it can be shown that duration is associated with repetition suppression of BOLD, it would also implicate particular predictive mechanisms in duration perception. Predictive mechanisms require a hierarchical system (Friston, 2005) with top-down feedback generating and passing down predictions as well as bottom-up sensory input. The effect of prolonged sensory input has been studied using adaptation (Section 1.3.1) effectively investigating the effect of bottom up input on perceived duration so the oddball paradigm and repetition suppression provides a method to investigate the contribution of stages further up the hierarchy and top down feedback to duration perception.

1.9. SUMMARY

Three questions have been highlighted in this review of the literature on time perception and will be investigated in this thesis. The first is do perceptual measures of duration have functional roles within the visual system? Secondly, how might neural systems encode duration? Finally, are there neurophysiological correlates of perceived duration in the visual system? Each of these questions shall require different paradigms to investigate. The functional role of duration in vision is explored using behavioural experiments using a visual adapter previously shown to compress perceived duration. A computational model is developed to show how neural systems might encode duration. The aim of this is to investigate if basic properties of neurons and neural systems can be used to encode duration in a distributed manner across sensory hierarchies and might exist in early sensory areas. Finally a study using both behavioural and fMRI experiments is performed to look for neural correlates of perceived duration. Overall, this thesis presents a multi-modal investigation of crucial questions in field of visual time perception and in particular the mechanism for encoding visual perception of time.

2. CHAPTER TWO - CONTRASTING PSYCHOPHYSICAL METHODS FOR MEASURING DIFFERENCES IN THE FLASH-LAG ILLUSION

2.1. INTRODUCTION

A central finding of Johnston et al., (2006) is that the explicit perception of duration can be adapted separately from the perception of temporal frequency (TF), which may be interpreted as an implicit duration measure. Further experiments show that perceived duration is also affected by adapting to high contrast (Bruno & Johnston, 2010), luminance (Ayhan et al., 2009) and motion (Curran & Benton, 2012; Marinovic & Arnold, 2011), so explicit duration detectors must share common mechanisms with the encoding of these visual properties. These mechanisms have been theorized to be localized in the Magnocellular pathway of LGN (Bruno & Johnston, 2010; Johnston, 2010; Johnston et al., 2006) and dependent on contrast gain adaptation in M-cells (Solomon et al., 2004). Marinovic and Arnold (2011) show that adaptation to motion, which compresses perceived duration does not change action timings, so this adaptation and the resulting change in judgments of explicit duration does not have a functional role in guiding movements.

The question asked in this and in Chapter 3 is why does explicit duration share common encoding mechanisms with these visual properties? I.e. is explicit duration used for further computations within the visual system or does it piggy back onto other mechanisms because it is not as important to have an accurate estimate of duration as other visual attributes? Perhaps, for the rare occasions when an explicit duration judgment is required, the visual system computes an estimate of duration from other visual properties thus, adaptation of these other properties also affects perceived duration.

It was decided to examine this question using an effect known as the Flash-Lag illusion. This is characterized by an illusory displacement of a moving object's position in the direction of motion relative to the position of a flash (Nijhawan, 1994). When both the flash and a moving object are aligned exactly an observer perceives them to be misaligned, with the moving object positioned further along the direction of motion than it is in reality, this is shown in Figure 2-1. Note the object is moving in a linear path as opposed to circular path or rotating, which is often the case. The reasons for this are discussed later in Section 2.3.

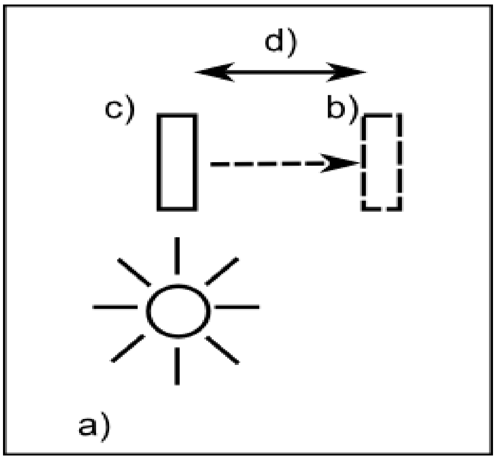


Figure 2-1: The Flash-Lag illusion. A flash (a) appears and the moving bar is perceived at (b) along the direction of motion (indicated by the arrow), when it is actually at (c) with an illusory displacement offset (d)that scales with the speed of the moving object.

The proposed mechanisms that cause Flash-Lag are fiercely debated and are discussed previously in Section 1.5.1. As each involves a temporal component, for the purposes of this study the argument over which provides the best model of the Flash-Lag Illusion is moot. The objective is to see if adaptation induced duration compression changes this time component in some way that would indicate that perceived duration is used in other visual mechanisms.

As Flash-Lag changes with object speed, it is likely that a change in perceived speed caused by TF adaptation (Hess & Snowden, 1992; Smith & Edgar, 1994) also affects the Flash-Lag illusion. Therefore, adapting to TF could change the Flash-Lag illusion irrespective of whether or not TF induced duration compression occurs, as TF adaptation changes perceived speed. It is necessary to measure the perceived change in speed in order to factor out its effect when measuring the effect of duration compression on Flash-Lag. Before conducting the experiment, it is important to show it is possible to separate the effects of adaptation on the Flash-Lag illusion, which is demonstrated in Section 2.2. The rest of this chapter will detail the methodologies used to measure the Flash-Lag illusion, first examining different stimulus designs to test that they cause the observer to perceive a Flash-Lag effect comparable to previous reports in literature. This will then lead to a comparison of psychophysical techniques for efficiently evaluating the effects of adaptation on Flash-Lag. Once a suitable methodology has been established, this will be used in Chapter 3 to measure the effect of temporal frequency adaptation on Flash-Lag.

2.2. PREDICTING EFFECTS OF TEMPORAL FREQUENCY ADAPTATION ON FLASH-LAG

Motion perception can be considered based upon two or three TF channels (Hess & Snowden, 1992; Smith & Edgar, 1994) where motion can be computed as a ratio of these channels (Smith & Edgar, 1994). Adaptation to a particular TF causes a relative reduction in sensitivity of one channel that has a repellent effect on perceived speed, so relatively faster moving objects are perceived to be even faster while slower objects are perceived to be slower still. As Flash-Lag is dependent on perceived speed of a moving object this means it is likely adaptation to TF will change the magnitude of the Flash-Lag illusion as well as any potential effects on the Flash-Lag time component.

Johnston et al., (2006) show an effect on duration after 20Hz TF adaptation only and an effect on perceived TF after both 5 and 20Hz adaptation. Since this work is based upon the duration compression effect reported by Johnston et al., (2006) it makes sense to use the same adaptation conditions. From which arise several different possible scenarios. If there is an effect at 20Hz and not 5Hz, this suggests it is change in the temporal component of Flash-Lag, not perceived speed causing the observed effect. However, this is not conclusive as the null 5Hz effect could be an artefact of TF adaptation similar to Smith and Edgar (1994) where the TF of the adaptor and adapted stimulus are closely matched so there is little adaptation. Alternatively, if there is an effect at both 5 and 20Hz adaptation on Flash-Lag this might mean there are effects of both perceived duration and perceived speed. In both cases, there needs to be a second experiment measuring the change in perceived speed so this can be factored out. If there is a significant difference in Flash-Lag after 20Hz adaptation and not 5Hz that cannot be explained by speed effects alone then this provides evidence of an effect of duration on the temporal component.

It is possible to show this quantitatively. Taking the data from Johnston et al., (2006) it is possible to estimate the perceived speed and duration effects caused by TF adaptation on Flash-Lag by distance, speed, time relationships. Here, distance relates to the Flash-Lag illusion magnitude, speed is the speed of the moving object and time is the Flash-Lag time component. The results of Johnston et al., (2006) where 5Hz adaptation increases and 20Hz adaptation reduces perceived TF (Smith & Edgar, 1994) broadly predict 5Hz adaptation should increase Flash-Lag while 20Hz adaptation reduces it, assuming Flash-Lag is dependent on perceived speed. The duration compression caused by 20Hz TF adaptation would suggest that it should shorten this time component by approximately 25% as Johnston et al., (2006) report, leading to a reduction in Flash-Lag. The alternative possibility is that the temporal component of Flash-Lag expands after adaptation, which while counterintuitive to Johnston et al., (2006), is observed as an effect of 20Hz TF adaptation on the perceived position of a moving object during a study by Hogendoorn et al., (2010).

Like speed, we can make predictions for the effect of adapting duration on Flash-Lag by using speed, distance, time equations, based on either duration compression or expansion. The time component of Flash-Lag is calculated by Distance/Speed using the same data as the speed prediction. If the effect of 20Hz adaptation on Flash-Lag is a compression of the temporal component, which reduces the Flash-Lag illusion, this is the same direction as the expected effect of the reduction in perceived speed caused by adaptation.

Therefore, the goal of this experiment is to measure the effects of 5Hz and 20Hz adaptation on Flash-Lag and perceived speed then to compare the pattern of adaptation between the two measures in the adaptation conditions and a control condition. The predicted effects of these are shown in Figure 2-2. If there were a significant deviation between the two, this would be a suggestion that 20Hz TF adaptation is changing the time component of Flash-Lag. TF adaptation has different effects on different speeds (Smith & Edgar, 1994). When adapting a particular speed using a particular TF, this might result in little change on perceived speed due to the TF of the adaptor being closely matched to the speed of the moving object. Thus, at least two speeds are required to observe a range of speed adaptations, whereas duration adaptation should remain the same.

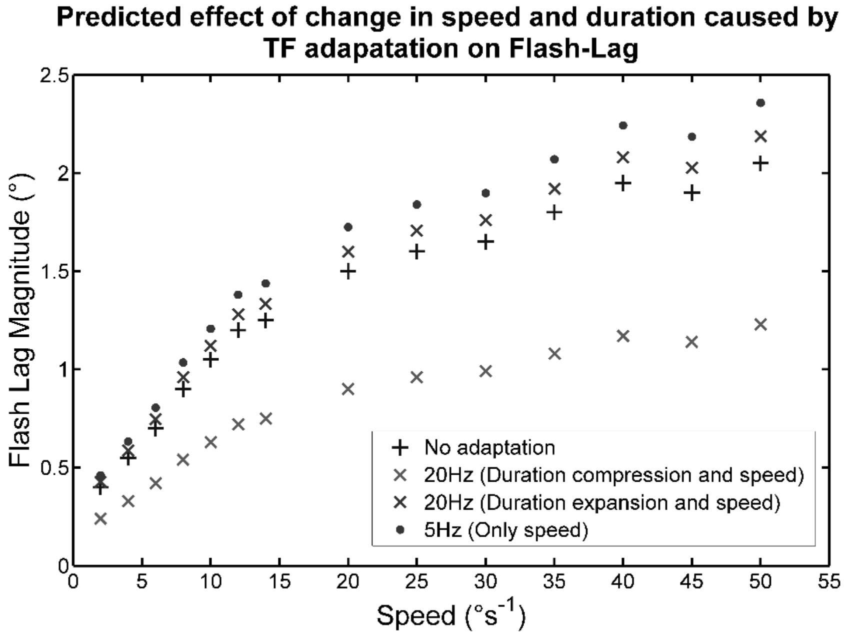


Figure 2-2: Data is taken from Wojtach et al, (2008). Predicted change in Flash-Lag caused by 5Hz and 20Hz adaptation. 5Hz adaptation is only expected to increase perceived speed of the moving bar, which should cause an increase in Flash-Lag magnitude as Flash-Lag scales with speed. 20Hz adaptation is expected to adapt speed but might adapt the time component of Flash-Lag also, causing either a compression or expansion effect.

2.3. MEASURING FLASH-LAG: STIMULUS DESIGN

The experiment requires a consistent and accurate measure of the Flash-Lag illusion so the experimental stimulus must be designed and tested to make sure it produces a consistent, and large enough illusion. The aim of the experiment is to measure change in the time component of Flash-Lag after temporal frequency adaptation by measuring the magnitude of the Flash-Lag illusion. Based upon previous work (Johnston et al., 2006), it is anticipated that should there be an effect on the time component of Flash-Lag that this will be a fractional reduction of the time component of approximately 25%. As Flash-Lag magnitude scales with speed, the faster the speed of the moving object the greater the magnitude of the Flash-Lag illusion, which would mean the larger any post-adaptation reduction of Flash-Lag would be in absolute terms. To measure a large Flash-Lag the stimulus needs to display the flash a large displacement away from the bar, so the experimental set up needs to accommodate this as well.

However, we need to take into account an implication of Weber's Law, a commonly reported property of sensory systems, that with increasing magnitude of a sensory property, errors in judgements also increase proportionally. For this experiment, it is likely there is a point where increasing speed of the moving object stops becoming helpful as the variability in participant responses will outweigh benefit from increases in the Flash-Lag magnitude for measuring any change in absolute Flash-Lag magnitude.

The Flash-Lag illusion is robust and there exists a variety of different set-ups that have been used successfully by a number of different researchers. In fact, there is evidence showing Flash-Lag is cross modal (Alias & Burr, 2003). Some examples of common stimuli include a rotating bar with the flash appearing at opposite sides of the bar, the stimulus originally used by Nijhawan (1994) and other setups using rotating stimuli, such as the annulus and disk stimuli used by Eagleman and Senjowski (2000) produce reliable Flash-Lag illusions.

These rotating stimuli do produce consistent Flash-Lag illusions and a rotating bar and flash setup was successfully used to investigate the temporal nature of the Flash-Lag illusion (Durant & Johnston, 2004). These stimuli are limited in the Flash offsets that can be shown, and the speed of the moving object is limited (in Durant & Johnston, 2004 the speed at the outermost edge was $5.7°s^{-1}$) and are not suitable for the purposes of this experiment. So which set ups are best for measuring high speed Flash-Lag? Wojtach et al (2008) use a set up with mirrors and stimuli projected using lasers for very high spatial precision to measure Flash-Lag accurately at much higher speeds than previous experiments. We do not require the full range of speeds in Wojtach et al (2008), but we will also use a linear, rather than rotating or circular bar path, this will allow a suitable range of offsets given the bar speed. The object path will be horizontal as, on a 4:3 ratio screen this is allows the longest path possible, required as we want to reduce the predictability of the flash and bar appearance points in space as predictability appears to reduce Flash-Lag magnitude (Namba & Baldo, 2004; Murakami, 2001). Similar set ups have been used before to investigate whether Flash-Lag occurs because of motion before or after the Flash (Nijhawan 2001). This set up allows for a consistent retinal speed across the length of the bar and an offset that is measured in visual distance rather than the angle of the bar. In later versions, we will see that flash and bar can be presented at the same distance from fixation. Due to the need to find the best set up that provides a large Flash-Lag effect using a high object speed that does not show too much variability, the stimulus design needs to be developed and tested before the full experiment takes place.

Another consideration for the final experiment is at least two speeds are required as TF adaptation has differing effects depending on the speed of the test object (Smith & Edgar, 1994). The possibility remains open that temporal frequency adaptation will have different effects on Flash-Lag depending on the speed of the moving object within the illusion. As discussed in Section 2.2 this could help tease apart any differing effects on the speed and the time component of Flash-Lag, so could prove useful. Or perhaps 20Hz temporal frequency adaptation, a stimulus that drives predominantly Magnocellular input (Xu et al, 2001) may have a greater, or exclusive effect on Flash-Lag using high speed stimuli that also drives Magnocellular response. The rest of this section is motivated by the need to develop a stimulus set up that can produce a reliable and consistent Flash-Lag illusion with a high speed moving object and decide upon which two (or more) speeds the final experiment will use. Once a suitable stimulus has been found it will be tested with an adaptor to check if it produces reliable pilot results with adaptation. Later on, this chapter will move on to investigating psychophysical techniques for measuring Flash-Lag and perceived speed in the most efficient, unbiased way.

2.3.1. FIXED PARAMETERS

Participants are required to fixate throughout the experiment upon a centrally positioned red circle (0.5° diameter) with a mid-grey background (63 cdm^{-2}). Each trial consisted of a white moving bar of size 0.33 x 0.66°, luminance: 124 cdm^{-2} that appeared on one side of the screen and moved horizontally toward the opposite side (path length 8°). At a point along the bar's trajectory a flash appeared (radius 0.33°, luminance: 124 cdm^{-2}, duration time 10ms/1 frame) and the participants judged if the bar was to the left or right of the flash when the flash appeared, in a two alternative forced choice design. The exact position of the flash, relative to the bar varied according to a Method of Constants (MoC) procedure, randomly chosen one each trial within a range of -1.5 to 2° with 0.5° steps. The exact appearance and disappearance position of the bar and flash position on screen was randomly jittered 1° trial to trial, so that it was impossible to predict exactly when and where the flash would appear. This setup meant that the participant could not predict in advance of onset where the flash would appear and where the bar would be in relation to the flash, while keeping the flash and bar reasonably close to central fixation. It also separates the flash and moving object in space, as opposed to an annulus and disc configuration that might lead to perceptual grouping confounds.

2.3.2. MEASURING FLASH-LAG MAGNITUDE

In this section, to measure the effect at each speed, each flash position is repeated multiple times (specified in each section), to generate a percentage judgment of where the participant perceived the bar to be relative to flash for each offset. A logistic psychometric function is fitted to these data where the 50% point is taken as the point of subjective equality (PSE), giving a measure of the illusion, whilst Section 2.4 details the use of adaptive methods to measure Flash-Lag.

2.3.3. EQUIPMENT

Stimuli were displayed on a linearized display Sony Trinitron monitor in a darkened room using a resolution of 800×600 pixels and refresh rate of 100Hz with a Cambridge Research Systems (CRS) ViSaGe system controlled by Mathworks MATLAB v7.5.0. Participants viewed stimuli with aid of a chinrest at a distance of 57cm from the screen, giving responses on a CRS CT6 remote button box with a CRS VET eye tracking system used to check fixation. Data analysis was performed using Mathworks MATLAB v7.5.0. Participants were the author and supervisor for initial piloting.

2.3.4. FIRST FLASH-LAG PILOT

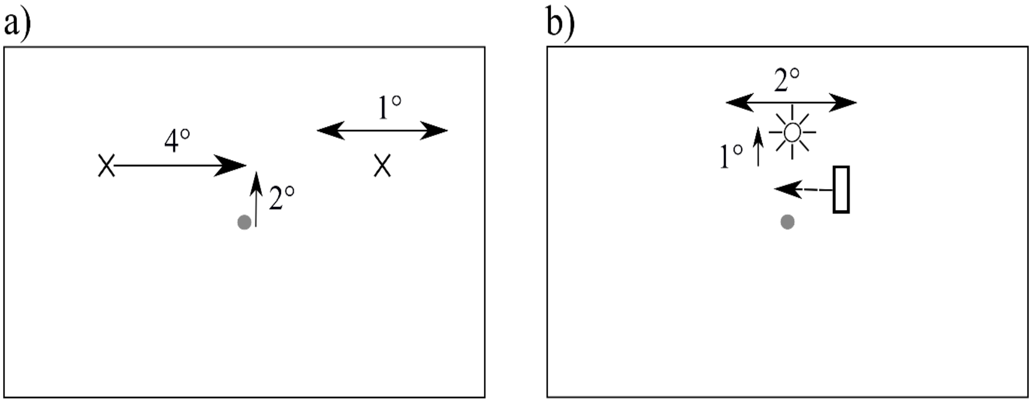


Figure 2-3: Stimuli for the first Flash-Lag pilot: a) shows central fixation and the appearance and disappearance positions (X) of the moving bar which are both jittered by 1°. B) shows the position of the flash relative to the moving bar, which is jittered by 2°.

Figure 2-3 shows a diagram of the initial pilot stimuli used. The vertical centre of the bar is 2° above the centre of fixation and the vertical centre of the flash is 2° above that of the bar. Flash-Lag was measured for two speeds: 9.1°s^{-1} and 18.2 °s^{-1}, chosen as these speeds should elicit a measurable effect (approx. 0.75° and 1.5° respectively with a 80ms time component typical for the Flash-Lag illusion (e.g. Nijhawan, 1994; 2002; Wojtach et al., 2008)). The bar moved from right to left. Each Flash-Lag illusion measurement was carried out once to produce a single psychometric function. The results in Figure 2-4 show the psychometric functions for the two speeds measured for a single participant. Each function forms a sigmoid from 0 to 100% response rate, which demonstrates the participant is responding sensibly and the range of Flash-Lag offsets is suitable for the task. This was fitted used the logistic function in Equation 2-1 (where the fitted function y is a function of the observed data x where α is PSE and β is slope) using a Newton-Gauss algorithm implemented by the MATLAB nlinfit function.

Equation 2-1

$$y = \frac{1}{1 + e^{-\frac{x-\alpha}{\beta}}}$$

The first results with the author as observer are shown in Figure 2-4. The fitted function for the faster speed shows a shallower gradient, meaning there is more uncertainty in the judgments, which is expected at higher speeds due to Weber's law. However, the PSEs (9.1°s^{-1}: 0.3°, 18.2°s^{-1}: 0.1°) for both show no effect or possibly a very small Flash-Lag at the slower speed. Much smaller than expected with a 80ms time constant (9.1°s^{-1}: ~0.75°, 18.2°s^{-1}: ~1.5°). It is not possible to get an accurate estimate of Flash-Lag from a single measure from a single participant, but since this first attempt produces an effect that is much smaller than expected, it suggests the setup is not producing a strong illusion and not fulfilling the requirements laid out in Section 2.3, thus prompting changes in the stimulus.

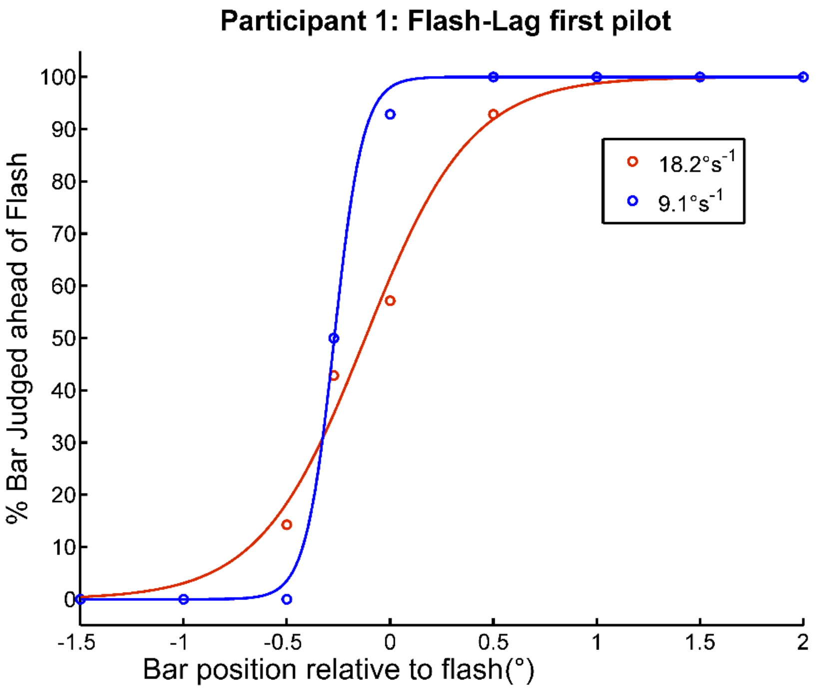
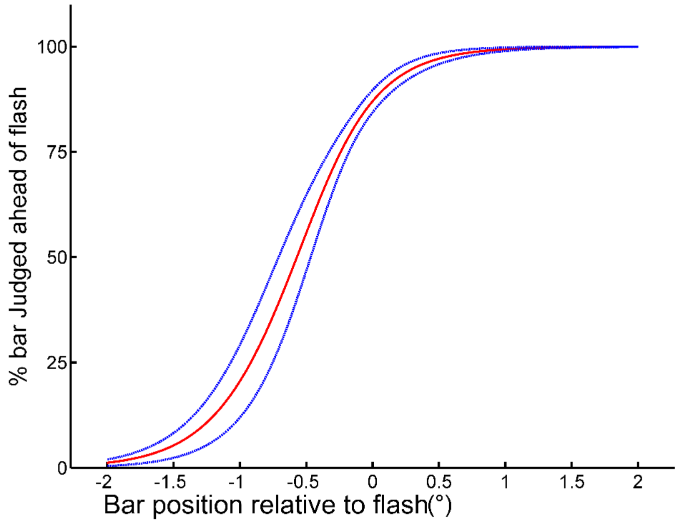


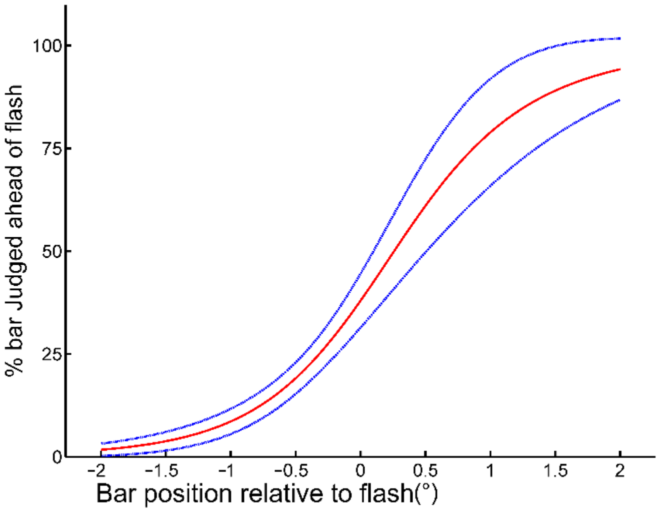
Figure 2-4: Responses showing the position of the bar relative to the flash (negative means flash is positioned ahead of the bar) and responses indicating when the bar was judged ahead of the flash. Psychometric functions are shown for a single participant for two bar speeds 9.1°s-1 and 18.2°s-1. Both speeds show a barely distinguishable Flash-Lag that is much smaller than commonly reported.

2.3.5. Second Flash-Lag pilot: two directions of motion

The experiment is changed to show the bar in both right to left and left to right motion paths to avoid motion adaptation, which may have affected previous results. Bar direction is interleaved in each block and the offset range is increased to $^{+}/_{-}$ 2° with 0.5° steps. Otherwise, the stimulus is the same as shown in Figure 2-3 and described in Sections 2.3, 2.3.3 and 2.3.1, except the start and end-points for right to left motion are reversed. Only the 18.2°s^{-1} condition is shown. The two main experimenters were the participants in this experiment. Figure 2-5 shows the shape of the psychometric function, indicating that the range is suitable. Only one of the two participants shows a Flash-Lag effect (participant 1:-0.5, participant 2 shows a Flash-Lead of 0.3), though this is much smaller than expected (~1.5°), indicating that, further changes are required.



a) Participant 1: Mean Flash Lag



b) Participant 2: Mean Flash Lag

Figure 2-5 : Psychometric functions and for the mean and standard deviations (n=4) of the data collected plotted as the position of the bar at the time of the flash versus the percentage the bar is judged ahead of the flash for a particular offset where a shift toward the negative indicates a Flash-Lag illusion. a) Participant 1 shows a significant Flash-Lag effect, but smaller than expected. b) While participant 2 (right) shows no effect, if anything is exhibiting a slight Flash-Lead effect in the opposite direction to Flash-Lag.

2.3.6. THIRD FLASH-LAG PILOT: CHANGING FLASH POSITION

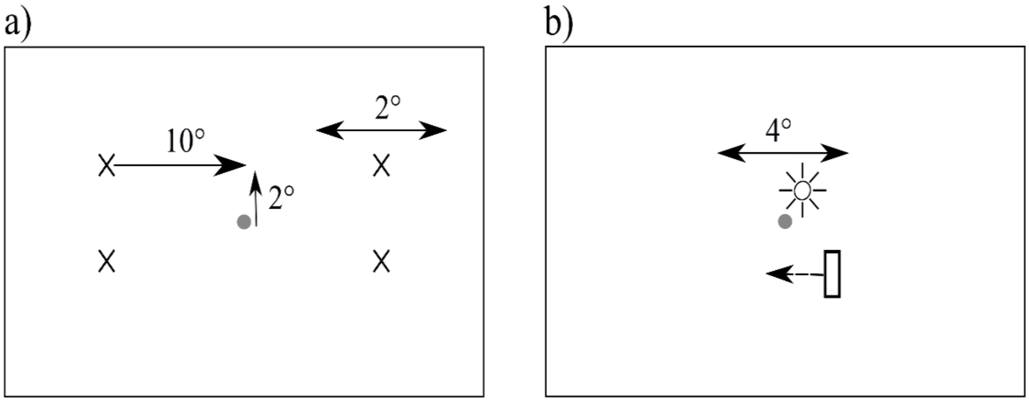


Figure 2-6: This shows the Flash-Lag stimulus design for the third Flash-Lag Pilot. a) The main change is the bar can now appear either side of fixation as marked using X. The distance the bar travels has increased to 20° from 8° and the jitter to 2° from 1°. b) shows bar and Flash with the Flash position jitter increased to 4° from 2°.

A possible explanation for the previous results is that the current arrangement, where both the flash and bar appear on the same side of fixation, encourages the participant to track the bar or shift fixation above the fixation point. Tracking the moving object by smooth pursuit removes the Flash-Lag effect (Nijhawan, 2001). A saccade to above fixation could also modulate the Flash-Lag effect as saccades are reported to compress perceptions of time and space (Morrone et al., 2005). At this point, we had no eye tracking to confirm this so this was set up using a CRS eye tracker so gaze could be checked via visual inspection of the traces.

A redesign of the stimulus overcomes this by having the flash and the bar on opposite sides of the fixation point instead of both above it (Figure 2-6). Therefore, the optimum strategy for the participant is to fixate in the centre to judge the position of both flash and bar equally well. A further change is the range of flash offsets which are set to $^{+}/_{-}$ 4° and the bar path distance increased to 20°, with the start and end points jittered by 2° allowing greater speeds to be used to accommodate the larger Flash-Lag magnitude.

This set up will be tested for three different speeds 18.2, 27.3 and 36.4°s^{-1}. The aim of adding two faster speeds is to see if this will produce a larger Flash-Lag illusion. The side of fixation the bar appears on is randomly selected for each trial and counter-balanced. The centre of the flash is now positioned 2 degrees vertically from the centre of fixation and each speed is now repeated for 12 trials so the four combinations of bar position (above or below fixation) and direction (left to right and right to left) are each shown 3 times. Other parameters are the same as Section 2.3.5.

The results are shown in Figure 2-7**Error! Reference source not ound.**. An increase in speed results in a shallower psychometric function slope to the point where the 36.4 °s^{-1} speed condition does not drop below 30% 'bar ahead of flash' response rate indicating the range of offsets do not extend far enough. The results show the flash offsets are suitably set to measure the effect for the other two speeds. Naïve, less practiced participants may not have as steep a sinusoidal function as this so it would be prudent to extend the range of flash offsets. The PSEs for each speed (1.6°,2.0° and 2.8° for 18.2°s^{-1}, 27.3°s^{-1}, 36.4°s^{-1} respectively) demonstrate a Flash-Lag effect, which is comparable to the expected illusion magnitude in literature given an 80ms time component (1.5, 2.2, 2.9° for 18.2°s^{-1}, 27.3°s^{-1}, 36.4°s^{-1} respectively). This is a statistically significant Flash-Lag as shown by one-sample t-tests (18.2°s^{-1}: $T_3 = 22.266$, $p < 0.001$. 27.3°s^{-1}: $T_3 =11.166$, $p < 0.01$. 36.4°s^{-1}: $T_3 = 6.780$, $p < 0.01$.). Flash-Lag is significantly different across the differing speeds, as shown by repeated measures ANOVA ($F_{3, 6} = 5.52$, $p < 0.05$). Overall these data show this methodology can produce a robust Flash-Lag effect comparable with previous reports for all speeds and an accurate estimate of psychometric function for 18.2 and 27.3 °s^{-1} speeds thus, fulfilling some of the objectives set out in Section 2.3 and provides the basis for the Flash-Lag experiments carried out in this and Chapter 3.

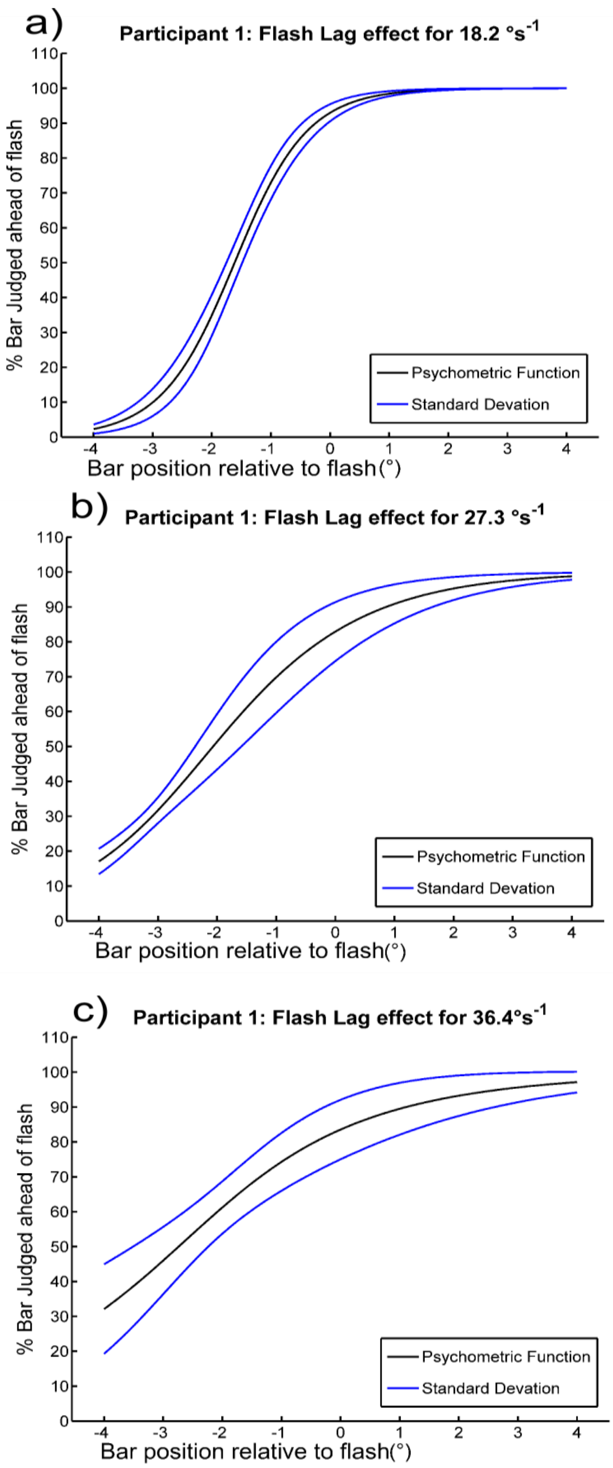


Figure 2-7: Psychometric functions and standard deviations (n=4) showing percentage of trials the bar is judged ahead of the flash for the bar's position relative to the flash. Both motion directions are collapsed, so a shift toward the negative indicates a Flash-Lag illusion. Each graph shows a different speed, which all show significant flash-lag effects. a) shows 18.2°s^{-1} speed, b) shows 27.3°s^{-1} speed and c) shows faster 36.4°s^{-1} speed.

2.3.7. ADDING TEMPORAL FREQUENCY ADAPTATION

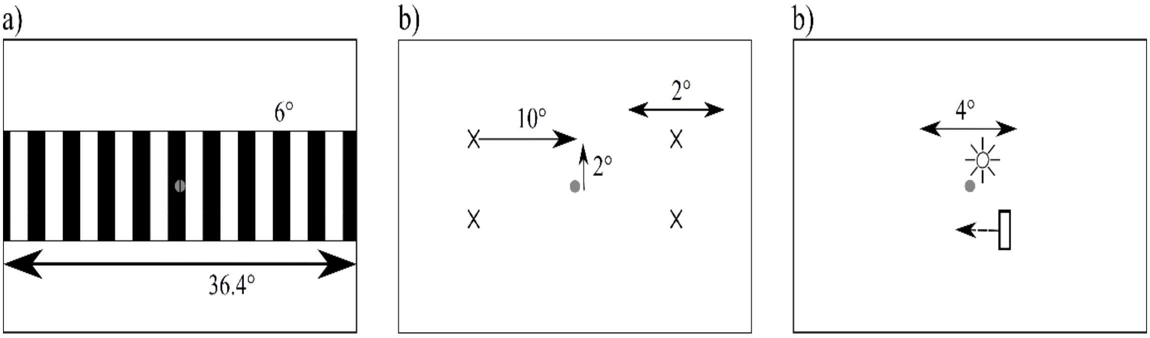


Figure 2-8: This shows the Flash-Lag stimulus with an adapting stimulus a) the adaptor covering the whole width of the screen appears in both the 5Hz and 20Hz adaptation conditions but not the control b) Shows the positions the bar starts and stops in c) shows bar and Flash with the Flash position jitter.

For measuring Flash-Lag with adaptation two changes were made, firstly the range of flash offsets was increased from 4 to 5° to make sure the full psychometric function is fully sampled and to shorten the experiment the number of repetitions is reduced to 8 and the flash offset step size is set to 1°. To adapt the Flash-Lag stimulus a squarewave grating (2 cycles per ° of visual angle) with a sinusoidal counterphase luminance flicker (Luminance: 41 - 82cdm^{-2}, Michelson contrast: 0.333) is used. This is set as counterphase flickering to avoid luminance after-effects and squarewave to avoid areas where no luminance change occurs, and thus no adaptation. This is shown in Figure 2-8.

Participants fixate as before and the grating appears centred in the middle of the screen on fixation for an initial 15s adaptation with 5s top up between trials to match Johnston et al., (2006). After adaptation, the Flash-Lag stimuli appear as in Section 2.3.6. There are two adaptation conditions 5Hz and 20Hz, making up three conditions altogether with the no adaptation control condition.

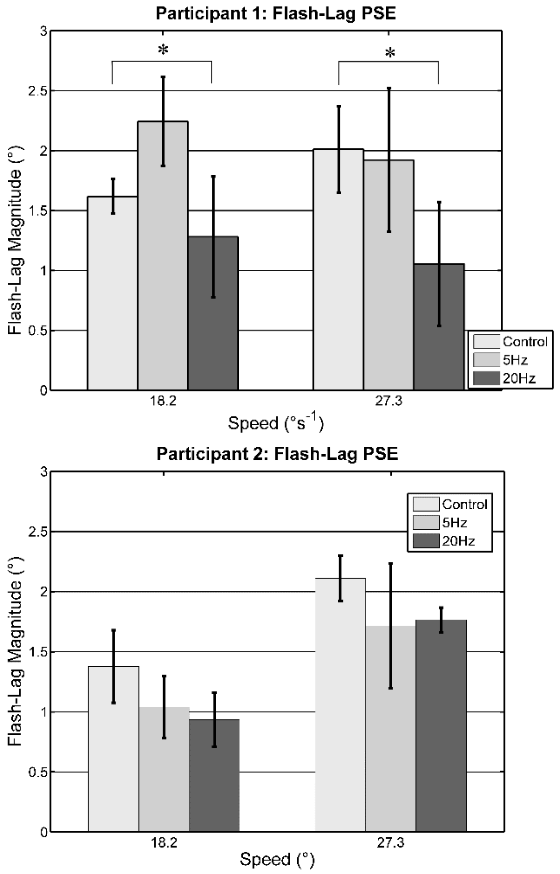


Figure 2-9: Shows measured Flash-Lag effects for two participants across all conditions. Flash-Lag magnitude is shown as a positive value, different to previous figures showing psychometric functions where a Flash-Lag is shown as negative. Bar grouping organised by speed. Both participants show similar changes because of adaptation with both 5 and 20Hz reducing Flash-Lag except participant 1 for 5Hz.

Results of adaptation for two participants are shown in Figure 2-9. The Flash-Lag effect for both participants in the control condition compares well to that expected with a 80ms time constant (participant 1 $18.2°s^{-1}$:1.6° $27.3°s^{-1}$:2.0° participant 2 $18.2°s^{-1}$:1.4° $27.3°s^{-1}$:2.1° and expected $18.2°s^{-1}$: ~1.5 $27.3°s^{-1}$: ~2.2). The pattern of change across the two participants shows adaptation reduces the magnitude of the Flash-Lag illusion with the exception of 5Hz adaptation at the $18.2°s^{-1}$ speed for participant 1. The effect of adaptation is significant for participant 1 across both speeds ($18.2°s^{-1}$: $F_{3,6} = 7.00$, $p < 0.05$. $27.3°s^{-1}$: $F_{3,6} = 4.44$, $p < 0.05$) but not participant 2 ($18.2°s^{-1}$: $F_{3,6} = 3.07$, $p = 0.10$. $27.3°s^{-1}$: $F_{3,6} = 0.78$, $p < 0.22$). There are no significant contrasts, indicating it is a combination of the adaptation effects at both 5Hz and 20Hz causing the significant difference for participant 1.

These data show two things. First, there is some indication of an effect of adaptation on Flash-Lag as shown by the significant results for participant

1, however though participant 2 shows similar trends in the results these are not significant, meaning that any effect on Flash-Lag may only be observable across a group.

Table 2-1: Shows the results from Section 2.3.7 using MoCs to measure the Flash-Lag illusion

PPT	1						2					
Speed	18.2			27.3			18.2			27.3		
Adapt	Ctrl	5	20	Ctrl	5	20	Ctrl	5	20	Ctrl	5	20 Hz
1 (°)	1.81	2.03	0.99	1.56	1.10	1.20	1.30	1.38	0.67	2.27	1.73	1.80
2 (°)	1.58	1.85	1.07	1.90	2.27	0.79	1.70	1.02	1.21	2.04	2.39	1.82
3 (°)	1.47	2.44	2.03	2.17	1.88	1.71	1.00	1.00	1.00	2.25	1.61	1.82
4 (°)	1.61	2.66	1.04	2.40	2.44	0.53	1.50	0.75	0.86	1.88	1.14	1.61
μ (°)	1.62	2.25	1.28	2.01	1.92	1.06	1.38	1.04	0.95	2.11	1.72	1.76
σ (°)	0.15	0.37	0.50	0.36	0.59	0.52	0.30	0.26	0.23	0.19	0.52	0.10

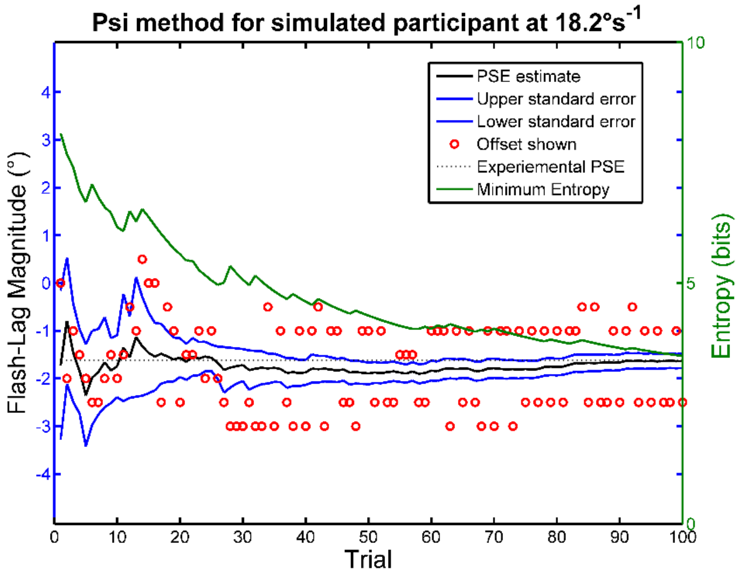
2.4. MEASURING FLASH-LAG: ADAPTIVE METHODS TO MEASURE EFFECT SIZE

The problem with the experiment so far is that to measure Flash-Lag across a range of speeds with TF induced flicker it will take 1 - 1.5 hours per condition, totalling up to 9 hours for the Flash-Lag experiment, depending on the number of flash offsets and repetitions required. This is not a reasonable demand on participant's time. An adaptive psychophysical method would reduce the number of trials the experiment requires. In this section, we test two adaptive methods: the Psi method and a simple up/down staircase as well as bootstrapping a single psychometric function to test if errors can be estimated rather than measured.

The Psi method (Kontsevich & Tyler, 1999) uses a range of pre-defined psychometric functions as a Bayesian Prior and indicates the likelihood that each function matches the real psychometric function. It chooses the independent variable value that is estimated to most reduce the entropy, and thus be most informative for the next trial estimating the function. It can accurately measure the PSE within 60 trials (MoC: 288) making it possible to measure Flash-Lag for all conditions in under two hours.

To determine the correct prior and the overall suitability of the Psi method it must be tested to see if it converges on a similar PSE to MoC. A psychometric function fitted to method-of-constants stimulus data is used to generate responses (with a 5% guess rate) input into the Psi method algorithms to estimate the PSE. This estimate can be compared to the MoC estimate testing if the Psi method can theoretically provide comparable estimates of Flash-Lag. Participant 1's control measure psychometric functions are used to test the Psi method, the results of which are shown in Figure 2-10. The Psi method prior consists of a range of logistic functions (Equation 2-1) with PSEs ranging between -4° to 4° in 0.5° steps and a gradient range set as 0° to 32° with steps of 4°.

Upon visual inspection of the Psi method estimate plots (Figure 2-10), they converge upon the experimental PSE within 30 trials (estimates, $18.2°s^{-1}$: 1.63° $27.3°s^{-1}$: 2.07° actual, $18.2°s^{-1}$: 1.6° $27.3°s^{-1}$: 2.0°) and remained stable throughout. The entropy, a measure of uncertainty in the PSE estimate, also showed an overall decrease, indicating the algorithm was able to measure PSE with increasing accuracy with more trials. This is also observed in the standard error of the PSE estimate, which decreases with increasing number of trials. This demonstrates that with a simulated observer producing responses based upon experimental data the Psi method produces an accurate measure of the Flash-Lag illusion.



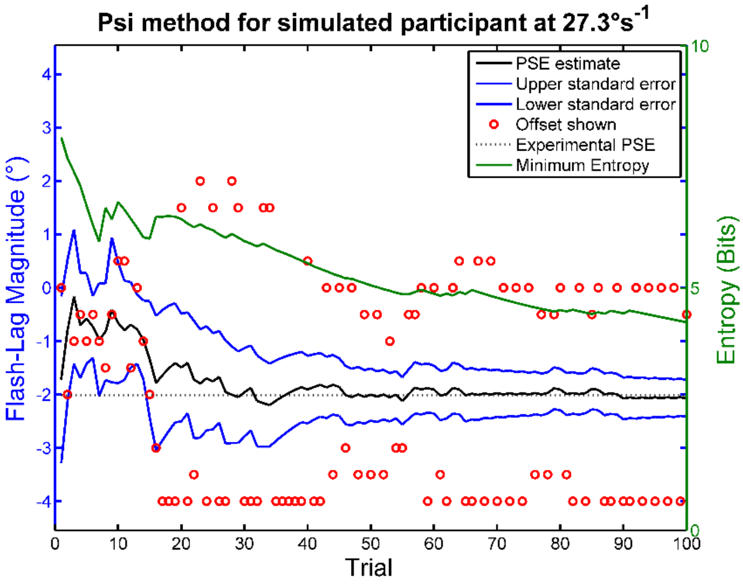


Figure 2-10: Flash-Lag estimates using Psi method for a simulated participant using MoC data for two speed conditions. Black lines show estimates from the Psi algorithm with dashed showing the MoC PSE. Blue shows the error estimate. Green shows the estimate entropy with red circles showing the flash-offset shown chosen by the algorithm. Both show convergence of the estimated PSE with the MoC PSE and a reduction in the error estimates and entropy.

2.4.1. PSI METHOD: MEASURING THE FLASH-LAG ILLUSION

Using the same experimental set up as Section 2.3.7, Flash-Lag is measured for two speeds, 18.2°s^{-1} and 27.3°s^{-1}, across three adaptation conditions, control, 5Hz and 20Hz adaptation for a single participant (author). The Psi method is implemented as before, with the exception that the number of trials is reduced to 30 and instead of one, two are run concurrently and randomly interleaved. With a single estimate, it is not possible to know if the Psi method is accurate or if it has found a local minimum in the error of the PSE estimate, so does not accurately estimate the PSE. Using two concurrent PSE estimates reduces this problem. If both PSE estimates differ drastically, this is indicative of one or both estimates representing a local minimum. The final estimate of Flash-Lag magnitude is given as an average between the two PSEs and the standard deviation computed as the square root of the sum of the estimated variance from both measures.

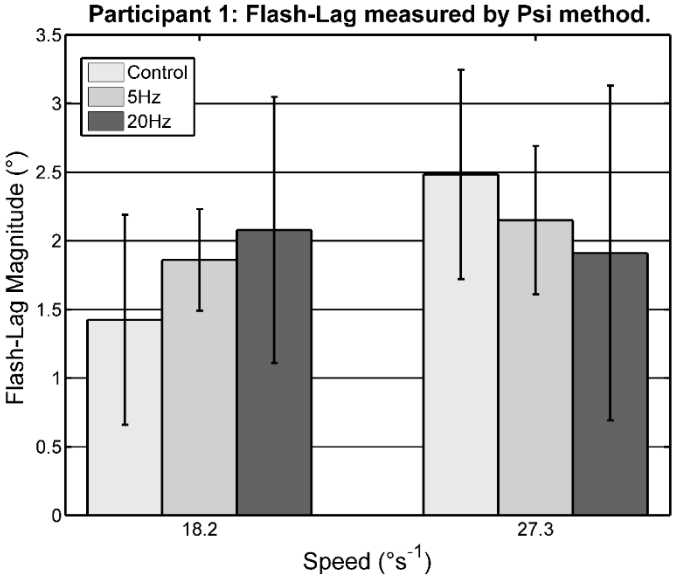


Figure 2-11 : *Shows estimates of the Flash-Lag effect measured by the Psi function. Bars are grouped by speed and coloured to indicate the adaptation condition. Error bars show the mean standard deviation calculated by the root of the squared variance estimate for each Psi method estimate for each condition*

Shown in Figure 2-11, the control condition, the PSI method estimates Flash-Lag to be 1.45° for the slow speed and 2.49° for the faster speed. Comparing this to the MoC measures (1.5° and 2.0° for slow and fast speed respectively) shows that for the slower speed both methods give similar estimates, the MoC estimate is within one standard deviation of the Psi estimate. The Psi Flash-Lag estimates scale with speed as expected, so this appears to be a good measure of Flash-Lag, despite the slight difference with method of constant stimulus estimates.

The adaptation conditions however, show a different pattern to that observed in method of constant stimuli. 20Hz adaptation at the faster speed reduces Flash-Lag in line with the MoC estimates but shows the opposite trend for the slower speed, indicating an increase in Flash-Lag. However, in both the MoC and Psi results the error bars of both the control and adaptation conditions overlap indicating there is not much difference between the two conditions. Examining the two separate Psi method estimates for each condition shows that for the 18.2°s^{-1} control, 20Hz and 27.3°s^{-1} 20Hz give quite different estimates (Table 2-2). Such that when comparing to the MoC results in Table 2-1, three of the estimate pairs in Table 2-2 exceed the largest standard deviation across all conditions for both participants in Table 2-1.

Table 2-2: Shows the estimated Flash-Lag effect for each concurrent run (labelled 1 and 2) of the psi method for each speed and adaptation condition for a single participant.

Speed	**18.2°s^{-1}**		**27.3°s^{-1}**	
Psi Measure	1	2	1	2
Control	1.86°	0.99°	2.62°	2.35°
5Hz	1.76°	1.97°	2.02°	2.28
20Hz	2.50°	1.66°	3.61°	0.22°

2.4.2. RANDOMISING FLASH OFFSET WITH THE PSI METHOD

The results described in the previous section are not due to the Psi method failing to converge, although this convergence is less meaningful when the two estimates differ greatly. Instead, methodological differences between the Psi and MoC might cause this. MoC displays a wider range of flash offsets in than the Psi method and in a random order. The Psi algorithm uses a greedy search to find local minima in choosing the next independent variable. This assumes moving from one local minima to the next is a sensible trajectory to find the global minima, which might not be true. Selecting the offset of the flash for half the trials at random so it samples across the entire search space could help solve this and by introducing more randomness into the experimental stimuli this would reduce any effect of predictable offsets on the participants' perception and/or responses.

The stimuli used for this experiment are as before in Section 2.3.5 with two speeds and only Flash-Lag in the control condition measured for a single participant. The number of trials in each Psi estimate increased to 40 with half chosen at random from $^{+}/-$ 4° according to a uniform distribution and half chosen from the Psi algorithm.

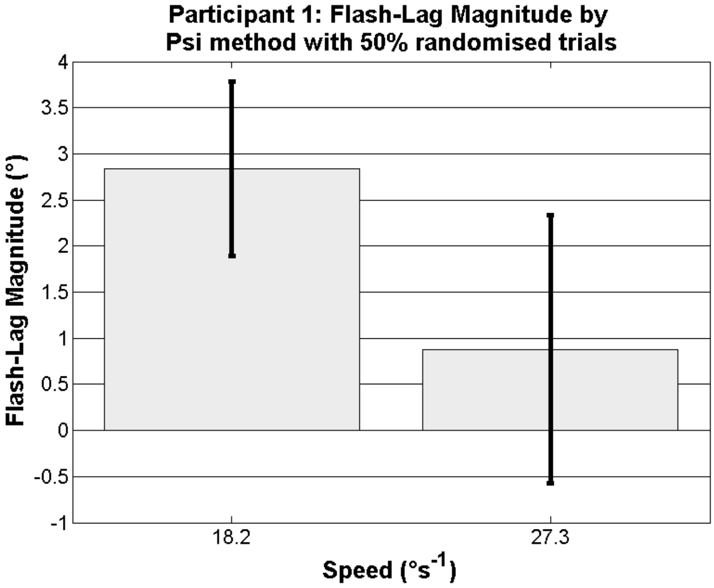


Figure 2-12: Shows Flash-Lag estimates using the Psi method for two speeds with no adaptation with 50% of the Flash offsets chosen at random rather than the PSI algorithm. This shows a smaller Flash-Lag with the faster speed, opposite to what is expected. Error bars show the mean standard deviation calculated by the root of the summed variance estimates for each Psi method estimate for each condition.

Figure 2-12 shows for the slower speed both estimates converge on similar PSE estimates though, this is larger than the estimate from MoC (Psi: 2.8°, Constants: 1.5°). For the faster speed the two estimates do not give comparable PSE estimates despite the estimate for each individual Psi algorithm estimate converging. One even measures a Flash-Lead as opposed to a Flash-Lag effect (Table 2-3).

This could be due to the non-informative points delaying the conversion towards an estimate and can be fixed with more trials though this would defeat the point of using the Psi method in the first place. Adding random flash offsets does not improve the Psi method for measuring Flash-Lag even though the Psi method is probably not drawn to mistaking local points of minimum error for the PSE estimate.

Table 2-3: Shows the estimated Flash-Lag effect for each concurrent run of the psi method for two speed conditions for a single participant.

Speed	$18.2^{\circ}s^{-1}$		$27.3^{\circ}s^{-1}$	
Psi Measure	1	2	1	2
PSE estimate	3.10°	2.57°	-0.35°	2.09°

2.4.3. MEASURING FLASH-LAG WITH A SIMPLE STAIRCASE

To test if the inconsistent estimates using the Psi method are an artefact of the particular algorithm or something we find with other adaptive algorithms, a simple up/down staircase is tested here. To check if a staircase works in theory, two staircases are used to estimate the PSE of response from a simulated participant set up before as in Section 2.3.

Both staircases choose flash offsets from $^{+}/_{-}$ 4° with 1° steps for 30 trials each and are randomly interleaved starting at each extreme. PSE and error estimates for each staircase are taken as mean and standard deviation of the last five reversals. The final PSE estimate is the mean PSE from the two staircases and error given as the square root of the sum of the variance from each staircase computed from the last five reversals. Figure 2-13 shows that both staircases converge upon the MoC data PSE indicating an accurate measure of Flash-Lag.

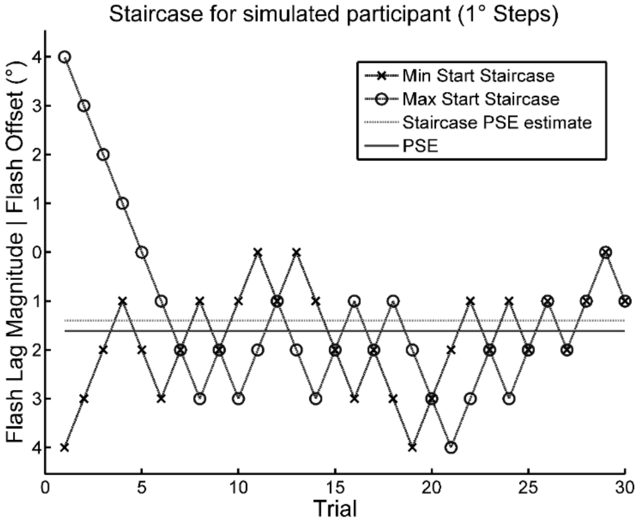


Figure 2-13: Flash-Lag magnitude estimate by staircase with simulated responses from method of constant stimulus data. x and o show the flash offsets chosen by each staircase starting at the minimum and maximum flash offsets respectively. Dark grey line shows the PSE as measured using method of constant stimulus while the light grey line shows the staircase PSE estimate as taken by the mean of the two staircases estimates. Each staircase estimate is computed from the mean of the flash-offsets at the last five reversals. Both staircases converge and the PSE estimate closely matches that of MoC.

There were some changes made to the staircase setup for the experiment compared to the stimulations. The range was increased from $^{+}$/- 4° to $^{+}$/- 5° and step sizes reduced to 0.5°, and the number of trials increased to 32 to show the same number of trials with each bar position (above or below fixation) and direction (left or right motion) combination.

These results are shown in Figure 2-14 and Table 2-4 for two bar speeds (18.2 and 27.3°s^{-1}). The estimated Flash-Lag magnitude for the slower speed is 1.9°, larger than the MoC estimate 1.4°, with the faster Flash-Lag estimate of 2.0° matching the MoC estimate at 2.0°. There is no real difference between the faster and slower speed Flash-Lag estimates. This is not expected considering Flash-Lag scales with speed in the literature and is a concern. In addition, the staircases for the slower speed do not converge on similar estimates, listed in Table 2-1. These experiments are piloting checks on the experimental methodology, limiting any interpretation of these results. These results show neither Psi nor staircase method provide a constant measure of Flash-Lag, comparable with the literature with the setup here.

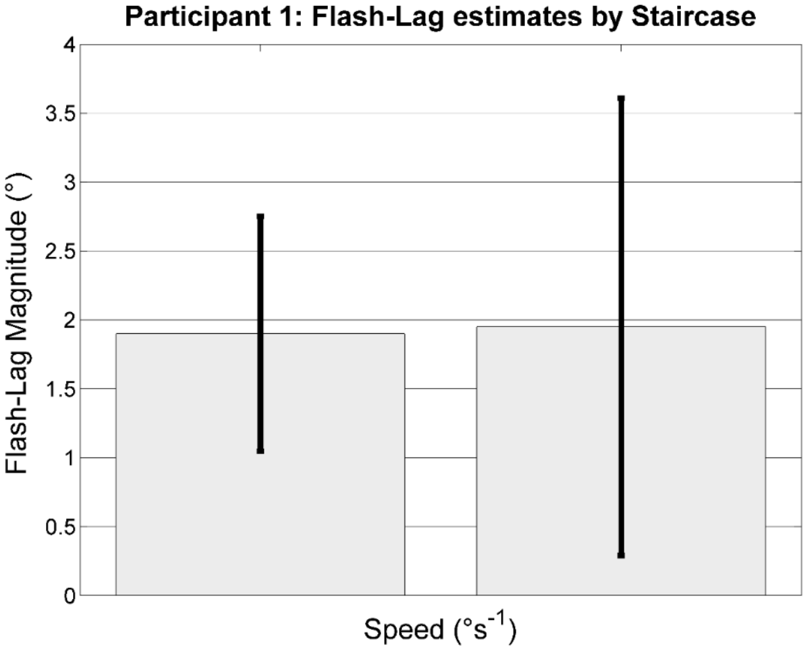


Figure 2-14: Shows Flash-Lag estimates using staircases for two speeds with no adaptation. There is little difference in Flash-Lag estimate for the two speeds where it is expected that Flash-Lag scales with perceived speed. Error bars show the mean standard deviation calculated by the root of the squared variance estimate for each staircase estimate for each condition

Table 2-4: Shows the estimated Flash-lag effect for each concurrent staircase run (labelled 1 and 2) for two speed conditions for a single participant.

Speed	**18.2°s^{-1}**		**27.3°s^{-1}**	
Staircase Measure	1	2	1	2
PSE Estimate	0.90°	2.90°	2.1°	1.8°

2.4.4. BOOTSTRAPPING ERRORS FROM A SINGLE PSYCHOMETRIC FUNCTION

The problem of how to reduce effectively the number of trials and therefore, time required for this experiment remains. MoC was the only method that measured the Flash-Lag effect consistently (in line with the literature) and accurately (with approximately similar results from multiple estimations) with the setup used here. Instead of four repetitions per measure, the procedure is performed once and individual error bars are estimated using bootstrapping.

Bootstrapping takes the fitted psychometric function and generates multiple data sets from the function, i.e. simulating multiple experiments based upon the original psychometric function. The PSE is estimated for each experiment simulation and a Gaussian function is fitted to the distribution of PSEs for all simulations(N=500), with the PSE and slope as free variables and error rate fixed at 0%. The standard deviation of the Gaussian fit is taken as an indication of the PSE estimate's accuracy. We test the bootstrapped standard deviations by comparing them to those computed from running Method of Constant Stimulus four times. These are shown in Table 2-5.

Overall there is no significant difference between standard deviations estimated from bootstrapping (Participant 1; $T_5 = -2.08$, $p = 0.092$. Participant 2; $T_5 = 0.65$, $p = 0.545$), this means bootstrapped standard deviations provide a sensible estimate of error for the Flash-Lag effect. The best way to measure Flash-Lag efficiently is collecting data to fit a single psychometric function and using bootstrapped standard deviations as measures of individual error.

Table 2-5: Shows the standard deviations of Flash-Lag effect measures from MoC compared to bootstrapped estimates (N=500) for two participants.

Speed	**Adaptation condition**	**Participant 1**		**Participant 2**	
		Bootstrap estimate (°)	MoCs estimate (°)	Bootstrap estimate (°)	MoCs estimate (°)
18.2°s^{-1}	Control	.18	.15	.28	.30
	5Hz	.38	.37	.28	.26
	20Hz	.34	.50	.29	.23
27.3°s^{-1}	Control	.25	.36	.35	.19
	5Hz	.41	.60	.33	.52
	20Hz	.46	.52	.28	.10

2.5. GENERAL DISCUSSION

This chapter demonstrates how it is possible to measure a Flash-Lag effect with a stimulus moving at high speed, and of a magnitude comparable with that found in literature with the typically recorded ~80ms time component. Initially there were problems, hypothesised as caused by adaptation to motion and/or uninstructed eye movements. However, it is not possible to confirm this without further measurements. The final stimulus design avoids these possible issues by randomly selecting half the trials to have the opposite direction of motion and designing the stimuli so that fixating upon the central point is the optimum viewing strategy for this experiment. It is worth bearing in mind for any experiment requiring visual fixation, to, where possible, design the stimuli so that fixating is the sensible option to perform the task. Overall, the method of measuring Flash-Lag presented here provides a good basis for further experiments in Chapter 3 investigating the effect of temporal frequency adaptation on the Flash-Lag illusion. The two established adaptive methods tested here: a simple staircase and Psi method in practice yielded less reliable results. This is unexpected as both methods are theoretically able to measure accurately the Flash-Lag effect when simulating responses from the MoC data and both methods converge as expected on an estimate, but two concurrent staircases or Psi algorithms converge on different estimates when used experimentally. That the adaptive methods appear to work as expected when simulating responses from experimental data might imply that the participant responses shown here were affected by the distribution of offsets shown. In both adaptive methods, the tendency is to show flash offsets across a small range as the estimate converges compared to MoC, which shows offsets from a wide range. An explanation for this is the adaptive methods affect participant perceptions of Flash-Lag by showing only offsets from a small range thus the distance between bar and flash on a particular trial is more predictable. This could result in a response bias or it could be that the Flash-Lag illusion is affected by the predictable nature of the stimuli. There is experimental evidence showing Flash-Lag changes based on the predictability of stimulus, (Namba & Baldo ,2004; Krekelberg &

Lappe, 2000b; Murakami, 2001) but as the results presented here are preliminary at best, this needs to be demonstrated by further experiments. Currently, it is more prudent to presume that adaptive methods struggle with measuring an accurate Flash-Lag illusion at higher speeds as participant responses tend to be more variable, which would provide a more straightforward explanation for the results here.

2.6. CONCLUSION

It is possible to measure a Flash-Lag illusion with a high object speed moving in a linear path reasonably consistently using a method of constants stimulus. For stimuli design, it is hypothesised that adaptation to motion and unwanted eye movements are factors that might prevent an accurate measure of Flash-Lag. We also show that method of constants stimuli provides a more consistent measure of Flash-Lag with a high-speed object than adaptive techniques for estimating PSE. The stimulus set up developed in this chapter can form the basis of future experiments using the Flash-Lag illusion with higher speed stimuli than has been typically used in other studies.

3. CHAPTER THREE - HIGH TEMPORAL FREQUENCY ADAPTATION COMPRESSES TIME IN THE FLASH-LAG ILLUSION

3.1. INTRODUCTION

The previous chapter details experimental data demonstrating how a Flash-Lag effect can be measured, giving consistent results comparable to previous findings. This chapter builds upon this work investigating whether adapting to visual stimuli shown to compress perceived duration can also affect the Flash-Lag illusion. Research shows that the perceived duration of visual events is compressed in specific spatial locations after adapting to properties of visual stimuli in those locations. Such properties include temporal frequency (TF) (Burr et al., 2007; Johnston et al., 2006), contrast gain (Bruno & Johnston, 2010) and motion (Curran & Benton, 2012; Marinovic & Arnold, 2011). These findings indicate that the visual system computes event duration based upon localized low-level visual properties and perceived duration is malleable in a spatially specific manner. One question that arises from this is does this effect of adaptation on perceived duration have other effects or is it simply a pure duration effect.

Investigating whether this duration mechanism has a functional role Marinovic and Arnold, (2011) find compressing perceived visual duration does not affect action timing, concluding there must be separate timing mechanisms responsible for vision and action. We ask a similar question by exploring if duration perception has a functional role in the visual perception of space and motion. To do this, the study measures the effect of 20Hz TF adaptation, shown to compress perceived duration (Johnston et al., 2006) on the Flash-Lag illusion where an observer views an object moving on a predictable path, perceiving the object displaced further along its motion path relative to a spatially localized flash. The Flash-Lag induced displacement can be described as increasing in proportion to object speed (Nijhawan, 1994). Although Wojtach et al., (2008) found a nonlinear relationship when extending the tested range over faster speeds, over the range 10°/s - 40°/s a linear relationship provides a good approximation. This linear relationship can be expressed as perceiving the bar advanced by a fixed amount of time relative to the flash (Durant & Johnston, 2004), i.e. the same time travelled at a higher speed leads to larger displacement.

Flash-Lag is often explained as an artefact arising from perceptual mechanisms compensating for delays in processing position of moving objects (Nijhawan, 2002). Delays in visual processing, e.g.: Retina -(Shapley, Kaplan, & Soodak, 1981) and V1 -(Maunsell & Gibson, 1992) pose a problem for estimating positon of objects in motion as by the time object position has been computed, the object has moved to a new position, meaning the visual representation of the environment is out of date. This delay is thought to be approximately 72ms for V1 neurons (Lamme & Roelfsema, 2000), so it is proposed that the visual system has developed compensatory mechanisms, otherwise interaction with moving objects would be prohibitively difficult. For example, a delay of 72ms means an object travelling at 30kph would result in a perceived positional error of 60cm. This is why according to the extrapolation explanation of Flash-Lag the flash apparently lags behind the moving object as the position of the moving object is shifted along its motion path in the direction of travel by the visual system to compensate for delays.

However there is little consensus as to whether such mechanisms lie behind this ‘lag’. Evidence showing Flash-Lag illusion is affected by motion after, not before the flash (Brenner & Smeets, 2000) suggests it is not a result of motion extrapolation, thus, others have proposed different mechanisms. Whitney and Murakami (1998) claim Flash-Lag is down to differences in processing speed between the flash and moving object so the moving object reaches a perceptual end point earlier than the flash creating the misalignment, a specific example of micro-consciousness (Zeki & Bartels, 1999). Two other explanations, motion integration (Krekelberg & Lappe, 2000a) and postdiction (Eagleman & Sejnowski, 2000; Eagleman & Sejnowski, 2007), both focus on the fact that motion after the flash continues to influence the illusion. Motion integration suggests that the position of the moving object is perceived as an average computed over a temporal window after the flash, so results in the shift observed in Flash-

Lag. Eagleman and Sejnowski (2000) apply a postdiction mechanism, similar to those used to explain effects such as colour-phi (a version of another motion illusion with a colour change) by Kolers and von Grunau (1976) and visual masking (Bachmann, 1989). This posits the visual system estimates position based upon expected events and when an unexpected event occurs, the visual system resets expectations, discarding information before the unexpected event and estimates the position of the bar at the time of the flash post-hoc, using motion after the flash only. This biases perceived position along the motion path of the moving object, creating the perceived offset.

All these proposed mechanisms use a temporal component. Extrapolation; how far ahead in time the moving object position is estimated, neural delays; difference in latency between moving and stationary objects, integration and postdiction; the size of the temporal window used for averaging the object position. Therefore, it is not necessary to know or make any claim as to which of these is the best explanation as any effect of duration adaptation on Flash-Lag can be accommodated by all these explanations.

One interesting suggestion from the pilot data from the previous chapter is that the Flash-Lag effect may be affected by the distribution of the relative spatial displacements between flash and moving object experienced over a period, such that, to measure reliably a Flash-Lag illusion, a wide range of spatial displacements is required across experimental trials. One feature of a wider range of displacements, as opposed to a narrow one is that the position of the flash is less predictable on a trial-to-trial basis. Stimulus predictability has been shown to change perception of time, such that predictable events are perceived shorter than unpredictable events (Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012; Schindel et al., 2011). Flash-Lag is reliably measured only with a wider, random distribution of displacements so trial-to-trial predictability is low. An unpredictable stimulus is perceived to last longer so one prediction from the research showing this is that if the time component of Flash-Lag and perceived event duration are linked, it could be that Flash-Lag is easier to observe, the less predictable the stimulus, similar to findings made by (Murakami, 2001).

Hogendoorn et al., (2010) indirectly investigated the same question using a paradigm reliant on the presentation of several moving clock faces, one of which was cued at a given time point, with participants reporting the position of the clock hand at the cued time. The perceived positions were compared with and without flicker adaptation. Although they never explicitly report the size of the Flash-Lag effect, from their results we can infer an increased temporal component – in the opposite direction to what we would hypothesize, as high temporal frequency adaptation compresses duration (Johnston et al., 2006), so would be expected to reduce the temporal component.

Our work aims to investigate this further by using the simplest form of the Flash-Lag effect and reducing it to a purely perceptual question of perceived alignment, removing any possible effect of shifting attention to the cued clock and reducing reliance on memory to judge position. Furthermore, by comparing the effect of adaptation on two speeds we can build a fuller description of the specific effect of flicker adaptation on the Flash-Lag illusion. High TF adaptation also reduces perceived speed (Hammett, Thompson, & Bedingham, 2000; Johnston et al., 2006; Smith & Edgar, 1994; Thompson, 1983), which could also reduce the Flash-Lag effect if it is dependent on perceived speed, thus the effect of perceived speed must be ruled out to infer direct duration adaptation, as in the Hogendoorn et al., (2010) study. Therefore, this study contains two main experiments, one measuring the effect of low and high TF adaptation on the Flash-Lag illusion and a second measuring the effect of low and high TF adaptation on the perceived speed of the moving object. Additionally we run a control experiment to verify that temporal duration compression has been induced in our stimulus set up. We find change in perceived speed cannot fully explain the change in Flash-Lag, concluding that TF adaptation compresses the Flash-Lag time component. This chapter is adapted from an article by Rowland and Durant (2014).

3.2. MATERIALS AND METHODS

3.2.1. PARTICIPANTS AND EQUIPMENT

The same six participants (authors ER and SD with four naive participants) with normal or corrected to normal visual acuity participated in Flash-Lag and speed experiments. An internal ethics board granted approval to perform this experiment in accordance with guidelines from the British Psychological Society, which follows the declaration of Helsinki. Stimuli were displayed on a linearized display Sony Trinitron monitor in a darkened room using a resolution of 800×600 and refresh rate of 100Hz with a Cambridge Research Systems (CRS) ViSaGe system controlled by Mathworks MATLAB v7.5.0. Participants viewed stimuli with aid of a chinrest at a distance of 57cm from the screen, giving responses on a CRS CT6 remote button box with a CRS VET eye tracking system used to check fixation. Data analysis was performed using Mathworks MATLAB v7.5.0 with the Palamedes toolbox (Kingdom & Prins, 2009) used for bootstrapping

3.2.2. FLASH-LAG EXPERIMENT PROCEDURE

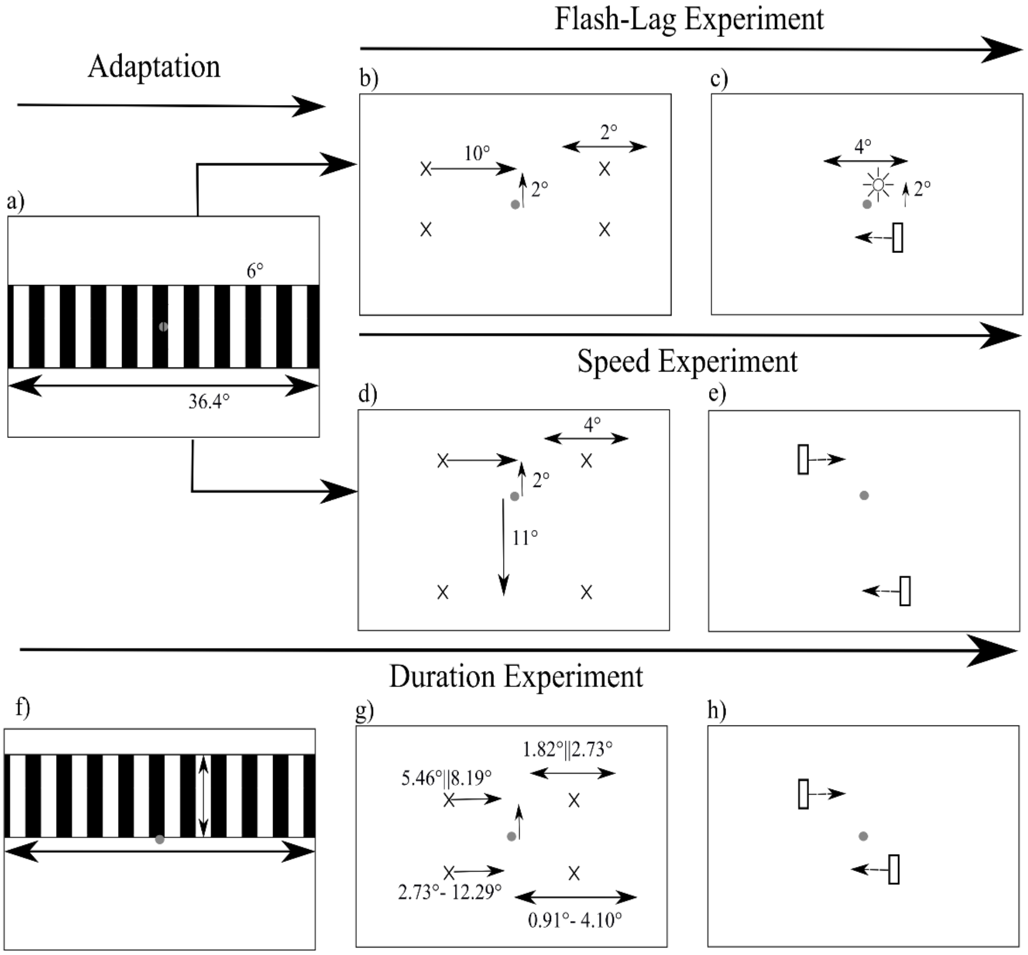


Figure 3-1: Stimulus diagrams. Frame a) shows adaptation phase, common to all conditions except the Flash-Lag control and duration experiment. Frames b) and c) show the Flash-Lag condition. In b) the bar appears at one of four crosses positioned 10° horizontally and 2° vertically from fixation, marking the points where the bar may appear on a particular trial before moving toward the opposite cross and disappearing. The appearance and disappearance position is chosen randomly on each trial with a 2° horizontal jitter. Frame c) shows the bar below and flash above fixation. The flash appears on the opposite side of fixation to the bar randomly jittered 4° horizontally about fixation for each trial. The centre of the flash is positioned 2° from the centre of fixation. Frames d) and e) show the speed condition with d) showing the positioning of the bars where the standard bar appears at one of two points 8° horizontally and 2° above from fixation with the comparison bar again appears at one of two points 11° below and 8° horizontally from fixation. Similar to Flash-Lag the appearance and disappearance of each bar is jittered by 4°. Both bars are shown in e), they appear at diagonally opposite locations so move in opposite directions. f) shows the adaptor for the duration experiment. g) shows positions of bars, the top two crosses and associated arrows give the position and jitter for the standard bar of duration 600ms for the high and low speed condition in the form low||high. The bottom two crosses and arrows give the position and jitter for the comparison bar, the distances vary depending on speed and duration of the comparison in the form min-max. h) shows the two bars moving in opposite directions.

The methods for this experiment are similar to those described in Chapter 2, section 2.5. Participants fixate on a centrally positioned red circle (0.5° diameter) with a mid-grey background (63 cdm^{-2}). In the 5Hz and 20Hz conditions, an adapting square-wave grating (36.4° x 6°, spatial frequency 2 cycles/degree - chosen to lie within a detectable range, allowing for many cycles to be displayed and it also approximates bar width) appears centred on screen (Figure 3-1a), counter-phase flickering in a sinusoidal temporal pattern (Luminance: 41 - 82cdm^{-2}, Michelson contrast: 0.333). For the control, no adapting grating was shown. A white (124 cdm^{-2}) horizontally moving bar (0.33° x 0.67°) appears in one of four points , either 2° above/below fixation and 10° left/right of fixation and moves toward fixation (all measurements are to the centre of the bar). The bar appeared ~0.6s after the adaptor with the exact appearance and disappearance positions are jittered +/- 1° trial-to-trial (Figure 3-1b). At a point along the bar's trajectory, a white circular flash (diameter: 0.33°) appears (10ms, 1 frame) vertically on the opposite side to the bar, 2° away from fixation, horizontally jittered +/- 2° from fixation (Figure 3-1c) and the bar continues to move until reaching the horizontally opposite side of fixation, where it disappears. The participant judges if the bar was to the left or the right of the flash by button press as a 2AFC. The displacement between bar and flash is varied across a range of +/- 5° with 1° steps in a method of constants procedure. Each displacement is shown 8 times except for ER where the range was +/- 4° with 0.5° steps, shown 12 times. We chose three adaptation conditions: a no adaptation control, 5Hz and 20Hz TF adaptation (15s initial, 5s top-up) with the two speed (18.2$°s^{-1}$, 27.3$°s^{-1}$) conditions, this makes six conditions in total. Trials are blocked according to adaptation condition. Blocks were carried out in separate sessions. The no adaptation block was shown first to confirm the Flash-Lag illusion was apparent at least one of the two speed conditions with each adapting condition randomly ordered afterwards, with the two speeds and flash displacements randomly interleaved.

3.2.3. SPEED EXPERIMENT PROCEDURE

We measure perceived speed by asking participants to indicate which of two bars moving in opposite directions has the greatest speed by button press to measure the effect of TF adaptation on perceived speed. One bar acting as the standard moves at one of two speeds (18.2° s^{-1}, 27.3°s^{-1}), the same as in the Flash-Lag condition. The comparison bar is varied in speed trial-by-trial in a range from 9.1° s^{-1} to 27.3° s^{-1} for the 18.2°s^{-1} standard condition and 18.2° s^{-1} to 36.4° s^{-1} for 27.3°s^{-1} standard condition, with 2.3°steps, each shown 8 times in a random order, in a method of constant stimulus procedure. As our aim with this experiment is to measure the effect of the above TF adaptation on perceived speed of the moving bar, we need to make sure the comparison bar is unaffected by adaptation otherwise this would underestimate the effect of adaptation. Receptive fields in motion sensitive retinotopic maps across the Medial Temporal area are quite large (~9° in humans - Amano, Wandell, & Dumoulin, 2009) , so we position the comparison bar 11° away from the adapting stimulus, where no adaptation will occur, in fact Ayhan et al., (2009) show that the change in speed caused by TF adaptation induced duration compression drops off by around 3° distance from the adaptor. The difference in the eccentricity of the bars may affect relative perceived speed even with no adaptation (baseline), but it is change from measured baseline that is of interest. The adaptation conditions and adaptation length are the same as Flash-Lag (Figure 3-1a). Except, a very low TF (0.1Hz) adaptor is used to equate attentional effects in the control condition as, unlike in Flash-Lag the adapter only covers part of the stimulus, so without this the adaptor would draw attention to the top over the bottom bar in the 5Hz and 20Hz conditions but not the control. This control adaptor TF should not affect the perceived speed of the moving bar. Comparing this baseline condition to the effect of 5/20Hz flicker adaptation is the best, most comparable way of measuring the effect of 5/20Hz flicker on the perception of the speed of the bar. Particularly when considering we are interested in the perceived difference in speed caused by adaptation. Participants fixate as in the Flash-Lag experiment. Two bars (0.33°x0.67°) appear (Figure 3-1d) on diagonally opposite sides of fixation (8° horizontally and 2° above fixation for the standard and 17° below for the comparison bar) and move on a horizontal trajectory to the horizontally opposite side of fixation (Figure 3-1e). The appearance and disappearance positions of both bars are jittered +/- 4° trial-by-trial as is the onset time +/- 35ms for the slower speed and +/-17.5ms for the higher speed, making it impossible for the participant to accurately judge which bar is fastest by indicating which bar moved across the length of its trajectory first. Separate blocks are presented for each adaptation/speed combination each adaptation condition was presented in separate sessions and ordered randomly with a break given between the speed blocks in the same session to avoid carry over effects of speed/temporal frequency adaptation. Participants indicated which bar appeared faster with a button press in a 2AFC.

3.2.4. DURATION EXPERIMENT PROCEDURE

A third experiment is run to test if the adaptor causes a compression of perceived duration with our moving bar stimulus. While 20Hz TF adaptation causes duration compression with gratings (Burr et al., 2007; Johnston et al., 2006) and a high speed adaptor causes duration compression with dot texture stimuli (Curran & Benton, 2012) and a moving object (Marinovic & Arnold, 2011), no experiment has shown duration compression of a moving object with a 20Hz TF flickering grating. Therefore, we run this experiment to check if the same effect responsible for compression of event duration has an effect on the Flash-Lag time component. The equipment is the same as the previous two experiments; the display is linearized with mid grey and white as in the previous two experiments. Participants fixate on a red fixation point as previously, with the same adapting stimulus appearing 3° above fixation covering the length of the screen. A white bar, same size as before of 600ms duration appears 3° above fixation moving horizontally at one of two speeds ($18.2° s^{-1}$, $27.3°s^{-1}$) as in the previous experiments. The duration the bar appears for is defined by the distance the bar moves before disappearing (10.92° or 16.38° for speeds respectively). Once the first bar has disappeared, there is a short, jittered delay (0.2-0.7s) before the comparison bar appears 3° below fixation and the adaptor, far enough apart to avoid adapting the comparison bar, as duration effects are spatially specific (Ayhan et al., 2009). The comparison bar starts at the opposite side of the screen, moving in the opposite direction to the standard. The duration of the comparison is varied between 300-900ms in 50ms steps, so the distance travelled varies between 5.46° and 16.48° with 0.91° steps for the low and 8.19° and 24.57° with 1.37° steps for the high speed. The horizontal centre point of each bar path is jittered by + or - one third of the total bar path about fixation so the start and end points are unpredictable. Once the comparison bar disappears, the participant indicates by button press which bar appeared for the longer duration. In each block, defined by the adaptation condition (0.1, 5 and 20Hz TF), each of the two directional combinations (standard moving left to right, comparison right to left and vice versa) is shown once for each of the four speed combinations (low-low, low-high, high-low, high-high). This gives eight measures for each different duration per block and these are interleaved within each of the three blocks. One session contained three blocks – one for each adaptation condition and participants performed two sessions in total on separate days. The control (0.1Hz) condition was always shown first so it was possible to check if they were performing the task correctly before proceeding onto the 5 and 20Hz blocks. The presentation order of the two adapting blocks (5 and 20Hz) was counterbalanced across participants. In total four participants took part, including the authors with two naïve to the purpose of the study. One possibility in this task is that participants use bar path length as a cue to judge duration, as the bar duration is defined by distance travelled. However, as the experiment requires comparisons between bars with different speeds and directions as well as the bars having jittered start and end points, this means that bar path length is not always a reliable cue. Therefore, we can take participants responses as a measure of perceived duration. In addition, there is enough data (eight repetitions per duration) to estimate psychometric functions for trials where bars have different and same speeds independently. This allows to compare participant performance when the distance cue is more informative (when bars are the same speed) or less informative (when the bars have different speeds), to show if this cue has a significant effect on performance.

3.2.5. PSYCHOPHYSICAL ANALYSIS

In all experiments, we fit a logistic psychometric function to the participant's response ratios, taking the 50% point on the curve as the point of subjective equality (PSE). This is interpreted as where the bar and flash are perceived as aligned in the Flash-Lag experiment, at what speed both bars are perceived to have the same speed in the speed measurement and the duration at which the bars are perceived to persist the same amount of time on screen in the duration experiment. In both Flash-Lag and Speed experiments ER and SD both repeat each measurement four times with a curve fitted to each and the PSE and standard error of the measurement calculated. Naïve participants performed each measurement once, a curve is fitted and bootstrapping can be used to estimate the standard error for each participant. As such, the measurements for the authors are more accurate, but can be analysed together with the naïve participants as they measure the same thing, but with more trials. For the duration experiment, both the naïve participants and authors participate with both viewing two blocks, making up a single measurement, to which a curve is fitted. As such, there is no difference between them in their analysis. In addition to fitting a curve to all trials from each adaptation condition, curves were fitted for trials where the bars where of different speeds, discarding trials where the speeds were the same and visa-versa where the two bar speeds matched. For each participant there were three different measures for each adaptation condition: one for different bar speeds, one for the same bar speeds and one for all bar speeds combined.

3.3. RESULTS

3.3.1. THE EFFECT OF TEMPORAL FREQUENCY ADAPTATION ON FLASH-LAG

All participants have a measured Flash-Lag effect in the expected direction for the 27.3 °s^{-1} bar speed, and only one does not for the lower bar speed, with a larger Flash-Lag at the higher speed as expected. We compare the mean across participants separately for each condition to examine the effect of adaptation Figure 3-2a). A repeated measures ANOVA for the 27.3° s^{-1} speed condition shows the change in Flash-Lag caused by adaptation is significant ($F_{2,10}$=4.31, p<0.05) with planned contrasts showing this is driven by the difference between control and 20Hz adaptation conditions (F_5=18.14, p<0.01), not change between 5Hz and control (F_5=0.11, p=0.76). There is no significant effect for the 18.2° s^{-1} speed condition ($F_{2,10}$=0.41, p =0.68).

3.3.2. THE EFFECT OF TEMPORAL FREQUENCY ADAPTATION ON PERCEIVED SPEED

The baseline measure for both speeds is greater than the comparison bar speed (Figure 3-2b) and one sample t-tests show this to be significant for both speeds (18.2° s^{-1}: t_5 = 2.68, p < 0.05. 27.3° s^{-1}: t_5 = 4.14, p < 0.01). Objects in peripheral vision appear slower (Johnston & Wright, 1986) and the adapter may draw attention to the standard bar (Cavanagh, 1992), which makes it appear faster so these effects would account for our results, however it is the effect that adaptation has on the baseline measure that is of interest. As with the Flash-Lag experiment, we average across participants' PSEs to compare the effect of adaptation on perceived speed (Figure 3-2b) separately for the two bar speed conditions. Repeated measures ANOVA shows that the change in perceived speed is significant at the slower speed ($F_{2,10}$ = 5.49, p<0.05) but not quite at the faster speed ($F_{2,10}$=2.81, p =0.15, Greenhouse-Geisser corrected). At the lower speed, planned contrasts show a significant difference between control condition and 5Hz adaptation (F_2= 16.68, p<0.05) but not 20Hz (F_2=0.45, p=0.53). In summary 5Hz adaptation has the effect of increasing perceived speed at the slower speed and no effect on Flash-Lag, whereas 20Hz has the effect of decreasing Flash-Lag at the higher speed and no effect on perceived speed.

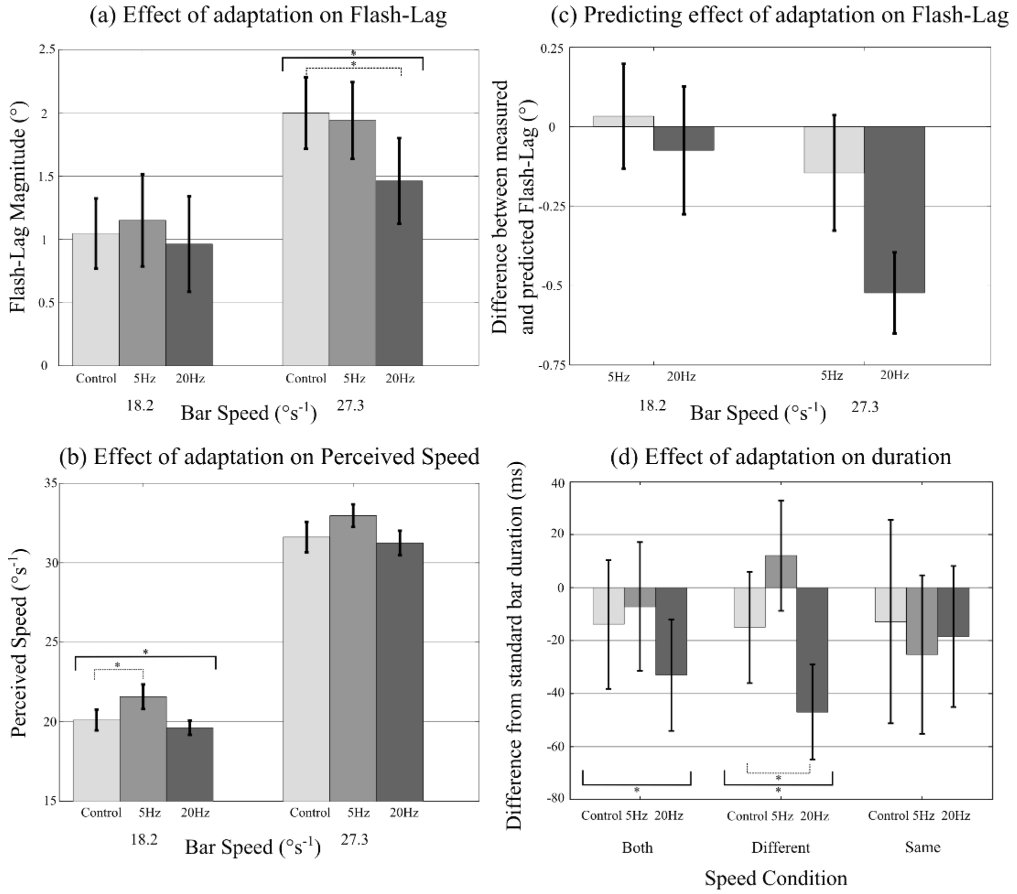


Figure 3-2: Results showing mean and standard error (N=6) for Flash-Lag. (a) where there is significant difference between control and 20 Hz adaptation in the faster speed condition, and Speed experiments (b) where there is a significant difference between control and 5Hz adaptation in the slower speed condition, * indicates significance at the 5% level with solid lines showing overall significant ANOVA and dashed lines indicating significant planned comparisons. (c) shows the mean of the differences between predicted and measured change in Flash-Lag after adaptation, error bars show standard error (N=6). Measured change shows a significantly greater reduction than predicted for 20Hz adaptation at the faster speed but not for any other, * shows significant effect at the 5% level. (d) Shows differences in perceived duration of a moving bar of 600ms where the standard and the comparison are moving at the same speed (18.2° s-1 or 27.3° s-1), different speeds (one bar 18.2° s-1, the other 27.3° s-1) or both different and same speeds. There is a significant effect of adaptation on both and Different conditions (* with solid lines) using ANOVA and a significant difference between 20Hz and control for different speeds (* with dashed line) in planned comparisons. Error bars show standard error (N=4).

3.3.3. EFFECT OF TEMPORAL FREQUENCY ADAPTATION ON PERCEIVED DURATION

As before, we fit curves for participants individually to estimate PSEs and then average the PSEs together to measure the effect. Repeated measures ANOVA shows a significant effect of temporal frequency when all trials are considered, ($F_{3,6}$=5.63, $p < 0.05$) and where only trials with different speeds are considered ($F_{3,6}$=11.61, $p < 0.01$) but not where only trials with the same speed are ($F_{3,6}$=0.24, p =0.80). Planned contrasts between both 5 and 20Hz with the control condition show that where trials with all speed combinations and only different bar speed trials are considered the effect at 5Hz is not significant (All: t_3 = 0.489, p = 0.54. Diff: t_3 = 2.474, p = 0.21) while 20Hz is significant for trials comparing the duration of bars moving at different speeds (t_3 =13.17, $p < 0.05$) but not quite when all trials are considered (t_3 = 7.919, p = 0.067). Overall, this experiment shows that 20Hz TF adaptation appears to compress the perceived duration of a moving bar, when comparing two bars moving at different speeds, i.e. when the distance travelled by the bar cannot be used as a cue.

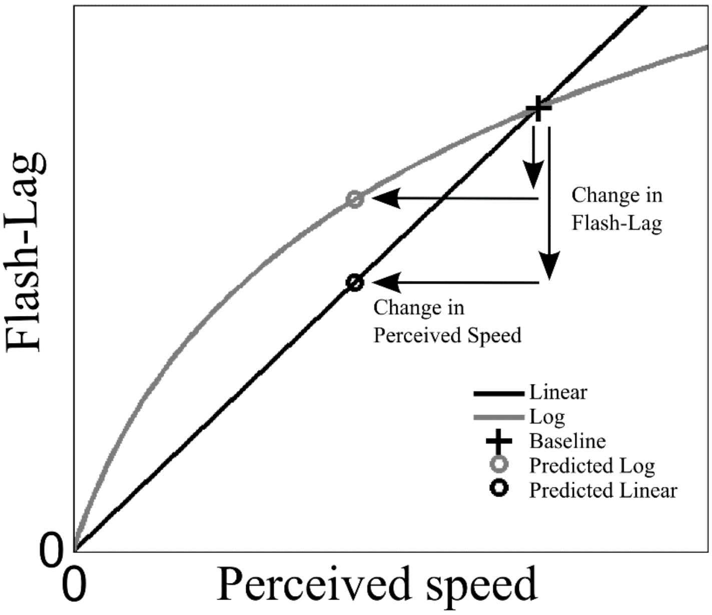


Figure 3-3: A linear relationship between speed and Flash-Lag passing through the origin and the baseline measure always predicts a larger change in the Flash-Lag Illusion given an observed change in perceived speed than a logarithmic relationship passing through the origin and the baseline measure. This means assuming a linear as opposed to logarithmic relationship between speeds and Flash-Lag gives the strongest test when compared to the duration compression hypothesis.

3.3.4. DOES CHANGE IN FLASH-LAG MATCH CHANGE IN PERCEIVED SPEED?

The pattern of the above results demonstrates an apparent dissociation between adaptation's effect on perceived Flash-Lag and perceived speed, which would not be the case if change in Flash-Lag was entirely dependent on the change in perceived speed caused by TF adaptation. We see in some conditions a drop in the size of Flash-Lag, whereas in some conditions perceived speed is increased, which should also increase the size of the Flash-Lag, if indeed Flash-Lag is dependent on perceived speed. The pattern of perceived speed adaptation is as would be expected, where adapting to low TF flicker causes a repulsion effect on TF, and hence speed (as spatial frequency is constant) causing a perceived increase in object speed and vice versa for high TF (Hammett et al., 2000; Smith & Edgar, 1994; Thompson, 1983). This means we are able to measure an effect on perceived speed and an effect of Flash-Lag, but they do not correspond. As Flash-Lag magnitude scales with physical speed, we needed to check whether a significant change in perceived speed would result in an equivalent change in Flash-Lag for that condition. Since this is not observed, this suggests another factor is involved in the observed Flash-Lag change other than a change in perceived speed alone. To confirm further that this is not due to lack of power and move away from comparing averages, we compared individual Flash-Lag measurements against the corresponding Flash-Lag predictions based on the change in perceived speed of the bar for each participant, assuming a linear relationship between Flash-Lag and perceived speed. We mentioned above that whilst the relationship between Flash-Lag and perceived speed is mostly linear at lower speeds, in fact it appears to be better described as logarithmic over a wider range of speeds (Wojtach et al., 2008). Figure 3-3 shows a logarithmic relationship would predict for the higher speed (where we observe a significant change in Flash-Lag, but not speed), a change in perceived speed to have a smaller effect on Flash-Lag than a linear relationship. This would make a reduction in perceived speed an even weaker explanation for the measured reduction in Flash-Lag. Therefore, by assuming a linear as opposed to logarithmic relationship we are pitting the hypothesis that 20Hz adaptation changes the time component of Flash-Lag against the strongest possible alternative hypothesis where change in speed is responsible for observed changes in Flash-Lag. In Figure 3-2c we see the change in Flash-Lag magnitude is underestimated if based on change in perceived speed after 20Hz adaptation at the high speed. This is not the case in any of the other conditions, as is confirmed by a comparison of predicted and measured Flash-Lags (2-tailed, paired sample t-tests, $18.2°s^{-1}$: 5Hz $t_5=-0.211$, $p=.841$, 20Hz $t_5=0.343$, $p = 0.746$; $27.3° s^{-1}$: 5Hz $t_5=1.061$, $p =0.337$, 20Hz $t_5=3.590$, $p <0.05$). However, we only measure a significant difference in perceived duration after 20Hz adaptation, not perceived speed, indicating duration compression

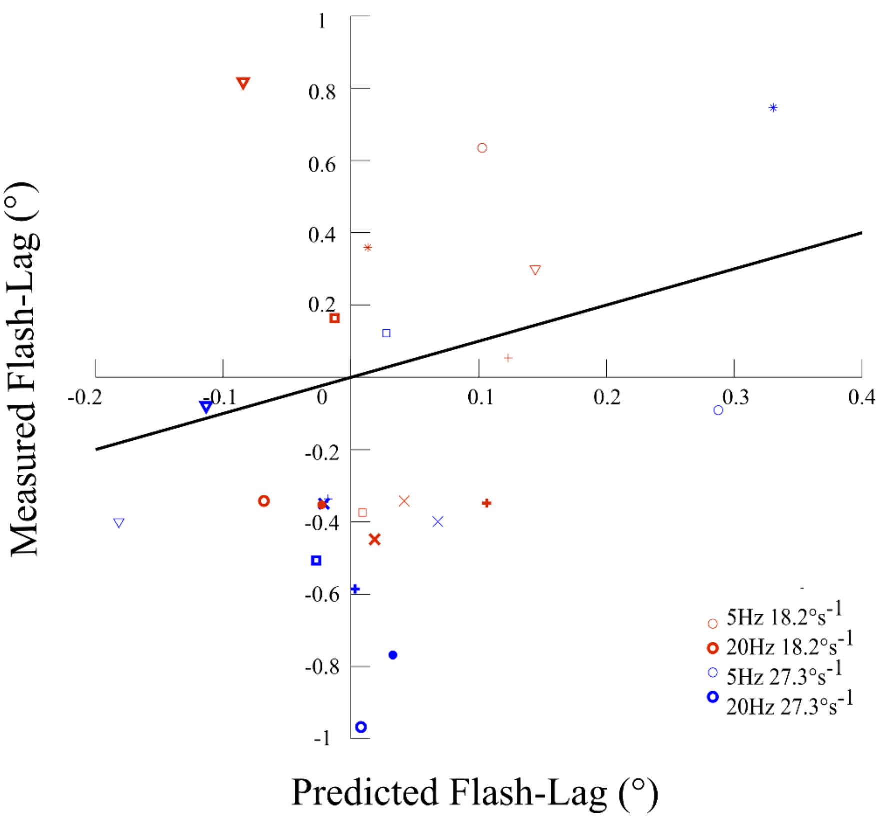


Figure 3-4: Scatter plot of predicted Flash-Lag from change in perceived speed versus measured change in Flash-Lag effects after TF adaptation. Different symbols correspond to different participants. Red shows slow while blue shows fast speeds with 20Hz results for both speeds are in bold and different symbols indicated different participants. Comparing results with the line of equality show all but a single participant have a larger than predicted drop in Flash-Lag for the 20Hz faster speed indicating change in perceived speed alone cannot explain the change in Flash-Lag for five out of six individuals.

effects of 20Hz adaptation have a stronger effect on Flash-Lag. Plotting each individual's data predicted by speed only versus measured Flash-Lag (Figure 3-4) shows a weak positive but non-significant correlation between these measures across all conditions (2-tailed Pearson's: $r_{24} = 0.333$, $p = 0.11$) reinforcing the finding that while perceived speed might have an effect on Flash-Lag it cannot fully explain the results collected. Given we show a compression of perceived duration an alternative explanation is that the time component of Flash-Lag is changing after 20Hz TF adaptation. To measure the magnitude of this effect we calculate the time component for each individual in each condition by time = Flash-Lag/perceived speed. For control and 5Hz adaptation, we found average time component of 54.2ms and 56.2ms for the lower and 64.0ms and 59.3ms for the higher speed respectively, fitting with previous estimates of Flash-Lag magnitude. At 20

Hz we found 50.8ms and 47.1ms time component, consistent with the time component shrinking by 8.3% (-3.4ms) in the slower speed condition, and 32.5% (-16.9ms) in the faster speed condition. This reduction in Flash-Lag time component is greater than the reduction in perceived bar duration which was 34ms (5.6%) for all trials and 47ms (7.8%) for trials with bars of different speeds, but the effect is in the same direction and would predict a reduction in Flash-Lag after 20Hz TF adaptation similar to what is observed.

3.4. DISCUSSION

We show two key findings in this study. The first is that TF adaptation changes the magnitude of the Flash-Lag effect and second, the change in Flash-Lag is not attributable to a change in perceived speed alone. In particular, Flash-Lag is reduced for the 20Hz adaptation condition only, by more than would be expected by speed adaptation alone. As 20Hz TF adaptation has been previously associated with duration compression (Johnston et al., 2006) and this is where we observe a reduction in Flash-Lag we conclude that 20Hz TF adaptation changes Flash-Lag in a manner that is consistent with the compression of the fixed time window associated with the Flash-Lag effect. Our estimation puts this compression of time at 32.5%, close to previous reports of around 22% (Burr et al., 2007; Johnston et al., 2006). We further confirm that duration compression does occur in our stimulus set-up. This implies that reducing perceived duration has an effect on these computations, which implicitly rely on duration based calculations. The lack of significant reduction in Flash-Lag at the slower speed after 20Hz adaptation may be due to the smaller baseline Flash-Lag displacement in this condition, making it harder to measure a reduction in perceived offset.

This effect on Flash-Lag ties in with results showing that both perceived time and space are compressed across saccadic eye movements, thought to arise from shifts in receptive fields anticipating eye movement, indicating an interlinked perception of time and space (Morrone et al., 2005). This is similar to what our experiments suggest, in that a compression of time is associated with a compression of space – in this case a reduced Flash-Lag offset, i.e. we show the compression with a moving object rather than eye movements. The mechanisms behind the effect shown by Morrone et al., (2005) are not clear, but saccades suppress magnocellular activity (Ross et al., 1996) and the attenuation of the Flash-Lag effect may be linked to the adaptation of the magnocellular (M) pathway, which is particularly sensitive to high TF flicker, as has been suggested by Johnston et al., (2006). It is possible then for computations carried out in the Magnocellular pathway to affect both perception of time and space simultaneously. This would also link our work in with results showing a reduction in the Flash-Lag effect when equiluminant stimuli (to which the M pathway is less sensitive) have luminance noise added (Chappell & Mullen, 2010).

The reduction in Flash-Lag time component can be explained by each of the proposed mechanisms underlying the effect. In motion extrapolation (Nijhawan, 1994), the position of the bar is extrapolated a shorter duration into the immediate future. For latency delay (Whitney & Murakami, 1998); either or perhaps both the processing of the flash is sped up or processing of the bar is slowed so the difference in their respective arrival at a perceptual end-point is reduced. For both integration (Krekelberg & Lappe, 2000a) and postdiction (Eagleman & Sejnowski, 2000) explanations there is a reduction in the size or possibly a shift in the position in time of the temporal window where the motion of the bar after the flash affects its perceived position.

One recent study (Bruno, Ayhan & Johnston, 2015) found that a Gaussian stimulus flashed in an area of the screen that had been adapted using a 20Hz temporal frequency stimulus resulted in that flash being perceived to appear sooner than a flash displayed in an unadapted area. This suggests a potential explanation of the results observed here is that the adaptor is causing the flash to appear sooner, therefore reducing the delay between perceiving the bar and flash (if such a delay causes the illusion). This results in the mitigated Flash-Lag illusion that is unexplained by changes in perceived speed observed here, i.e. less directly caused by duration compression per se, although the advancement of the flash is tied in with the effect of adaptation on time (Bruno et al., 2015). This might indicate 20Hz adaptation is reducing the relative delay between the static flash and moving bar but does not exclude other explanations. The high-speed flicker may prime the internal model of the environment to expect rapid changes in the environment, such as a flash, therefore reducing the need to discount the motion prior to the Flash. Modifications to this paradigm, most obviously adapting only the area covering the moving bar or the flash separately could provide further insight into the mechanism responsible for Flash-Lag and duration perception. Results of such an experiment would show if high TF adaptation affects the bar, flash or is an interaction between the two.

Since Flash-Lag magnitude is affected by prior knowledge regarding the distributions of object speed in the environment (Wojtach et al., 2008) and the predictability of flash locations (Namba & Baldo, 2004) it may be that time perception effects processes based upon expectations in the visual system. This provides a link with work on expectation and time perception (Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012; Schindel et al., 2011). One implication of the finding reported here is that for duration to affect other processes the visual system must encode perceived duration and this information must be spatially localized as duration compression effects of high temporal frequency adaptation are only observed within a couple of degrees of the adapting stimulus position (Ayhan et al., 2009).

There have been some proposed mechanisms for encoding duration such as state dependent networks (Karmarkar & Buonomano, 2007) which are computationally effective though difficult to conclusively verify, though there is evidence that neural systems encode time intrinsically (Goel & Buonomano, 2014). The neural energy hypothesis (Eagleman & Pariyadath, 2009) proposes that time is encoded by the amount of neural activity associated with an event. This framework aims to explain a number of duration effects including those caused by expectations and adaptation. Expected events show a suppression in BOLD, a strong correlate of neural activity (Larsson & Smith, 2012; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008), thus expected events are perceived to be shorter in comparison to unexpected events. In this interpretation duration, compression occurs after adaptation as adaptation reduces neural activity and thus reduces perceived duration. However, this does not explain why it appears only after adaptation to high temporal frequencies, so clearly this needs refining. Nevertheless, neural energy does offer a general framework to explain how duration is encoded within the brain. This topic is explored further in the following chapter.

Other work (Hogendoorn et al., 2010) has demonstrated that high speed TF adaptation causes a moving clock hand to be perceived further around a clock face than an un-adapted hand after accounting for change in perceived speed - the opposite direction to our finding. Furthermore, in the above study Experiment 3 shows that a hand on a clock face, in an area adapted to a 20Hz temporal frequency stimulus is perceived ahead of a hand in an unadapted area or adapted to 5Hz, when the outer circumference of the clock briefly (20ms) changes colour 1-2s after onset of the clock stimulus, something that our data apparently contradicts. Hogendoorn et al., (2010) explain this as a shift in the representation of the time course of events. Our explanation for our results is the Flash-Lag temporal component is compressed by high temporal frequency adaptation that reduces the (illusory) distance between moving bar and flash. We randomly varied the duration of the moving bar (the clocks were always presented for the same amount of time), and the relative position of the bar to the flash was not in any way connected by the task to the perceived duration of the bar. This requires the participants to focus on judging the perceptual offset, not when in the time course of the moving bar did the flash appear, so the explanation for Hogendoorn et al., (2010) does not quite apply to our results on the surface. Rather, by measuring the Flash-Lag explicitly as a relative spatial judgment participants are reliant on the fixed temporal component used in this calculation and it is this that is compressed. One point that Hogendoorn et al., (2010) make is that any mechanism that shifts the time of events backwards might also be able to shift it forwards as well. This suggests that a measure of duration or the effect of 20Hz temporal frequency adaptation on this measure of duration is task dependant so the way the visual system uses time is likely to be complex given the results across these experiments, this is perhaps an explanation that accounts for the results here and those of Hogendoorn et al., (2010).

We also find evidence of 20Hz TF flicker adaptation reducing the duration of a moving object that has not previously been demonstrated before, although this effect is smaller (47ms or a 7.8% perceived reduction from the actual duration of 600ms) than other reports that put duration compression magnitude at ~20% (Burr et al., 2007; Johnston et al., 2006) as well as our estimates of Flash-Lag time component compression. This may be due to (as we have seen) the bar trajectory providing an additional cue to duration. In addition, our estimate of compression does not allow for the fact that the change in perceived speed may have also had some effect. Importantly however, we are not claiming that it is the reduction in perceived bar duration over its entire presentation per se that reduces the size of the Flash-Lag magnitude, as there is still a great deal of debate as to what underlies the temporal component of the Flash-Lag illusion. However, we can say that the same effect of 20Hz temporal frequency adaptation that reduces perceived event duration here and repeatedly in literature (Ayhan et al., 2009; Burr et al., 2007; Johnston et al., 2006) also compresses the time component in the Flash-Lag illusion.

3.5. CONCLUSION

Although we cannot differentiate between the different Flash-Lag theories with our data, the main conclusion is that as all these theories rely on a fixed averaging/predictive/delay time component, and that component is compressed by high TF adaptation, suggesting that duration perception is intimately linked with motion and position computations, rather than being a separate process. Previously it has been suggested that the Flash-Lag illusion may be due to compensatory mechanisms, but interestingly in this example as the Flash-Lag magnitude is reduced, this provides a more veridical perception of the stimulus, which may be advantageous in an environment containing rapid change (signalled by high TF flicker), where such compensatory mechanisms may not update speedily enough. Specifically, locally malleable time perception may play a key role in position calculations.

4. CHAPTER FOUR - A MODEL TO ESTIMATE DURATION

4.1. INTRODUCTION

There has been a general shift from central clock mechanisms, such as those discussed in Chapter 1 (Gibbon, 1977; Gibbon, et al., 1984; Treisman et al., 1990; Wearden, 1991), leaving a gap in the literature regarding what mechanisms might be used to measure event duration in the brain. Recent evidence suggests that duration is computed within sensory systems (Ayhan et al., 2011; Bruno & Johnston, 2010; Burr et al., 2007; Johnston et al,. 2006; Marinovic & Arnold, 2011; Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012; Schindel et al., 2011), which follow a distributed, hierarchical information processing structure.

The purpose of this chapter is to demonstrate how event time can be estimated using basic, biologically plausible properties of neural systems, then test the limitations of the model with the aim of providing a useful 'back-pocket' model of a duration encoding mechanism for evaluating experimental evidence. The input signal encodes a presence of a sensory event, so a value of zero indicates that there is no stimulus and values above zero encode the magnitude of a particular stimulus property. For example, for encoding luminance, a brighter object provides a higher input magnitude. The stimulus lasts for a particular duration, which is represented by how long the input magnitude is greater than zero in a step on-off function. From this on-off signal, the model estimates how long the stimulus persists in the visual field or receptive field of a neuron, encoding this duration without employing an oscillator as a timing signal.

Initially, it may be tempting to encode and compare the onset and offset times to provide a measure. However, this does not solve the problem, as it requires encoding the time of when onset and offset occur, passing the task of measuring duration to another level rather than solving the problem in the local process itself. Evidence suggests that onset and offset times can be manipulated after TF adaptation (Bruno et al., 2015). However, reported changes in duration can be manipulated in a manner that cannot be accounted for by changes in perceived onset and offset time (Johnston et al., 2006) implying that, to some extent, perceived duration is processed separately from perceived onset and offset times. Instead, the model presented here will use time variant properties of neural systems to encode duration similar to the approaches taken by Goel and Buonomano (2014) and Johnston (2010).

4.2. MODEL OUTLINE

One fundamental property of neurons is acting as a low pass filter. Low-pass filters can describe dynamics of many systems within the brain. From the scale of ion channels in the Hodgkin-Huxley model (Hodgkin & Huxley, 1952) neurons and Integrate-and-Fire models (Abbott, 1999), to forming a basic requirement of motion-detector circuits, such as Elementary Motion Detectors (Borst & Egelhaaf, 1989) and the response of populations of neurons to form channels such as those used for coding the temporal frequency of a visual stimulus (Hess & Snowden, 1992).

A low-pass filter can be described by its temporal response function (Equation 4-1), and the model makes use of these temporal dynamics to estimate duration. The low-pass output monotonically increases over time approaching a final value, proportional to the intensity of the input (here arbitrarily scaled to unity). This means the stimulus has to persist for a minimum duration for the filter output to match the input magnitude at a given level. It is crucial to notice that for relatively short durations, as compared to the filter time constant, the filter output growth is approximately linear. This temporal property of low pass filters, offers a method to estimate the input duration.

A second component of the proposed model is a threshold (T). The low-pass output is passed to a threshold switch, so if the low-pass output is greater than T, it activates the switch, causing it to generate an output of 1, if it is less than T, the switch output is 0. Effectively, the non-zero switch output indicates if the input stimulus has persisted for a particular duration.

This duration estimate is determined by two variables: the low-pass filter time constant, τ and the threshold, T. τ defines the slope of the low-pass filter's response. With a larger τ, the response gradient becomes shallower and so the stimulus has to last a longer time for the filter output to reach T. For larger values of T, the output has to reach a greater magnitude to activate the switch. Thus, the input stimulus has to persist for a longer

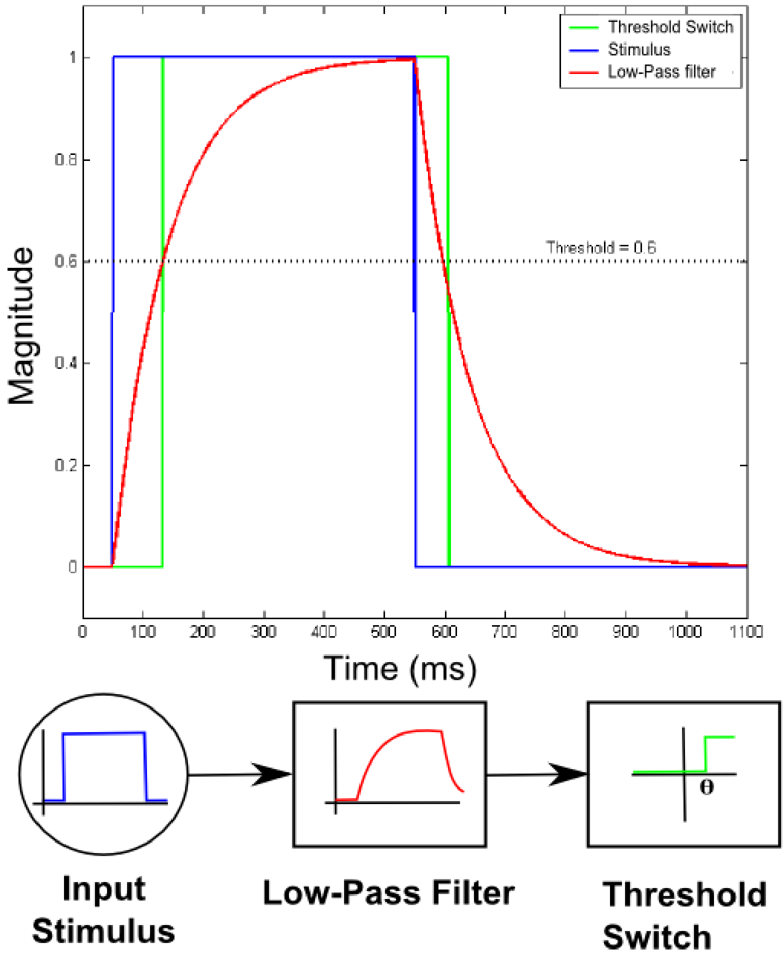


Figure 4-1 Showing the components of a Simple Duration Detector (bottom) with an on/off input passed through the low-pass filter, which feeds, into a threshold switch where the output state is dependent on whether the input from the low-pass filter exceeds a set value (T) and provides the final output of the detector of 1 or 0. The graph (top) shows the output for different components of the Simple Duration Detector with a low-pass time constant (τ) of 100ms and a T of 0.6 in response to a square wave on-off stimulus of 500ms duration coloured according the bottom illustration of the components.

duration. In the proposed model we set the threshold at a constant meaning the time that threshold is reached is entirely defined by the filter τ. Together, these two components; the low-pass filter outputting to a threshold switch gives what is termed a 'simple duration detector' or SDD and forms the key component of the model.

4.2.1. REPRESENTING EVENT DURATION

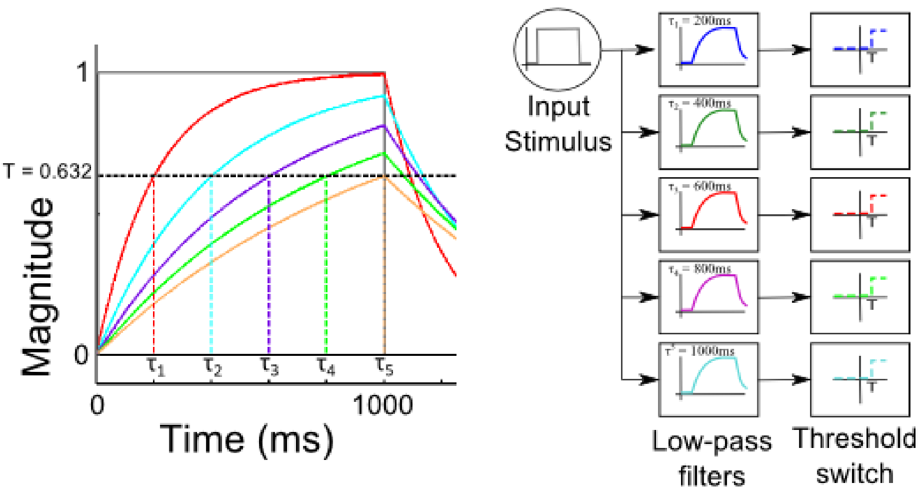


Figure 4-2: A population of SDDs is shown, receiving an input of duration 1000ms with 5 different low-pass filter responses to that input (blue, green, red, purple, cyan lines). The graph on the left shows a step on/off input (grey) and the low-pass filter response with five different values of τ (200,400,600,800 and 1000ms) representing filters in a SDD population (right – coloured respectively). Each filter output crosses the threshold (0.632 – black dotted line) at a time equal to the filter constant τ (coloured respectively - dotted) where the SDD output switches from zero to one.

A single SDD can indicate if the input stimulus has passed a particular duration defined by the filter time constant τ and threshold T. Clearly, any duration encoding mechanism will need to encode duration across a range, so the proposed model uses a population of SDDs with a range of time constants to encode the duration of an input signal by a labelled lines method (Figure 4-2).

Labelled lines are the simplest way of thinking of encoding information within neural systems across modalities. It is used in models, for example detecting motion direction in MT (Maunsell & Van Essen, 1983). Labelled lines are also used in representing space in retinotopic maps - where a neuron responds to a stimulus at a particular area in the visual field, which can be thought of its spatial 'label' (Wandell, Brewer, & Dougherty, 2005), to representing sensory homunculi in the somatosensory cortex (Kaas, Nelson, Sur, Lin, & Merzenich, 1979). Similarly, labels have been used as a basis of reading output from models for the olfactory system (Kauer & White, 2001).

In the present model, the last SDD to reach threshold indicates the most recent stimulus duration estimate and is updated every time a detector switches on, by the SDD label of the latest detector to switch on. This allows a measure of duration whilst still receiving an input signal, as the value updates in real time. The low pass filter output does not increase when there is no input and decays when input drops to zero, so cannot trigger the threshold switch. The last detector to switch on indicates how long the event has lasted during the event itself. When an event has ended, the value indicated by the last detector to have switched on needs to be stored in memory after the event has past, raising the question of how the label is stored, but this is less a problem of sensory perception and more of memory, so is beyond the scope of the model.

A key property of this model is that while a final duration estimate requires a stimulus to be present for a given time, it is not dependent on the absolute time of stimulus onset or offset, and it is explicitly represented in the system. To create a labelling scheme, the threshold is fixed at a value of 0.632. This value is chosen as τ represents the time it takes for the low pass filter output to reach $1 - e^{-1}$ (~ 0.632) of the input stimulus intensity. This value is arbitrary and not crucial to model function but it is chosen for two reasons. Firstly, low pass filter response is approximately linear up to this point, which means the durations encoded by a population are also linear. Secondly, the filter time constant τ corresponds to the time after onset where a detector switches on, making the duration encoded by each SDD intuitive to interpret and representative of the SDD properties.

One possible alternative to this would be instead of a population, to use a single low pass filter with a larger τ and multiple thresholds to indicate duration. The problem here is the low-pass filter response is non-linear over time so such a coding scheme would have to consider this. This would also effectively involve directly measuring the duration of a stimulus in terms of the duration of response of a single ‘timer’ neuron, which is something we are trying to avoid as this becomes too similar to the idea of a more centralised timing area. There is one key assumption at this stage in this chosen, single threshold-labelling scheme, that the input level I is always equal to 1 when a stimulus is present. Changing this value changes the duration estimate from the model. For example, if the input value is 2, the filter output gradient will be twice the assumed gradient, causing the detector to switch on in half the time (with this fixed rather than proportional threshold value).

This creates a problem, as the model cannot encode duration unambiguously without knowing input magnitude itself, thus also encoding some property of the stimulus. This will be discussed in Section 4.2.4 and resolved in Section 4.3, leading to interesting implications for the model. At this stage, however, the model will assume a normalised input intensity of 1, so the basic properties of the SDD population can be examined.

4.2.2. MATHEMATICAL FORMALISATION OF THE MODEL

The first stage in the proposed model computes the temporal response of a first-order low-pass filter *(*O_{LP}*)* at duration *(d)* with time constant (τ) in an individual SDD to the input stimulus (I), Equation 4-1. In the computer program implementing the model, the filter output at a particular duration *d*, $O_{LP}(d)$, is computed iteratively as a difference function as defined in Equation 4-2 where Δd is defined as the size of the timestep.

Equation 4-1

$$\mathrm{O_{LP}(d) = I\left(1 - e^{\frac{-d}{\tau}}\right)}$$

Equation 4-2

$$O_{LP}(d) = I\left(\frac{\Delta d}{\tau + \Delta d}\right) + O_{LP}(d-1)\left(\frac{\tau}{\tau + \Delta d}\right)$$

$$\text{Where } O_{LP}(0) = 0$$

The second step calculates the threshold switch output at a particular point in time *$O_{TS}(d)$* as

Equation 4-3

$$O_{TS}(d) = \begin{cases} 1, & O_{LP}(d) > T \\ 0, & otherwise \end{cases}$$

The duration (D) indicated by the SDD is shown in Equation 4-4 for a constant input magnitude(I_{μ}), which with the normalised input amplitude of $I_{\mu} = 1$ reduces to Equation 4-5

Equation 4-4

$$D = O_{TS}\frac{\tau}{I_{\mu}}$$

Equation 4-5

$$D = O_{TS}\tau$$

Computing duration estimates for a population of n SDDs using Equation 4-5 generates a set of indicated times (P) as

Equation 4-6

$$P = [D, \ldots, D_n]$$

The largest value D_I of set P finally provides the duration of the input I as Equation 4-7

$$D_I = \max(P)$$

4.2.3. MEASURING EVENT DURATION FOR A SIMPLE ON-OFF STIMULUS (STEP FUNCTION)

The model is run to show that the SDD population works across a range of durations. The input consists of a step function varying from 0 to 1, then back to 0 again, with the duration the step function set at 100, 250, 500 and 1000ms, with ‘off’ periods of the same duration as the step function before the start and after the end of the stimulus.

The population consists of 100 SDDs with τ values of 10ms to twice the input duration using 10ms steps; this dictates the temporal resolution of duration detection. The threshold of 0.632 as in Figure 4-2 is kept constant across the population. We show raster plots for the filter and final outputs for each duration in Figure 4-3 and Figure 4-4, the overall value calculated from the population measure of duration is plotted against actual duration in Equation 4-5. Figure 4-3 shows that the low-pass output is homogenous if the population τ scales with duration output, with aliasing visible at the shorter durations as the population τ resolution does not scale with duration, if it did the four low pass output graphs would look identical apart from the axis numbers. This temporal aliasing is also visible in the duration detector output in Figure 4-4 again due to the population τ resolution.

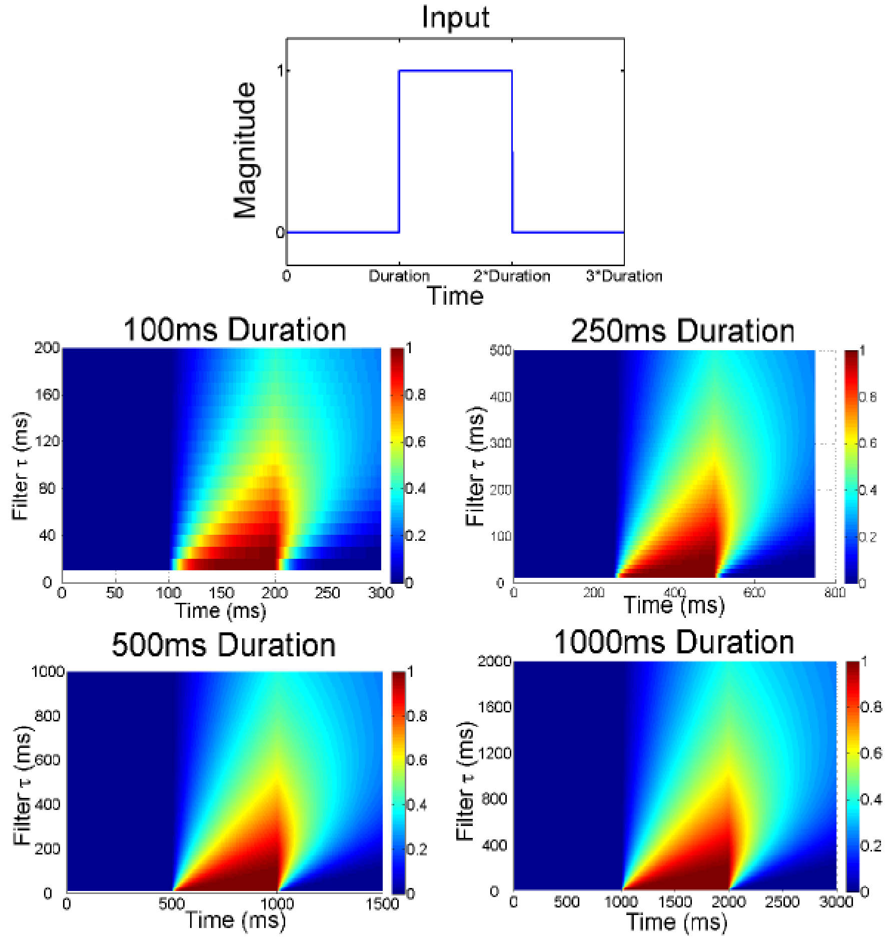


Figure 4-3 : The output of the Low-pass filter component in response to the input (top). The input graph shows the magnitude of the input (y-axis) and the time (x-axis). The bottom four graphs show the low-pass filter output for different stimulus durations. X-axis shows time, y-axis is the τ of the particular low pass filter and the colour shows the output magnitude given by the colour bar.

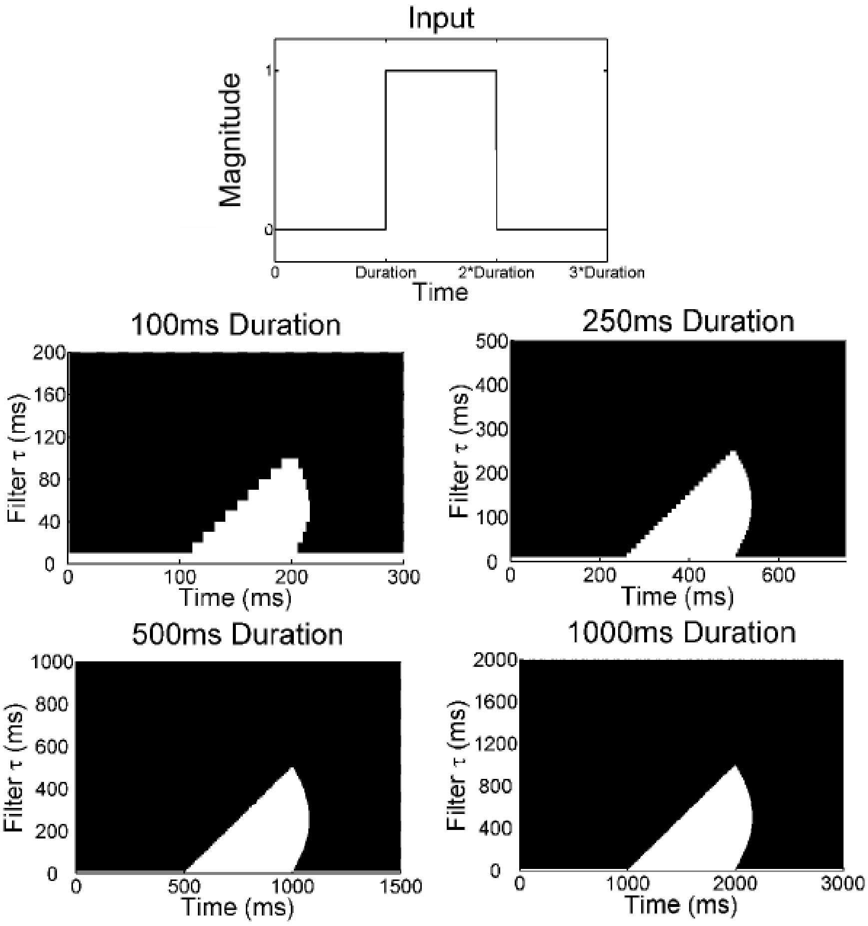


Figure 4-4: Shows the output of the threshold detector with the threshold set at 0.632 in response to the input from the low pass filters' (shown in Figure 4-3) response to the model input (top).). The input graph shows the magnitude of the input (y-axis) and the time (x-axis). The output of each detector is shown in the four graphs below x-axis shows time, y-axis is the *τ* of the particular low pass filter, black shows an output of zero, white shows and output of 1.

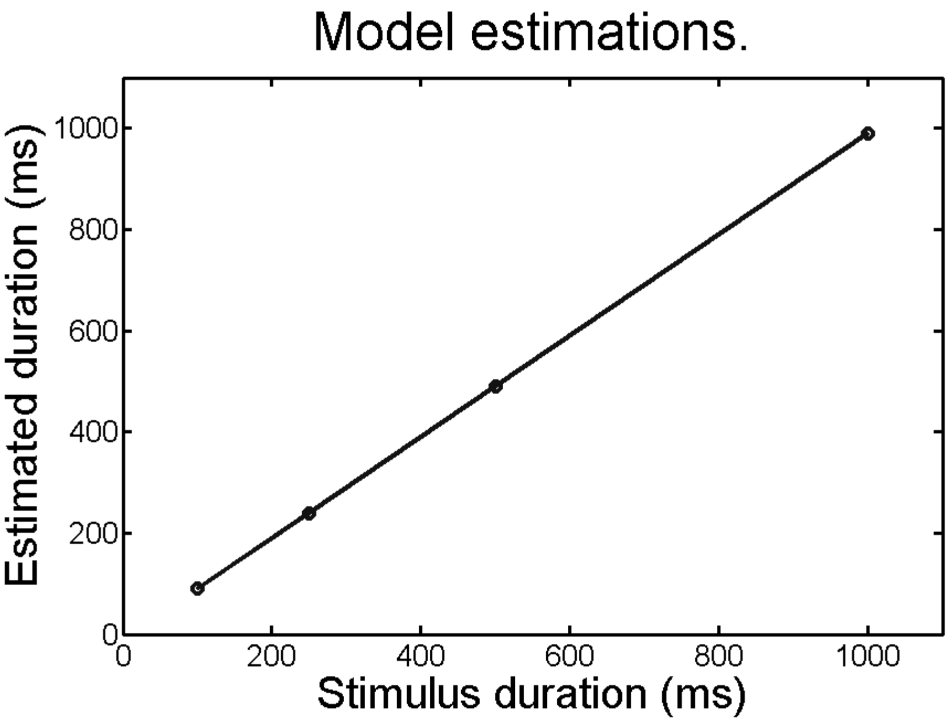


Figure 4-5 Shows duration estimates versus actual durations for 100, 250, 500 and 1000ms. The estimates match stimulus duration.

4.2.4. EFFECT OF SIGNAL MAGNITUDE ON DURATION ESTIMATES

As stated before and shown in Equation 4-4 and Equation 4-5, the model can only be expected to give consistent duration estimates if the input magnitude of the model is constant. Estimates for stimuli of differing input magnitude are gathered for range from 0.75, to 2 magnitudes with 0.25 steps of 200,400,600 800 and 1000ms. Figure 4-6 clearly shows that the duration of the stimuli vary according to their input magnitude. This is not a realistic model for duration estimation in its current form as the duration estimation is as much based on the stimulus properties represented by the input signal magnitude as it is on the stimulus duration.

There is some evidence in literature showing perceived duration increases with the magnitude of various stimulus properties such as brightness (Brigner, 1986; Terao, Watanabe, Yagi, and Nishida, 2008), speed (Brown, 1995; Kanai, Paffen, Hogendoorn, & Verstraten, 2006) or temporal frequency (Kanai et al., 2006) and size (Xuan et al., 2007). However, these effects show fractional relative variations not on the scale of the relationship observed in the model. This means the basic SDD model is not feasible without additions to control the input signal magnitude through a form of signal normalisation discussed in Section 4.3.

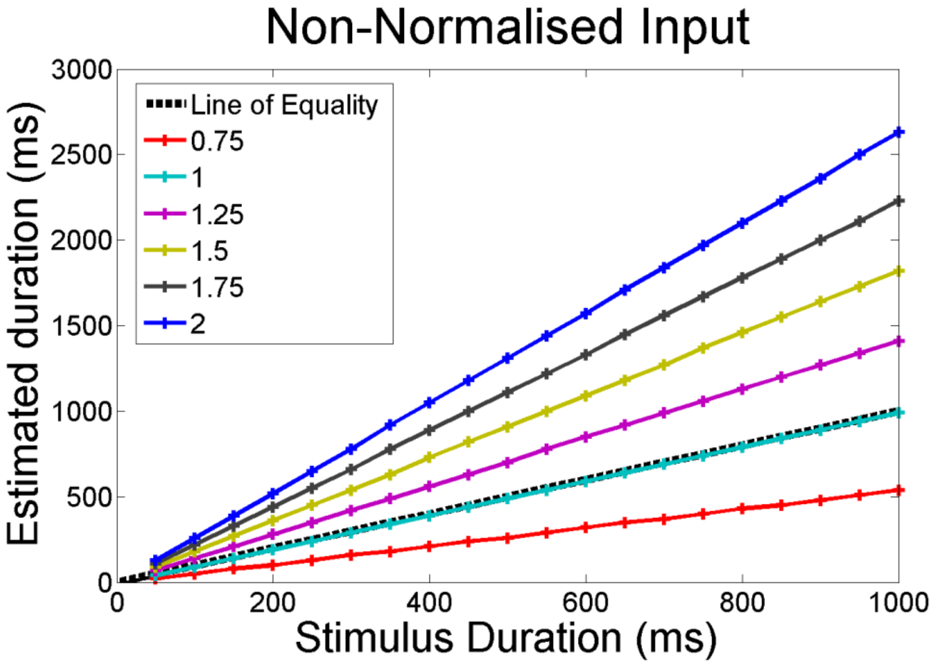


Figure 4-6: Above shows model duration estimates versus actual durations for stimuli of varying input intensities (coloured). This shows that duration estimates are as much influenced by the input signal magnitude as they are the duration of the stimulus as indicated by Equation 4-4.

4.2.5. ESTIMATING DURATION OF AN IMPULSE (δ DIRAC) FUNCTION

An impulse is an input of infinite magnitude over an infinitely small period-of-time. It is used to demonstrate the temporal dynamics of a system and provides an interesting test for the model to investigate its output. It is impossible to use an impulse as input into the model because the low-pass output is computed iteratively meaning an infinite input over an infinitely small period would result in an undefined output. Instead, an input of 1ms (a single timestep) with a magnitude of 2000, 1000 times greater than the largest magnitude that is used elsewhere, forms a suitable approximation of an impulse response. The SDD population has τ of 200-1000ms with 200ms steps in this example. The output is shown in Figure 4-7. The shape of these impulse response functions convolved with the input gives us the response to all possible signals at this stage in the model.

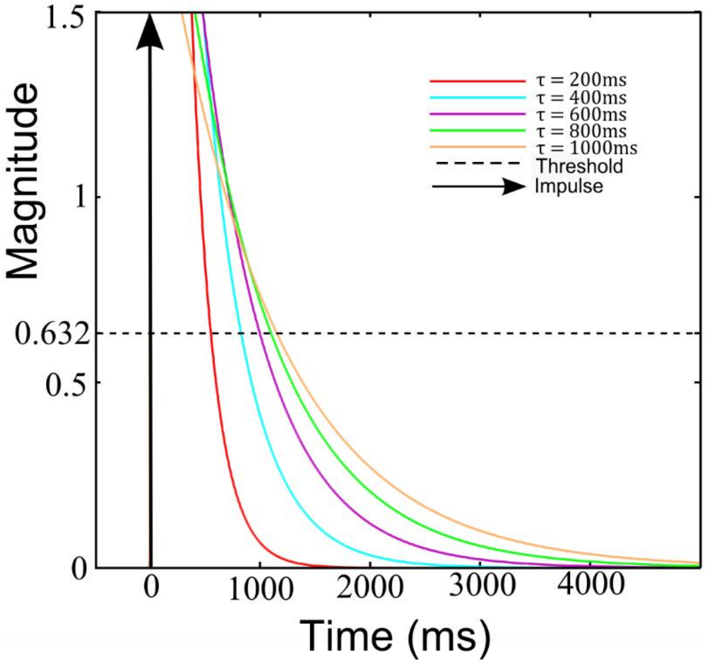


Figure 4-7: Impulse response of low pass filters in an SDD population (coloured) to an approximated impulse at time = 0 (Black arrow). All filter outputs exceed threshold (black dashed), so the model duration judgment is the label of the SDD with the largest τ, in this case 1000ms.

After the threshold stage the SDD population estimates the duration of the input to be 1000ms as this is the longest duration the population can encode. What this demonstrates is the impulse drives the output of all low pass filters to exceed threshold. Therefore, the duration indicated by the SDD with the largest τ gives the duration of the impulse.

Another interesting question to ask is what is the smallest possible impulse magnitude to drive a detector of time component τ to output a value of greater than 0.632, i.e. switch it on? It is possible to show this from Equation 4-2. Output $O_{LP(d)} = T$ or 0.632, and Δd is 1, the smallest possible duration we can input into the model, which gives Equation 4-8 . This can be rearranged in terms of the input I, shown in Equation 4-9 that can be used to determine the smallest impulse magnitude to switch a detector on.

Equation 4-8

$$T = I\left(\frac{1}{\tau + 1}\right)$$

Equation 4-9

$$I = T\tau + T$$

With our labelling scheme set up so detector τ is the duration indicated by the detector it is possible to rearrange Equation 4-9 in terms of τ, taken to be the estimated duration of the input $D_{(I)}$ shown in Equation 4-10.

Equation 4-10

$$D_{(I)} = \frac{I - T}{T}$$

Hence, this shows the relationship between input magnitude *I* and duration estimate $D_{(I)}$ so that with increasing input intensity the duration estimate also increases, as shown in Section 4.2.4. In fact, given no limit on the maximum duration measurable by the population the model would estimate the duration of the impulse with a magnitude of 2000 as ~3163ms, depending on the spacing of the time constants of the detectors. However, at the other end of the spectrum, given our population of detectors, the size of an impulse needs to be of magnitude 6.95 to trigger a shortest duration detector with τ=10ms. Compared to the size of our standard input of magnitude 1, this is ~7 times larger, so it would need to be a very large impulse to trigger any duration detectors. Inputs of less than T would result in negative duration judgements. This is not sensible, instead negative durations can be interpreted as have a duration of zero, this makes practical sense as the input will not be strong enough to cause any detectors to switch on. What does this mean for the model? If the input magnitude represents a stimulus property, e.g. luminance, then the input represents an extremely short and bright flash. The model predicts the duration of a very bright, very short flash to be perceived as lasting a much longer than reality. There is some evidence of this with brighter flashes being perceived to last longer, although this may be due to photoreceptor properties also (Bowen et al, 1974).

4.2.6. ESTIMATING THE DURATION OF TIME VARIANT STIMULI

So far, the stimulus used here does not change over time between onset and offset, whilst many sensory stimuli will do, such as flickering or moving stimuli. The next test is to use the model to estimate durations of sine and square wave inputs. The mean input intensity is set as 1, as before, so the square and sine waves have a peak magnitude of 2 and minimum of 0. The SDD population is set up as before with the input stimulus lasting 200,400, 600, 800 and 1000ms for a 10Hz input varying between 0 and 2 magnitude. These durations are chosen so the 10Hz input completes 2, 4, 6, 8, and 10 cycles for each duration respectively, as if the input ends in the middle of a cycle the input magnitude would not average 1. Figure 4-8 shows the duration estimates.

There is little difference in duration estimates between the different input types, showing the model is robust towards stimulus type, thus can estimate durations of time variant stimuli. This appears promising but temporal frequency of a stimulus has in fact been empirically found to have an effect on perceived duration. Kanai et al., (2006) show that increasing temporal frequency increases the perceived stimulus duration which is not observed here.

Square and sine waves exhibit a consistent but minor underestimation. This is caused by the nature of the time variant signal. Each oscillation can be broken up into two halves, the first 180° of the oscillation where it peaks in magnitude and the second 180° with the trough of the oscillation. Immediately preceding offset, the signal passes through the trough phase meaning the input to the detector population is reduced through this period when compared to an on-off step input despite fixing mean intensity at 1 over the duration of the stimulus. As established in Section 4.2.4, a reduced signal magnitude means an underestimation of duration that is observed here that explains why time variant signals are perceived to be shorter in duration.

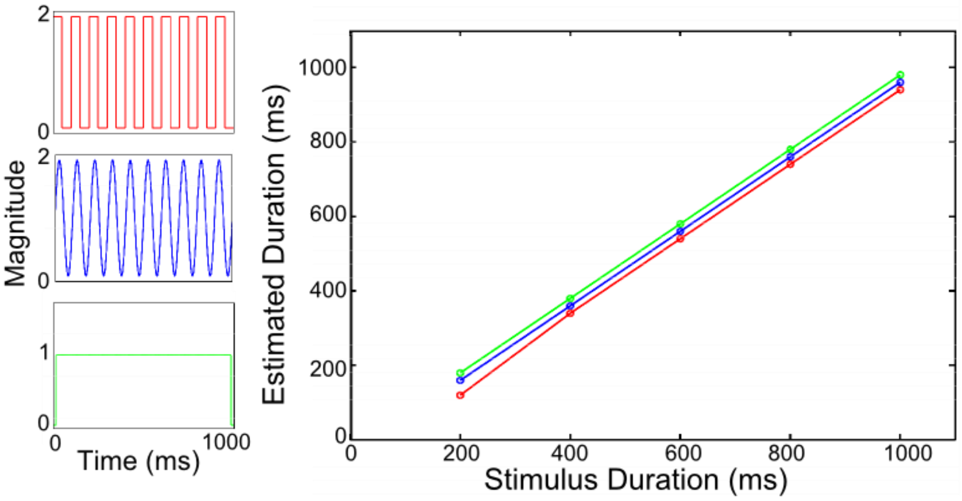


Figure 4-8: Shows the stimulus vs estimated duration of sine, square (both 10Hz) and continuous inputs (coloured respectively) each with a mean magnitude of 1 across the duration of the stimulus. There is little difference between the estimations of time-variant and continuous stimuli.

4.2.7. EFFECT OF CONTRAST ON DURATION ESTIMATES OF TIME VARIANT STIMULI

Another stimulus property that varies in the real world is stimulus contrast, i.e. the difference between the smallest and largest input magnitude of a stimulus varying over time or space. The simplest example of this is luminance contrast, though the stimulus could also represent other properties such as position or velocity of an object moving in a repetitive, back and forth motion. 10Hz sine waves with differing Michelson contrasts (Equation 4-11) with the same mean magnitude (Table 4-1 for full values) and durations of 200, 400, 600, 800 and 1000ms are input into the model.

As shown in Figure 4-9 the input contrast does not affect duration estimates, which again shows the model is robust toward differences in stimulus properties. This is because low-pass filters integrate the input over time effectively blurring the signal, so transient changes in the input do not change the model estimations, only the mean input magnitude over time. There is slight mismatch in duration estimates of different contrasts, but this is due to the differences in peak magnitude of the inputs of differing contrast. The direct effect of the contrast on the stimulus' perceived duration has not been reported so far, rather it is the intensity of the stimulus that seems to have an effect (e.g. Alards-Tomalin et al., 2014) so this matches with current knowledge. Albeit rapid adaptation to high contrast does affect duration (Bruno & Johnston, 2010) and this will be investigated later in this chapter.

Equation 4-11

$$\frac{I_{max} - I_{min}}{I_{max} + I_{min}} = \ Contrast$$

Table 4-1: values for the stimulus input in Figure 4-9.

Max Magnitude	Min Magnitude	Mean Magnitude	Michelson Contrast
1.1	0.9	1	0.1
1.5	0.5	1	0.5
2	0	1	1

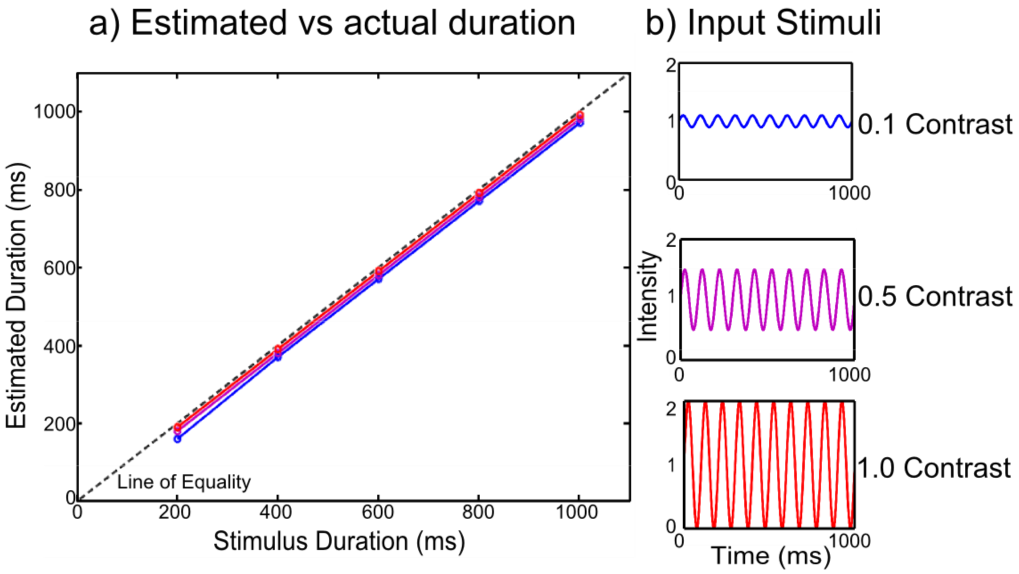


Figure 4-9: a) Shows the input of three sine waves with values from Table 4-1 varying in contrast and shown in b) with respective colours. The stimulus and estimated durations match closely as indicated by the line of equality (Black, dashed) and contrast does not appear to affect the estimates.

4.2.8. EFFECT OF TEMPORAL FREQUENCY ON DURATION ESTIMATES

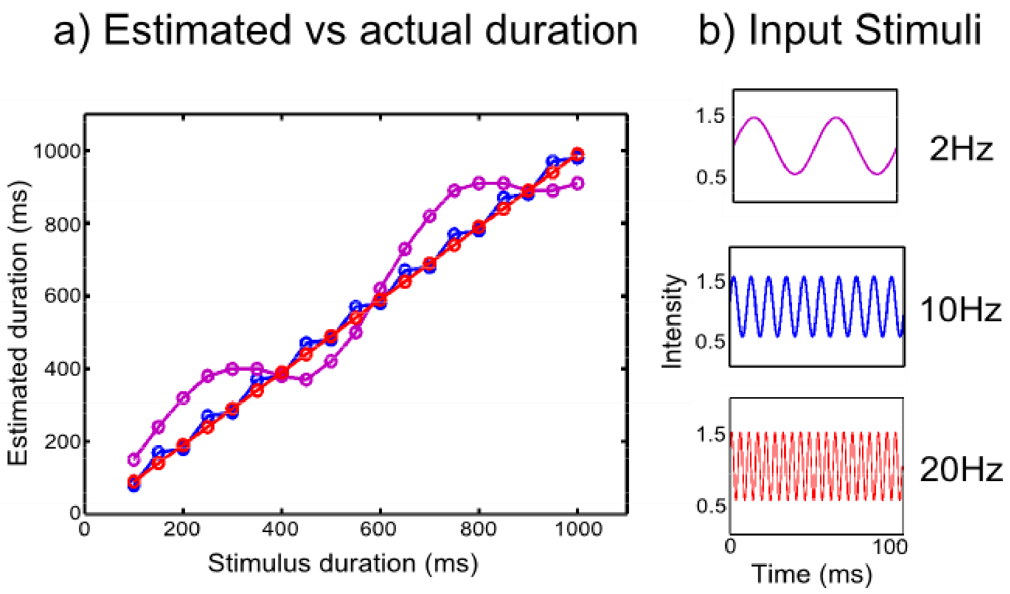


Figure 4-10 Right shows input of differing frequencies and left shows the estimated verses actual durations for the different frequency inputs, coloured respectively. There is a variation in the duration estimates depending on the input phase at that point in time, an artefact of variations in mean magnitude at that point in time.

One property of time variant stimuli is their temporal frequency, which corresponds to speed of a moving periodic stimulus or rate of change in the environment. The model is tested for sine-wave inputs of varying temporal frequency (2, 10 and 20Hz) for durations of 50ms to 1000ms with 50ms steps and magnitude oscillating between 1.5 and 0.5 keeping a mean magnitude of 1. Figure 4-10 shows the estimated durations for each stimulus.

Here, there are variations in the duration estimate depending on the stimulus duration and the temporal frequency of the input stimulus. 20Hz shows a clear linear relationship between the stimulus and estimated duration as observed previously, while both 10 and 2Hz stimuli are under or overestimated compared with 20Hz depending on the duration. This is a feature of the effect described in 2.2.

Time variant inputs are underestimated compared to a continuous input due to a reduction in input magnitude preceding offset. As a wider variety of durations than the previous two sections (50ms, rather than 200ms steps) are shown and the input durations have not been selected as to match a whole number of oscillations, sometimes the duration is overestimated, and sometimes underestimated depending on the oscillation phase at offset. This means the difference between duration estimations of signals with differing temporal frequencies is not due to the temporal frequency per se, but the variations in mean input magnitude at offset. This could provide a limitation for the model as at lower temporal frequencies duration estimations vary, but it also shows a potential strength of the model regarding flickering or moving stimuli. Time variant stimuli for example: a light switching on and off, analogous to the square wave input here, have two durations associated with them, the duration the light has been switching on and off for and the duration of the on phase.

A question arising from this is how can the visual system estimate both the duration each time the light comes on and how long the light has been flickering for at the same time? As we see the duration estimates oscillate as a function of the input frequency, this shows oscillation duration affects the duration estimate in the model.

There might be possible ways to extract the information about the duration of the input phase, which could reduce the problem of the input frequency distorting duration estimates. One is to have separate populations of SDDs, encoding different duration ranges, i.e. one for longer and one for shorter durations, allowing simultaneous readouts of both the duration of each oscillation and the overall stimulus duration. Although this relies on prior knowledge about the stimulus frequency to set effective cut-offs.

Another way would be to separate out the stimulus component frequencies and estimate the duration for each using a separate SDD population. What also affects the duration estimates is the resolution of the duration detectors. The estimates for the 20Hz in Figure 4-10 appear linear as the SDD population resolution is such that it coincides with the wavelength of the stimulus input so it is not affected by variations in the stimulus magnitude.

4.3. NORMALISATION OF THE INPUT SIGNAL

Section 4.2.4 demonstrates that when the input signal violates the constant mean input intensity assumption it creates large errors in duration estimates. To correct this issue the input signal can be fed through a normalisation stage before passing to the SDD population (Figure 4-11). This mechanism controls the mean input to the SDD population so that it approximates a set value over time, meaning the constant mean input assumption is reasonable.

The mechanism uses normalisation, a process where the signal intensity encodes relative magnitude of a particular property rather than absolute magnitude to achieve this. There are many examples of normalisation in the visual system, for example; a neuron encoding luminance contrast with a particular receptive field will receive inhibitory input summated from other neurons encoding luminance contrast in the areas surrounding its receptive field (Carandini & Heeger, 2011). The model uses a form of the normalisation equation from Carandini and Heeger (2011) to normalise input to the SDD population, shown in Equation 4-12.

Equation 4-12

$$I_D = \frac{I}{\sigma + I_\mu}$$

Where I is stimulus input to the model, I_μ is the normalisation factor, it is a running average defined by the temporal window across which the input I is averaged. σ is a normalisation constant acting as free variable to fit experimental data as well as avoiding dividing by zero at the instance of stimulus onset where I_μ would be 0. Finally, I_D is the input to the detector population.

The normalisation mechanism in the model normalises the signal over time by dividing the input at a particular point in time by a running average of the signal intensity by using a low-pass filter (another one, separate to those that form part of the SDDs described in Equation 4-1 and Equation 4-2). Normalisation is often implemented spatially but dynamic normalisation, similar to that shown here, has also been used previously to model neural systems (Louie, LoFaro, & Webb, 2014; Wilson & Humanski, 1993).

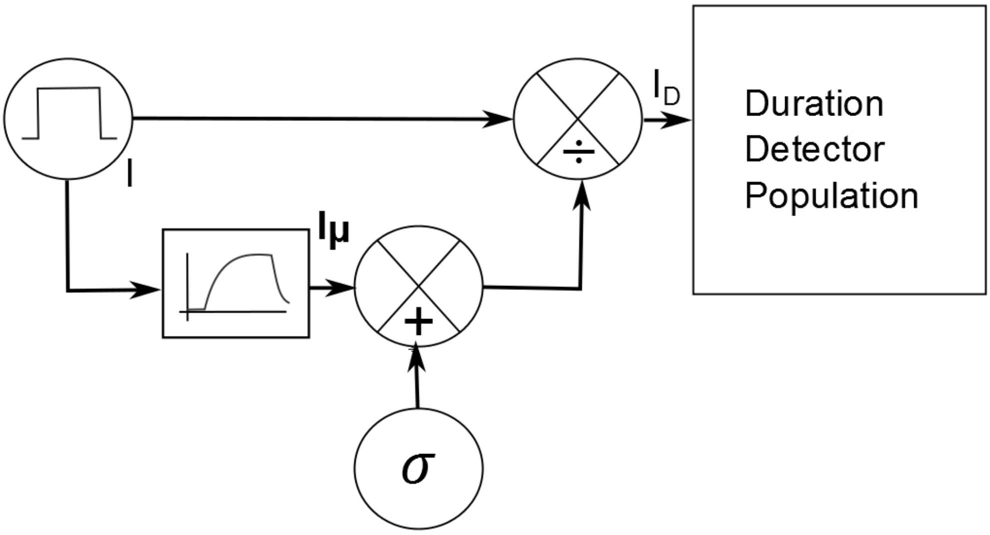


Figure 4-11: A circuit diagram of the normalisation process used in this model so that the duration detector input (I_D) can be assumed to approximate a set value. The input stimulus (I) passes through a low-pass filter to compute a running average of the input signal magnitude (I_μ), given by Equation 4.1 before summing with a constant (σ). The instantaneous input is divided by the running average plus the constant, to give the input to the SDD population (I_D).

A low pass filter is used, as previously discussed, it is a good approximation of neural function, so is a plausible way of implementing a running average in neural systems with the running average being exponentially weighted in the case of using the low-pass filter. Thus, the full temporal normalisation equation used is shown in Equation 4-13 and the input signal is normalised over a temporal window defined by the time constant for the normalisation stage (τ_μ).

Equation 4-13

$$I_D = \frac{I}{\sigma + I\left(1 - e^{\frac{-d}{\tau_\mu}}\right)}$$

4.3.1. SETTING NORMALISATION PARAMETERS: THE RUNNING AVERAGE TIME CONSTANT (τ_μ)

Within the normalisation equation, there are two free parameters, σ and the low-pass filter time constant τ_μ, which need appropriate values. Here τ_μ gives the size of the window for the stimulus running average. The time taken for the low-pass output to approximate the input magnitude of a continuous, time invariant stimulus is $3\tau_\mu$ (the output after $3\tau_\mu$ is 95% of an input step change), which gives the temporal window across which the input magnitude is integrated.

As such, τ_μ cannot be too large as this would mean the temporal window for computing the normalisation factor will exceed the duration of the input stimulus, thus the stimulus will not drive the low-pass filter for long enough to allow the filter output to approximate the input I . This means the input to the SDD population will never be fully normalised. The appropriate value of $\tau\mu$ should be set so that $3\tau_\mu$ is sufficiently less than the stimulus duration.

As the aim of this model is to encode sub second durations, τ should be small. However, it cannot be too small as for time variant stimuli it will not provide a good estimate of the mean intensity. Ideally, τ_μ should be set so that a single oscillation of the input signal is less than $3\tau_\mu$. For the moment a τ of 100ms will suffice as the filter response will be sufficiently rapid enough to normalise sub second durations except those of less than 300ms ($< 3\tau\mu$). The model will not fully normalise inputs of less than this but will not distort the waveform of temporal frequency inputs greater than 3.3Hz with oscillations of length 300ms or greater.

4.3.2. SETTING NORMALISATION PARAMETERS: NORMALISATION CONSTANT (σ)

The constant σ has two functions, which become apparent when considering the effect of normalisation on the input signal. If the normalisation stage low pass filter output was zero, without σ divide-by-zero errors would occur. In addition without σ, when the normalised I_{μ} is very small relative to the input I (just after signal onset, as there has not been a signal to average in the recent past), the input to the detectors, I_D , becomes very large. This means the system gain will be very large. A large gain is unwanted for two reasons, the initial amplification of I_D will unduly distort duration estimates (as input magnitude affects duration estimates – Section 4.2.4) and high gain is unrealistic in neural systems. This suggests a larger σ value would be best in this model to reduce the initial amplification of I_D. A larger σ also has problems as it means as I_{μ} approaches I, the bigger sigma is, the less well I_D approximates 1 as assumed for the input, causing distortions in duration estimates.

Equation 4-14

$$I_D = \frac{1}{\sigma + 1}$$

In Equation 4-14 a large σ will result in $I_D << 1$ which would violate this assumption and result in duration underestimations.

Therefore, it is important that σ be set to a value giving a balance between reducing initial amplification and keeping the input as close to the assumed input value as possible. An σ of 0.05-0.25 is reasonable given these limitations. For the rest of this chapter a value of $\sigma = 0.15$ is used unless stated otherwise.

4.3.3. CENTRAL TENDENCY IN TIMING (VIERORDT'S LAW) AND THE NORMALISATION CONSTANT (σ)

One property of time perception the addition of σ appears to capture, is referred to as the central tendency effect, which states that relatively short durations are perceived to be longer and relatively long durations are perceived to be shorter than they are. This is also referred to Vierordt's law, which is named after Karl von Vierordt, the first person to report this effect in the 19th century (For an English translation of Vierordt's early work on this see Lejeune & Wearden, 2009).

This aspect of time perception is robust across sensory modalities where no feedback is given (Lejeune & Wearden, 2009); when participants receive feedback during duration reproduction tasks on the accuracy of their judgements the effect does not occur (Lewis & Miall, 2009). Considering the model with a fixed τ_μ and σ, this means that events with relatively short durations, which have not been completely normalised during the event i.e. where the mean of $I_D > 1$ will lead to over estimations in duration as I_D will be greater than the assumed input to the detector population (Section 4.2.4). For longer durations where over the course of the event, mean $I_D < 1$ the reverse is true, meaning longer durations are underestimated. This is an interesting property of adding a normalisation stage to mitigate the effect of assuming $I_D = 1$ (section 4.2.2) in the model.

This demonstrates that adding normalisation, a process that occurs at many different levels within the brain improves the model's plausibility when compared to known properties of time perception.

4.3.4. NORMALISING STIMULI OF DIFFERENT MAGNITUDES

To test the normalisation stage, stimuli with durations of 50-1000ms and magnitudes of 0.25-2 are run through the model to output duration estimates. An SDD population described in section 4.2.3 was capable of estimating the duration to the nearest 10ms (the resolution of the SDDs) and for the normalisation stage σ was set to 0.15 and τ to 100ms based upon the considerations describe in sections 4.3.1 and 4.3.2. The durations of inputs with magnitude 0.25 to 2 are tested with 0.25 steps with results shown in Figure 4-12.

Stimuli without any normalisation vary greatly in estimated duration and only where $I_D = 1$ generate accurate estimates of duration. Stimuli where $I < T$ are excluded from the non-normalised data, because the model cannot estimate durations of this input magnitude as the SDD low-pass filters never reach threshold. When normalising the input durations of lower magnitude input (0.5) can be estimated accurately except for the lowest intensity input (0.25).

The normalisation stage gives estimates that are more consistent across different magnitudes but there is still a clear effect of increased input magnitude leading to larger duration estimates corresponding with larger input magnitudes. This finding is consistent across the literature with reports of increased perceived duration correlating with a number of properties that

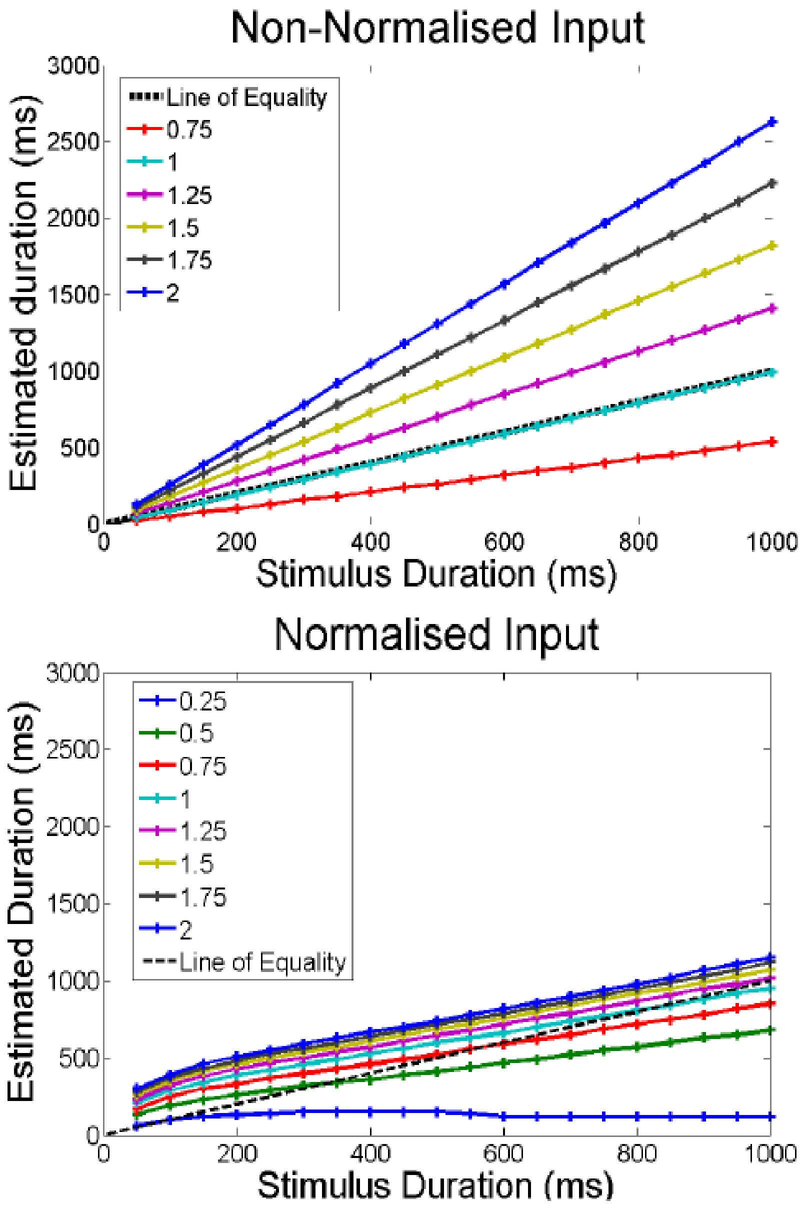


Figure 4-12: Top panel shows the model's duration estimates versus stimulus durations for a non-normalised input with magnitudes of 0.75-2 with 0.25 unit steps and is the same as Figure 4-5. The bottom graph shows the model's estimates for a normalised input using stimulus magnitudes from 0.25 to 2 with 0.25 steps. The normalised estimates are far more consistent and show the central tendency effect, where shorter durations are overestimated and longer durations underestimated. Note that the model can estimate durations for stimulus magnitudes smaller than the fixed SDD threshold when using the normalised input demonstrated as the model estimates durations for the 0.5 stimulus magnitude only when normalised.

could be considered as input magnitude. This includes, increased stimulus brightness (Brigner, 1986; Terao et al., 2008), speed (Brown, 1995; Kanai et al., 2006), temporal frequency (Kanai et al., 2006), size (Alards-Tomalin et al., 2014; Ono & Kitazawa, 2007; Xuan et al., 2007), colour saturation (Alards-Tomalin et al., 2014), and numerosity (Xuan et al., 2007). See Eagleman and Pariyadath, 2009 for a summary of some of this research.

4.3.5. IMPULSE RESPONSE WITH THE NORMALISATION STAGE

It is also worth considering the effect of an impulse on the model with the normalisation stage. We know the response of the low pass filter performing the running average to an impulse would show an exponential decay from an initial peak in response from Section 4.2.5. The output of the averaging filter (O_μ) at the instance of the impulse with no prior input is given by Equation 4-15 from Equation 4-2 with τ_μ as the normalisation stage time constant.

Equation 4-15

$$O_{\mu(d=1)} = I\left(\frac{1}{\tau_\mu + 1}\right)$$

This can then be substituted into Equation 4-12 to give the input into the detector population from the normalisation stage to give Equation 4-16. σ is the normalisation constant and I_D is the input into the detector population.

Equation 4-16

$$I_D = \frac{I}{\sigma + I\left(\frac{1}{\tau_\mu + 1}\right)}$$

When combined with Equation 4-10 for the duration estimate of the population to an impulse of magnitude I, this gives Equation 4-17.

Equation 4-17

$$D_I = \frac{\left(\frac{I}{\sigma + I\left(\frac{1}{\tau_\mu + 1}\right)} - T\right)}{T}$$

As after normalization duration is linearly dependent on the normalized intensity, if the denominator in Equation 4-176 is greater than 1 this will act to reduce duration estimates from the population, if it is less than 1 then this will increase the duration estimates compared to the model without normalisation. The value of I above which will result in reduced duration estimates is shown in Equation 4-18.

Equation 4-18

$$I = \tau_{\mu} - \sigma\tau_{\mu} + 1 - \sigma$$

Which when substituting the values chosen in sections 4.3.1 and 4.3.2 gives I as 86, i.e. when input magnitude over one time step produces a large enough input averaged over time τ_{μ}. Since the impulse magnitude used in section 4.2.5 is greater than this, we can conclude that the normalisation stage would reduce duration estimates in this case. When calculating the estimated duration for this with an input of 2000, the output is a duration estimate of ~158ms, much less than 3163ms, the estimate with no normalisation stage. From this example, it is clear that with the addition of the normalisation stage, the model estimates vary less with the magnitude of the input and are therefore more dependent on the duration of the input. Interestingly, inputs of a lower intensity, where the denominator is less than 1 will actually be intensified, meaning they will register a duration at a lower intensity. Therefore, with the normalisation stage the model's ability to estimate durations for weaker inputs is increased.

4.3.6. COMPARISONS WITH EXPERIMENTAL FINDINGS ON SPEED AND TEMPORAL FREQUENCY

It has been established that the model's duration estimates vary with input magnitude and that this is supported by the literature. One particular interesting result is from Kanai et al., (2006) who provide a detailed example of this magnitude effect, showing that overestimation scales with object speed logarithmically (Figure 4-13) similar to previous findings by (Brown, 1995) and further experiments show this effect is driven by change in temporal frequency. This is contrary to some of the results from the model. Section 4.2.5 shows the model's estimates of time do not vary with temporal frequency of a time variant input, which would mean the model does not predict the results of Kanai et al., (2006) which is shown in Figure 4-14. This result is achieved by varying the temporal frequency of a sine wave input (peak: 1.25, trough: 0.75 normalisation parameters: σ =0.15 and τ_{μ} = 100ms).

However, there is another way of representing temporal frequency within the model. Instead of modifying the frequency of a time varying input signal, temporal frequency can be represented in the magnitude of the input, so a greater input magnitude represents an input stimulus with a higher temporal frequency. There is evidence showing that cells in V1 and V2 demonstrate a reduced response to lower temporal frequencies (Hawken, Shapley, & Grosof, 1996). Changing input magnitude is also how speed is represented to get the results from the model in Figure 4-13. It has been suggested that speed could be encoded as a rate code in MT as suggested by the high proportion of neurons tuned to high speeds (Cheng et al., 1994; Johnston et al., 1999) so there is support in the literature to justify encoding speed and/or temporal frequency in this way.

The SDDs in the model are considered to be receiving input from cells such as these that encode speed in terms of their firing rate, in this example. Here, we test if the model can account for the findings of Kanai et al., (2006) by modifying how temporal frequency is represented in the model. We test with a step on/off input of 200-1000ms and normalisation parameters of σ =0.15 and τ_{μ} = 100ms with varying input magnitude to represent differing speed/temporal frequency.

On visual inspection, Figure 4-13 shows the model estimates of duration for inputs of differing intensity match the trends observed by Kanai et al., (2006) for perceived speed. The results from Kanai et al., (2006) and the model for temporal frequency are shown in Figure 4-14. Since the normalisation parameters have been set to values based upon general guidelines, these results are not a result of precise variable fitting but are an emergent property of the model.

Another finding from Kanai et al., (2006) is a lack of effect for spatial frequency on duration. If the model input magnitude is said to encode spatial frequency then the model would predict a similar result to the effect of temporal frequency on duration running contrary to Kanai et al., (2006). This suggests that only neurons that scale their response with temporal frequency feed into estimates of duration perception and not spatial frequency. Indeed neurons do not tend to scale their output with SF, but rather show tuning for a specific spatial frequency (DeValois & DeValois, 1988). What can be taken from both the findings of Kanai et al., (2006) and the model is an indication of what stimulus properties might or might not affect perceived duration based upon how these properties are encoded in sensory systems, which could provide avenues in designing experiments to validate the model.

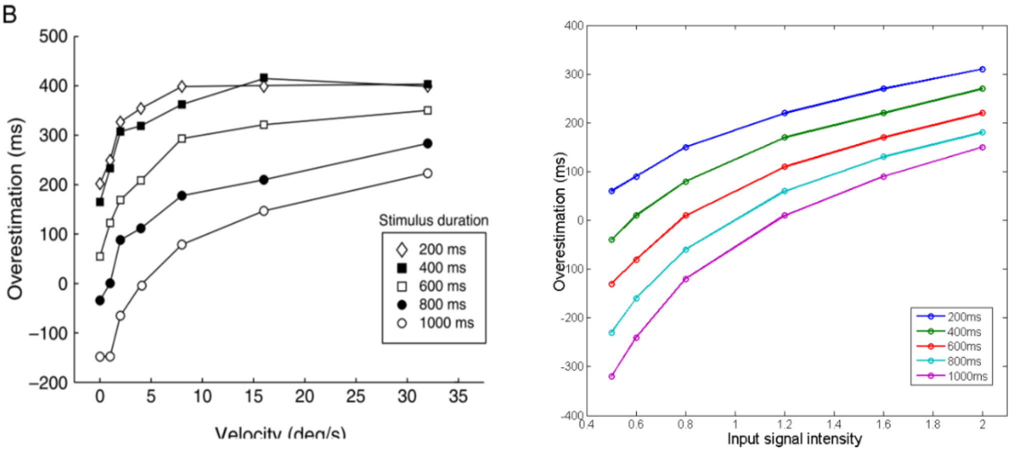


Figure 4-13: The left graph shows the results from (Kanai et al., 2006) experiment 1 showing the speed induced time dilation effect where the greater the velocity, the larger the overestimation of event duration according to a logarithmic trend. It also shows Vierordt's law with shorter durations showing a larger overestimation than longer durations. The graph on the right shows data from the model using k =0.15 τ = 100ms in the normalisation stage, except instead of speed the x-axis shows input signal intensity which in this case is assumed to encode speed. The model output reflects the logarithmic trend observed by (Kanai et al., 2006)

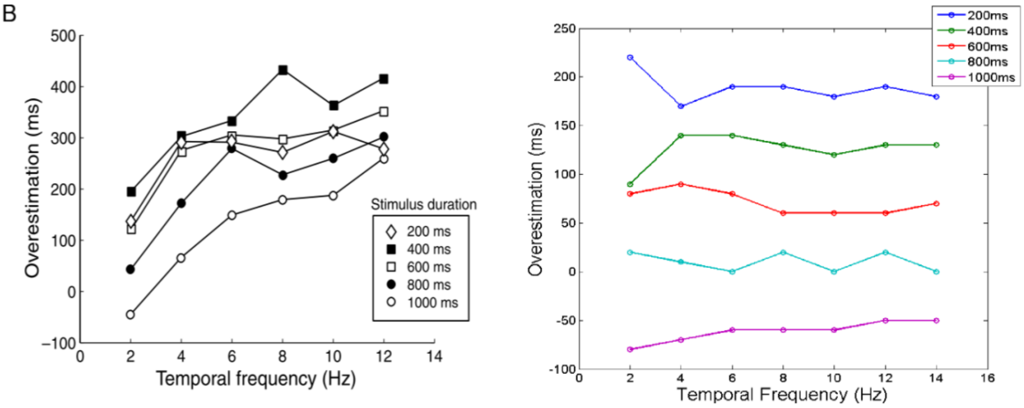


Figure 4-14: The left graph shows results from (Kanai et al., 2006) experiment 4 showing a temporal frequency induced time dilation effect following a logarithmic trend with temporal frequency and Vierordt's Law. The model estimating the duration of a sine wave input varying between 0.75 and 1.25 intensity does not show the same logarithmic relationship as the experimental data.

4.3.7. WEBER'S LAW

One aspect of duration perception is the scalar property, a manifestation of Weber's Law where errors increase with size of estimates. This is claimed to be a robust feature of time perception where the Weber fraction, given by the judgement variance over the mean estimate, is approximately constant in animal experiments (Gibbon, 1977) and humans (Wearden, 1992). However, it should be pointed out that this does not always seem to hold as other experiments with humans have found a decrease in Weber fractions with duration (Bizo et al., 2006; Grondin, 2010b; Lewis & Miall, 2009). To test the model's compliance with Weber's law, Gaussian noise is introduced by adding noise to the stimulus (I in Equation 4-12 and Equation 4-13) to simulate a noisy stimulus or environment. Alternatively, noise is introduced internally by adding it to the output of the low-pass filters within each SDD (O_{LP} in Equation 4-1 and Equation 4-2) to simulate noise in processing the input.

Estimates are computed using a continuous input of durations 250, 500, 750 and 1000ms with a magnitude of 1, which is normalised using $\tau =$ 100ms, $\sigma = 0.15$ as before. The standard deviations of the internal noise were set at +/- 0.05, 0.1, 0.15 and 0.2. Initial testing on internal noise demonstrated the system to be sensitive to the noise and produces large overestimations in duration. Consequently, only the lowest two noise levels 0.05 and 0.1 were used for internal noise. 100 duration estimates were generated for each noise level and duration combination, allowing Weber fractions to be computed by dividing the standard deviation by the mean of the 100 estimates.

The results in *Figure 4-15* shows that internal noise has a much greater effect on model variance, the Weber Fractions show an increase of around an order of magnitude compared to external noise. External noise shows Weber fractions decreasing with increased duration, to be expected by the law of large numbers that states with enough random samples over time the mean value of those samples will converge. Noise is added at each time step (1ms) in the input, changing the input magnitude at that step and the duration estimate is based upon the mean input magnitude (section 4.2.4).

Interpreted using the law of large numbers, the input magnitude at each time-step is a random event and with a longer duration input, there are a greater number of random events, so the average of these events, i.e. the input magnitude converges over time resulting in less variance over the 100 trials for longer inputs and hence reduced Weber fractions. A different trend is apparent with internal noise, Weber fractions exhibit less relative change across durations, with the lower noise level showing increasing Weber fractions and higher noise level demonstrating the opposite. The scalar property of timing (Gibbon, 1977; Gibbon et al., 1984; Wearden, 1991) is a case of Weber's law applied to duration perception that states errors in duration estimates should increase proportionally to the duration estimate itself, meaning the Weber fractions should stay constant across a range of durations.

Adding external noise does not exhibit this effect; instead, the model shows a reduction in Weber Fractions with time, closer to the results of Lewis & Miall (2009), who show a reduction relative to Weber's law with timing. Internal noise shows a relatively small reduction or increase in Weber fractions depending on noise levels. Since results showing the scalar property of time perception do exhibit a large variation (Gibbon, 1977; Wearden, 1991), the model could still be said to fit with behavioural data despite not exhibiting constant Weber fractions. These results also provide a way to reconcile the differences in experimental observations, where the scalar property of timing is not obeyed (Bizo et al., 2006; Grondin, 2010b; Lewis & Miall, 2009). External noise, either from the environment, stimulus or task difficulty is the main driver of non-scalar time estimations, where internal noise in the model produces variability more closely aligned with the scalar property.

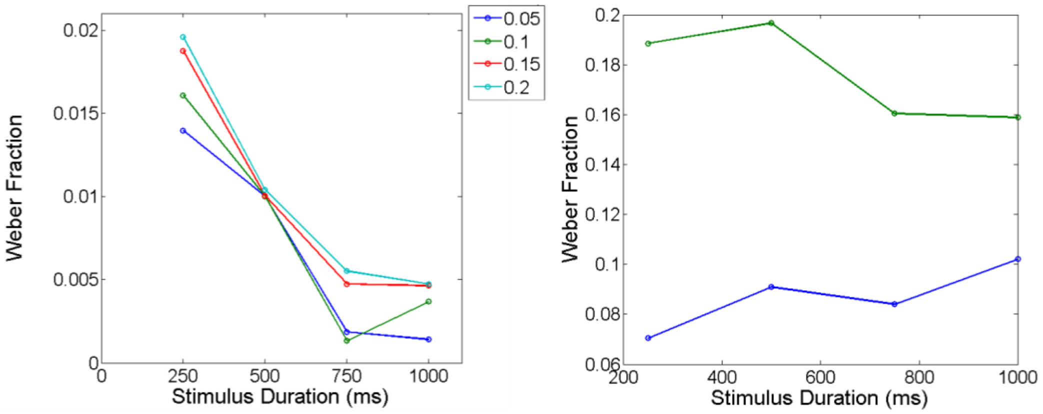


Figure 4-15: Showing Weber fractions (standard deviation/ mean of duration estimates) for external (left) and internal (right) noise. With external noise, Weber fractions are generally higher with more noise and decrease with the stimulus duration. Internal noise shows Weber Fractions an order of magnitude greater than external noise (right) and do not exhibit the same overall trend. Lower noise (blue) shows a slight increase in Weber fractions whilst the higher noise (green) shows a slight decrease.

4.3.8. NORMALISATION ACCOUNTS FOR ADAPTATION INDUCED DURATION COMPRESSION EFFECTS

There is a body of evidence showing adaptation to high temporal frequency and high contrast grating stimuli causes duration compression (Bruno & Johnston, 2010; Burr et al., 2007; Johnston et al., 2006). Both high contrast and high temporal frequency stimuli cause contrast gain adaptation in M, but not P Cells in macaque monkeys (Solomon et al., 2004). It has been theorised (Johnston, 2010; Johnston et al., 2006) that the duration compression effect is a result of adaptation in M-cells in LGN, implicating a low-level mechanism contributing to duration compression.

The normalisation stage in the model is effectively a form of gain control defined by the normalisation factor I_μ and constant σ; as such, it is possible to posit that this normalisation stage in the model is analogous to the function of M-cells. Solomon et al., (2004) show that adaptation creates a shift in the contrast sensitivity function of M-cells so that they are more sensitive to higher contrast stimuli, which is a result of a reduction in gain. In the normalisation stage, an increase in σ is effectively a decrease in gain. It is possible that the long-term suppression in M-cells caused by high contrast or high temporal frequency adaptation and the resulting changes to contrast sensitivity and suggests the effects on duration compression can be explained by variations in σ within the normalisation stage. By increasing σ and simulating the model's response to a stimulus this can be said to represent the change in response of M-cells after adaptation.

To test the effect of increased σ on duration estimates of step function on-off inputs with three input intensities (0.5,1,1.5) with a range of durations (200-1000ms, 200ms steps) were computed. The model normalisation parameters are set to τ_μ= 100ms and σ set to 0.15, as before, acting as the 'unadapted' condition as well as σ = 0.2 and 0.25 both acting as 'adapted'conditions. Figure 4-16 shows reductions in duration estimations when increasing σ to reduce normalisation gain. This reduction is consistent across stimulus durations and input magnitudes. Figure 4-17 shows the duration compression ratios (unadapted/adapted condition duration estimates for the same stimulus duration) for inputs of different intensities, showing a compression in perceived duration of around 10-40% (shown in Figure 4-17 as compression ratios of 0.9-0.6 respectively) depending on the value of σ used. This compares reasonably well to duration compression effects of approximately 20% in Johnston et al., (2006); showing that high contrast or high temporal frequency adaptation induced duration compression could be explained by changes in gain of the model's normalisation stage implemented by increasing the normalisation constant σ.

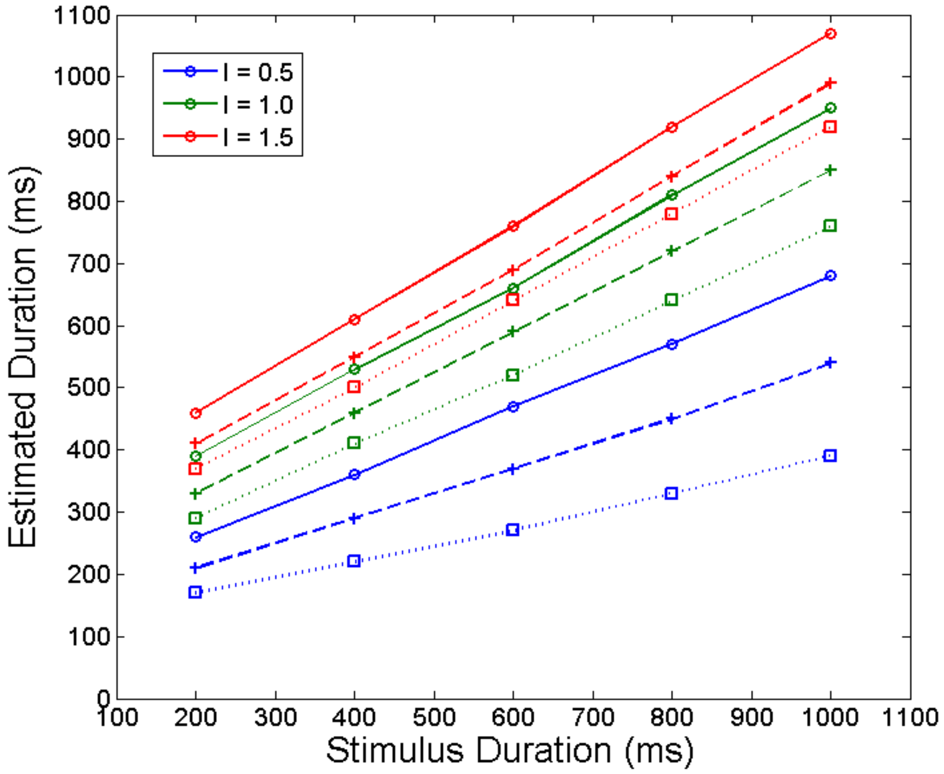


Figure 4-16: Shows the effect of increasing σ (Solid: $\sigma = 0.15$, Dashed: $\sigma = 0.20$, Dotted $\sigma = 0.25$) on duration estimates for stimuli of different intensities (coloured) this shows a duration compression effect for increased σ across different intensities.

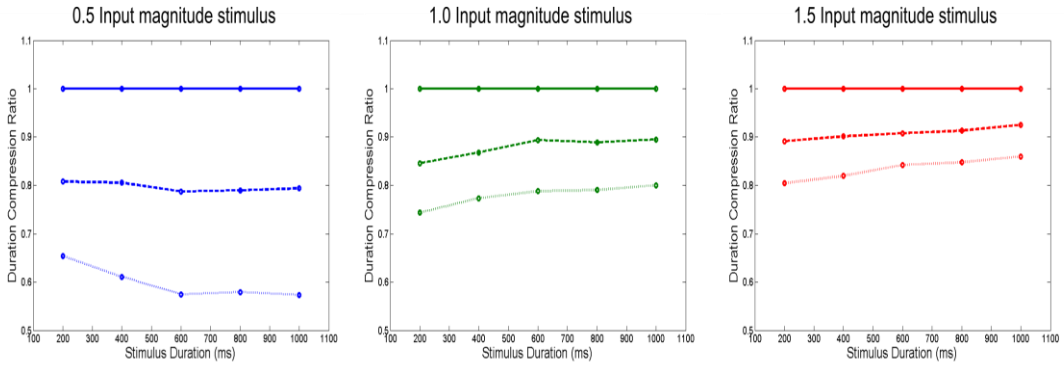


Figure 4-17: Shows the duration compression ratios for stimuli of varying magnitudes relative to $\sigma = 0.15$ (Solid) where the stimulus is considered 'unadapted' and the where the stimulus has been 'adapted' where $\sigma = 0.2$ (dashed line) and $\sigma = 0.25$ dotted line. Both adapted conditions show a reduction in duration across a range of durations for all inputs as observed by the compression ratios of less than 1.

4.3.9. NORMALISATION STAGE AS A GAIN CONTROL MECHANISM

We have shown that reduction in the model's normalisation stage gain shows a reduction in duration estimates comparable with adaptation results in the literature. This section follows on by investigating whether the normalisation stage implemented in the model could be considered equivalent to the contrast gain control mechanism in the M pathway observed by Solomon et al., (2004) even though this model has not been designed to encode contrast.

It has been mentioned before in Section 4.3.6 that signal magnitude could act as a variable to encode stimulus properties. So here the input (I) and output (I_D) magnitude of the normalisation stage is assumed to encode luminance contrast, where I is the contrast of the stimulus and(I_D) is analogous to the neural response to the stimulus i.e. the mean spike rate encoding contrast. Although, the normalisation is designed to set I_D to the same level no matter what the magnitude of I. If the output contrast is taken as the average intensity across the first 100ms after stimulus onset, where the output of the normalisation stage has not fully normalised, we see variation in the output intensity, which can be interpreted as the contrast sensitivity function of the model. Figure 4-18 shows the change in contrast sensitivity in M-Cell spike rates observed by Solomon et al., (2004) and the results from the model.

With increasing gain, the model output shifts rightward along the x-axis with increasing contrast, which is the same direction as the contrast sensitivity function observed by Solomon et al., (2004). However, there are clear differences in the shape of the sensitivity function between the model and experimental data. The recorded spike rate function is sinusoidal while the model shows an exponential sensitivity function. This might be explained as a saturation effect as there are limits in the spiking output frequency of neurons. In fact, this limitation makes the contrast gain change perceptually desirable as the decrease in gain means higher contrasts are more discernible from the cell spike rate, making the visual system more sensitive to subtle changes in a high contrast environment.

Overall, changing σ to reduce gain means the model approximates data from in-vivo cellular recordings and could be made to match them closely with the addition of a ceiling effect. This is despite the model not being conceived to explain contrast gain adaptation. σ in the normalisation stage is equivalent to c_{50} in contrast gain normalisation equations detailed by Solomon et al., (2004) who indicated that the change in contrast gain control is the result of inhibitory input to M-cells from retinal ganglion cells that persists for several seconds after adaptation to high contrast stimuli.

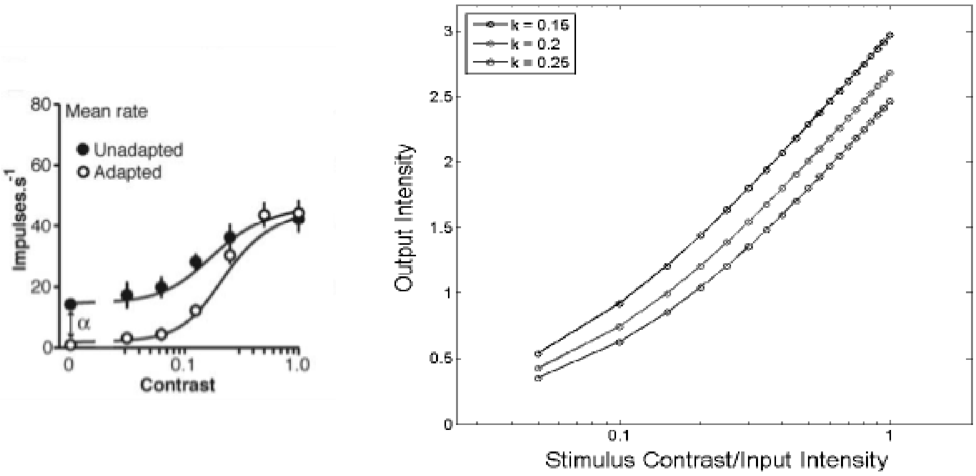


Figure 4-18: Left shows effect of adaptation to a high contrast grating to the contrast sensitivity profile of M-cells from Solomon et al., (2004). Right shows the normalisation stage output given the input stimulus contrast represented by the input intensity for different values of k where increasing σ is analogous to contrast gain adaptation. Both model and data show a shift in the sensitivity profile in the same direction though the model output is not sinusoidal, exhibiting a saturation effect like the recorded data.

4.4. DISCUSSION

This chapter shows that a model using varying temporal responses of neural systems, represented by low-pass filters, can encode the duration of a stimulus whether the input stimulus is continuous or time variant. A feature of the model proposed here is that at no point before the final duration value from the last-off method is duration explicitly represented in the system. Instead, signal magnitude represents a particular property of the stimulus. Therefore, the low-pass filters can represent neurons, or populations of neurons encoding that particular stimulus property and can be placed anywhere in the visual system. This means duration can be encoded in addition to other stimulus properties given that the neurons or populations of neurons vary in their temporal response to the stimulus.

When the input magnitude is not known or cannot be determined beforehand, a requirement of this model is that the input needs to be normalised (a process carried out across multiple systems in the brain (Carandini & Heeger, 2011). This fits in with the distributed nature of the model in that using normalisation does not limit where in the brain or on what level in the sensory processing hierarchy the model might exist. The literature shows that the magnitude of a stimulus property does affect estimates of duration as has been shown experimentally in many visual modalities (stimulus brightness-Brigner, 1986; Terao et al., 2008, speed – Brown, 1995; Kanai et al, 2006; temporal frequency - Kanai et al., 2006; size – Alards-Tomalin et al 2014; Ono & Kitazawa, 2011; Xuan et al., 2007), colour saturation (Alards-Tomalin et al., 2014), and numerosity (Xuan et al., 2007). These results are matched well by the fact that the normalisation stage mitigates the effect of input magnitude on duration estimates.

Changing the parameters in the model's normalisation stage explains results from experiments showing that adaptation to particular visual stimuli changes perceived duration (Ayhan et al., 2011; Bruno & Johnston, 2010; Burr et al., 2007; Burr et al., 2011; Johnston, 2010; Johnston et al., 2006). This also corresponds to shifts in sensitivity functions of M-cells (Solomon et al., 2004) that indicate a possible mechanism for duration compression after adaptation. The requirement for a normalisation stage not only describes the result of these studies, it can also explain why adaptation and stimulus property magnitude affect perceived duration, which is because the signals in the brain coding for these properties are also used in computing event time. This corresponds to proposals that duration uses a shared magnitude system with properties such as size and numerosity (Walsh, 2003). This may explain why properties like size (Alards-Tomalin et al., 2014) and numerosity (Xuan et al., 2007) also affect duration as there is a suggestion these are processed in the same, broad pathway (Bueti & Walsh, 2009; Walsh, 2003).

A duration estimation mechanism cannot use the raw signal magnitude to estimate event time because this leads to large errors in estimates that are untenable. Adaptation is not limited to one system or stage in processing within sensory systems, so it is likely that a duration mechanism of this kind may use sensory signals that have been fed through several adaptation stages. There is some evidence of this with directionally selective adaptation also affecting duration (Curran & Benton, 2012; Latimer et al., 2014). High concentrations of directionally selective cells are most commonly found in extra striate visual areas (Maunsell & Van Essen, 1983), implying adaptation stages further up the visual hierarchy affect duration estimates in addition to the proposed M-Cell gain change.

It may be suggested that the simplicity and flexibility of the model leaves it somewhat underdetermined and thus unfalsifiable, but there are some findings presented here and from literature that might serve to pin down mechanisms with the proposed model. The evidence from the adaptation studies (Bruno & Johnston, 2010; Johnston et al., 2006) as well as the results relating the normalisation stage to contrast gain control in M-cells implicated the Magnocellular and not Parvocellular pathway in time perception. A finding also supported by the results of Kanai et al., (2006) who find that spatial frequency, for which P-Cells are selective (Xu et al., 2001) does not affect perceived time. Results showing adaptation to motion has similar effects also implicating motion sensitive areas (Curran & Benton, 2012; Marinovic & Arnold, 2011).

This can be tied into another problem with the model, which is that it requires the time constant of the duration encoding neurons to be equal to the duration being encoded requiring neurons with slow time constants that might not be realistic. There are models showing how ramping activity evolving over seconds can be produced with a single cell (Durstewitz, 2003) and within a population (Simen, Balci, Cohen, & Holmes, 2011; Standage, You, Wang, & Dorris, 2013). There is also neurophysiological evidence showing cells in LIP encode time delays in actions using ramping firing rates (Janssen & Shadlen, 2005; Leon & Shadlen, 2003). It is not possible to say that these neurons act as the low-pass filters in this model, particularly as they are involved in action timing, not visual perception but the function of the low-pass filters in the model could be performed by neurons exhibiting similar temporal properties. The Magnocellular pathway, MT and LIP are all considered to make up the dorsal/action pathway in the visual system (Goodale & Milner, 1992; Nassi & Callaway, 2009), which has been proposed as the where/when pathway (Battelli, Pascual-Leone, & Cavanagh, 2007), implicating its involvement in duration perception. This means the most likely location of an analogue of the proposed model in the visual system is in the dorsal/action pathway as properties that affect perceived duration are processed within it and neurons that exhibit properties similar to the low-pass filters used in the model exist.

An unresolved problem with the model is if duration is encoded across sensory hierarchies, how do sensory systems arrive upon a final duration for an event? This is an example in the temporal domain of the generic sensory binding problem (Revonsuo & Newman, 1999): when a system processing sensory attributes is using different sub-systems, it needs to work out which properties need to be bound together to produce a coherent and unique object percept. This is an interesting broader issue that is not exclusive to duration perception or this model, but is relevant to the study of perception as a whole.

4.4.1. SDDS SHARE COMMONALITIES WITH OTHER MODELS

This model demonstrates that it is possible to estimate event duration by using fundamental properties of neural systems. A common theme of this model is that changing the input into the SDD population by manipulating magnitude either by changing the input stimulus representing the sensory event or by manipulating the input gain in the normalisation stage, results in changing the duration estimates.

This approach shares at least some similarities with previously proposed explanations for duration. Perhaps the clearest link is the neural energy proposal (Eagleman & Pariyadath, 2009) that duration is encoded by the amount of neural activity associated with an event. This is similar to the SDD model where in a single detector time is represented by whether or not the output of a low-pass filter has reached a specified threshold so also depends on the amount of neural activity. Neural energy provides only a descriptive account of time perception as opposed to the more precise quantitative model proposed here. In the SDD model, neural energy may not just relate to the input to the model but also to the way duration is encoded using the SDD population. The low-pass filter output of an individual SDD increases over time and more SDDs switch on in accordance with the event duration. If either the low-pass output or the number of detectors switching on is analogous to neural activity, such as firing rate of a single or population of neurons then this is a direct demonstration of how neural energy can represent time.

The SDD itself is similar to the memory strength model (Staddon & Higa, 1999) which uses low-pass filters and thresholds to represent duration in the strength of an event's representation in memory that can decay over time. The concept of what a memory is and how it is stored is ill defined. The SDD model can exist in sensory systems on top of mechanisms encoding sensory properties that, depending on the property in question, are reasonably well defined in literature so improves upon these shortcomings.

It also has similarities with pacemaker-accumulator models (Gibbon et al., 1984; Treisman et al., 1990; Wearden, 1992). The main difference is instead of having an accumulator counting inputs from a central pacemaker the input signal from the environment acts as a pacemaker, which is normalised to give an approximately constant input. The input then drives low-pass filters, which act as accumulators producing a ramped output. The main fundamental deviation of the SDD model from internal clock models is that a central pacemaker is not responsible for the time sense but it is instead sensory systems compute duration according to local input.

Sensory systems use distributed parallel processing on multiple hierarchies so it follows that sensory systems compute duration in a similar distributed fashion. The SDD model is completely compatible with this view. With the normalisation stage showing evidence that it could map onto functions performed by M-cells in LGN and the SDD population occurring as a second stage the model shows a hierarchical structure.

4.5. CONCLUSIONS

The key conclusion of this chapter is that it is possible to estimate event time quantitatively, based upon established, basic, temporal properties of neural systems without the need for a central timer, instead being more compatible with the neural energy hypothesis. The implication of this is that event durations can be computed locally across sensory systems, making use of shared mechanisms when required. The perceived duration of a sensory event is therefore dependent on the signal properties encoding the event duration and on processes, such as adaptation, that affect the encoding of these properties.

5. CHAPTER FIVE -EVENT PREDICTABILITY AND PERCEIVED DURATION: A BEHAVIOURAL AND NEUROPHYSIOLOGICAL STUDY

5.1. INTRODUCTION

One proposal is that perceived time and expectation are linked (Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012). The classic example often given to support this claim is the oddball paradigm originally demonstrated by Rose and Summers, (1995) where unexpected objects appear to last longer. This is not necessarily an effect of low-level adaptation due to stimulus repetition (Schindel et al., 2011), and is likely due to expectation (Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012). This is an important finding as changes due to expectation affect BOLD signal which shows a suppression effect when a stimulus is repeated, not entirely due to simple BOLD adaptation to repeated stimuli (Grill-Spector et al., 2006; Larsson & Smith, 2012), implying a link between BOLD repetition suppression and stimulus expectation in the oddball paradigm of Pariyadath and Eagleman (2012). A reduction in BOLD signal due to expectation can be considered a signal indicating a mismatch between perceptions and predictions i.e. an error signal, which could link duration to theories of perceptual learning such as those proposed by Friston (2010).

The previous two chapters have focused on the effects of sensory adaptation based upon previous work (Ayhan et al., 2011; Bruno & Johnston, 2010; Curran & Benton, 2012; Johnston et al., 2006; Marinovic & Arnold, 2011; Solomon et al., 2004). To obtain a full understanding of how time is perceived, top-down effects such as expectation need to be considered as well, since the representation of duration in the visual system may be linked to expectation related modulation in the visual system (Pariyadath & Eagleman, 2012). It has been suggested that perceived duration is related to the amount of neural activity associated with processing an event (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012). Such a link is also proposed with the model in Chapter 4, where the model estimates of duration are correlated with the output magnitude of individual low-pass filters or the mean across a population of filters that are said to represent the output of individual or populations of neurons. Although, the model in its current form does not account for expectation effects, similar to how a reduced input to the SDD population because of low-level adaptation predicts an effect on duration; reduced BOLD might indicate a reduction in input due to expectations that would have a similar effect on duration estimates. BOLD signal can be broadly interpreted as a correlate of input to and processing within a local population of neurons (Logothetis, 2003; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001), so this proposed link provides a way to relate perceived duration to neural activity.

As the oddball effect is a result of expectation (Schindel et al., 2011) the BOLD correlate must be repetition suppression produced by expectations (Summerfield et al., 2008) which Larsson and Smith (2012) show can be removed, leaving only the effect of repetition suppression from adaptation. The aim here is to do the opposite, removing repetition suppression due to adaptation, thus leaving only suppression due to expectation. This would link duration estimations to mechanisms involved in predicting future events and generating expectations (Friston, 2010; Grill-Spector et al., 2006).

5.2. DO EXPECTATIONS SUPPRESS BOLD IN EARLY VISUAL AREAS?

Two studies show the effects of expectation on repetition suppression (Larsson and Smith, 2012; Summerfield et al., 2008) using face stimuli that activate higher visual areas such as the FFA, which respond to complex combinations of visual features (Kanwisher, McDermott, & Chun, 1997). Some of the work discussed in previous chapters suggests the involvement of precortical and/or early cortical areas in duration perception (Ayhan et al., 2009; Bruno & Johnston, 2010; Johnston et al., 2006). As basic stimuli such as Gabor patches or gratings have properties such as orientation, which are encoded in early cortical visual areas (i.e. very different orientations are likely to cause markedly different patterns of activity in early areas), using these will show if repetition suppression in these areas is also correlated to perceived event duration.

Is there evidence for suppression using stimuli that drive differential responses mostly in early visual cortex? Kok, Jehee, and de Lange (2012a) used an auditory tone to cue the orientation of two sequentially presented grating stimuli. These two gratings had the same broad orientation (both were either roughly 45° left or right from vertical) but differed slightly in contrast and orientation (so one grating was slightly clockwise or anti-clockwise of the other). By cueing for broad orientation (the tone signalled 45° left or right from vertical) and asking participants to determine which of the two was either orientated clockwise or had the highest contrast, both an expectation is created and task relevance is manipulated. Results show a smaller V1 BOLD response in trials for the expected orientation direction for both the orientation and contrast discrimination tasks and a larger suppression when the cued expectation was relevant to the task. In a control experiment they show this relationship cannot be down to stimulus repetition (that would imply bottom-up adaptation), so must be due to the expectation invoked by the cue.

This result demonstrates that effects of expectation are not exclusive to higher visual areas but propagate down to or are derived locally in lower level areas such as V1, according to the expectation of low-level stimulus properties encoded in V1. Therefore, expectation is a general mechanism across the visual cortex. They also find this expectation enhances differences between stimulus properties, as reflected in the information contained in the BOLD signal, but as there is no effect of expectation on visual areas V2 and V3, this means either expectation only enhances representations in early visual areas or that it enhances representation in areas which are most tuned to the cued stimulus property.

What this means for this experiment is it provides a proof-of-concept, showing suppression as a result of expectation in early vision using low-level stimulus properties. This is of interest as adaptation studies suggest early or pre-cortical involvement in visual perception of duration (Ayhan et al., 2009; Bruno & Johnston, 2010; Johnston et al., 2006). Using Gabor stimuli of different durations will allow not only to investigate the effects of repetition suppression, but also to examine a BOLD correlate of duration perception and examine the effects of expectation on the BOLD duration correlate.

5.3. REPETITION SUPPRESSION: PERCEPTUAL EXPECTATION OR ATTENTION?

Attention has been shown to reduce suppression in BOLD (Larsson & Smith, 2012). In addition to investigating the effects of suppression due to expectation on early visual areas Kok et al., (2012a) also investigate the interaction between goal directed attention and perceptual expectation. They find that responses to gratings with the expected orientation are more easily discerned using multivariate pattern analysis (MVPA) showing an increase in stimulus representational clarity despite the corresponding measured drop in BOLD. This effect was not dependent on task (orientation or contrast discrimination), and was reflected in the behavioural data. As the effect was task independent, it was claimed there was no effect of attention to a particular feature and so is a result primarily of expectation priming, similar to that proposed by Lee and Mumford (2003), rather than feature based attention (Maunsell & Treue, 2006). However, Larsson and Smith (2012) show that when attention is removed by adding a distractor there is a reduction in expectation induced suppression, suggesting for some tasks, attention at least helps expectations to form, if not an explanation in itself. Summerfield and Egner (2009) hypothesised that attention and expectation are two complementary mechanisms that aim to enhance synergistically relevant sensory signals, improving the precision of sensory systems in a resources efficient manner. Attempts to untangle effects of attention and expectation were carried out in a separate study (Kok, Rahnev, Jehee, Lau, & de Lange, 2012b), where perceptual expectations and attention were manipulated independently so that they were either task relevant or not. Suppression of BOLD in response to predictable stimuli was observed for unattended stimuli (areas V1, V2 and V3), but there was a reversal in suppression when the attention was cued to the same side the stimulus appears on, so unexpected stimuli exhibited a reduction in BOLD compared to predictable stimuli (areas V1, V2 and V3). The findings are interpreted as supporting the hypothesis that attention mitigates the effect of expectation on stimulus response (Feldman & Friston, 2010). This could be considered the opposite effect to Larsson and Smith (2012), who found that suppression is reduced when using a distractor task to divert attention. This is perhaps due to methodological differences, Larsson and Smith (2012) distract attention from the stimuli completely while (Kok et al., 2012b) distract attention by making the expectation irrelevant to the task but do not distract from the stimuli, signifying a difference between spatial and feature based attention. A further study (Jiang, Summerfield, & Egner, 2013) sought to disentangle between these seemingly contradictory error signal suppression and amplification effects of attention. The experiment finds that attention increases the ability to distinguish between unexpected and expected stimuli using MVPA, across two areas selective for the different stimulus categories, the FFA for faces and Parahippocampal place area (PPA) for scenes, thus enhances the perceptual error signal. The authors explain differences in this finding with Kok et al., (2012a) as a difference in question as in Jiang et al., (2013) the question was does attention affect the error signal induced by expectation?, whilst the previous study investigates the effect of attention on the ability to decode the stimulus response. Jiang et al., (2013) show a similar univariate effect of attention and expectation as Kok et al., (2012b), where the average BOLD response of FFA or PPA is increased (for the relevant area's preferred category) when the stimulus is expected and attended relative to unattended and/or unexpected stimuli. The finding by Jiang et al., (2013) also matches Larsson and Smith (2012), who show that removing attention reduces repetition suppression. These studies show that attention facilitates the computation of prediction errors as evidenced by greater suppression, increasing the fidelity of the error signal as shown by improved MVPA decoding. This supports theoretical work (Feldman & Friston, 2010; Friston, 2005). These studies also show that suppression due to expectations in BOLD can be manipulated by both expectations themselves and task relevance.

5.4. THE HAEMODYNAMIC RESPONSE AND STIMULUS DURATION

fMRI studies often use a linear model (Boynton, Engel, Glover, & Heeger, 1996; Heeger, Huk, Geisler, & Albrecht, 2000) to estimate the BOLD response of a stimulus by convolving the stimulus profile with an impulse response function representing the haemodynamic response of the vascular system within the brain. As change in BOLD is driven by neural activity, deviations from baseline in the estimated BOLD response to a stimulus are interpreted as being caused by neuronal activity. Significant deviations from baseline estimates of BOLD are considered a result of differences in neuronal response to stimulus properties, thought most likely to be spatially localised input and processing similar to that measured by LFPs (Logothetis, 2003; Logothetis et al., 2001). There are many examples of this with visual properties such as orientation (Tootell et al., 1998), luminance contrast (Goodyear & Menon, 1998), motion (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998) and colour (Engel, Zhang, & Wandell, 1997), where a localised change in BOLD is interpreted as neurons responding to that property. This provides a cornerstone of neuroimaging in vision science as visual areas can be mapped using BOLD response to particular stimulus (DeYoe et al., 1996; Engel, Glover, & Wandell, 1997). fMRI studies on timing show evidence of multiple areas and brain structures involved in timing such as the cerebellum, basal ganglia, frontal cortex and supplementary motor areas (Coull, 2004; Coull et al., 2004; Hinton & Meck, 2004; Jueptner et al., 1995; Lebedev et al., 2008; Livesey et al., 2007; Mathiak et al., 2004; Rao et al., 2001), which have been claimed to either be evidence of a central timing mechanism or a network of areas contributing to time perception. Trying to localise time functions might be misguided if timing is not performed by a central mechanism, such as a clock (Gibbon, 1977; Gibbon, et al,. 1984; Treisman et al.,1990) and is instead performed across distributed mechanisms (Grondin, 2010a; Ivry & Spencer, 2004). Given that the temporal resolution of the BOLD response is on the order of seconds due to the slow change in blood flow (TRs used in the following experiments are 2500ms, typical for capturing this change), differences stimulus durations that are perceptually easy to distinguish but are both less than a second would not necessarily show differences in BOLD. As such, any significant differences in the visual cortex between two distinguishable, sub-second durations could be down to their explicit durations encoded in neural firing rates and reflected in the BOLD signal. Furthermore, measuring differences in the perceived duration of stimuli provides a means for testing the relationship between perceptual expectations, BOLD suppression and perceived duration. Expectation induced repetition suppression in BOLD is localised to areas where neurons exist that respond to the particular stimulus (faces – FFA: Summerfield et al., 2008, places- PPA: Jiang et al., 2013 and gratings – V1: Kok et al., 2012a Kok et al., 2012b).

A demonstrable relationship between BOLD suppression and duration in the visual cortex would provide evidence for distributed processing of duration in the visual system. V1, MT, MST and MT+ (combined MT and MST) are the visual areas targeted by this study. V1 is chosen as neurons in this area encode orientation, the stimulus property that is predictable based upon the probe where BOLD response changes in accordance with expectation using orientation grating stimuli (Kok et al., 2012a Kok et al., 2012b). MT, MST and MT+ are chosen as these areas have been linked to time perception (Curran & Benton, 2012; Sadeghi et al., 2011).

5.5. GENERAL METHOD

The motivation for this study is to test the hypothesis that temporal expansion of unexpected stimuli can be a result of repetition suppression induced by perceptual expectation. The experiment needs to remove confounding effects of bottom-up adaptation, effectively the opposite approach to Larsson and Smith (2012) who remove the effect of top-down mechanisms on repetition suppression. This is not possible with the standard oddball design, as the stimulus is repeated, which induces adaptation, therefore another method of creating expectations is required.

To create an expectation, each trial consists of a pair of stimuli: a prime stimulus appearing first, followed by a probe stimulus. The prime is one of two different stimuli, labelled A or B. The probe can also be one of two stimuli, labelled X or Y. To create expectation, the probability of a particular probe stimulus following a particular prime stimulus is manipulated so that on presentation of prime A there is a greater chance of probe X appearing than probe Y, this probability is reversed for prime B, so probe Y is more probable after prime B than probe X (Figure 5-1). Having an equal number of Prime A and B trials, randomly interleaved within a block means the probe stimuli X and Y are also displayed an equal number of times, given that the probabilities of X and Y appearing after B are opposite and equal for appearing after A. This factors out any adaptation effects from seeing one stimulus more often within a trial block, whilst creating a perceptual expectation for more probable pairings.

The prime stimuli will be Gaussian patches coloured red or green. The probe stimuli are Gabor patches orientated left or right. As orientation is encoded in V1 by orientation tuned neurons, it is hypothesised that expectations of orientation will have an effect in early visual areas as has been shown to occur with pre-learnt relationships (Kok et al., 2012a), so the experiment can test for duration and suppression effects in early visual areas. Another aim of this experiment is to investigate if it is possible to induce expectations by unconscious processing (i.e. not pre-learnt pairings) with no effect of adaptation taking place and using simple Gabor stimuli to test if expectation is an automatic process that occurs in early visual areas.

Participants were uninformed of the relationship between prime and probe stimuli beforehand in similar experiments (Larsson Smith, 2012; Summerfield et al., 2008) and when asked if they spotted a relationship after completion of the experiment, they indicated that they were not aware of it. Despite this, these studies exhibit significant repetition suppression in face processing areas. If BOLD suppression for expected stimuli, outside of awareness were found this would provide a link between it and research showing the MMN in EEG experiments as MMN is also shown outside of awareness (Garrido, Kilner, Stephan, & Friston, 2009).

This result could pave the way for future studies on BOLD suppression with EEG - as it has much greater temporal resolution than fMRI it would provide a way to measure population activity in real time. Furthermore, by using a variation of the oddball stimulus that does not cause differential adaptation in the probes we directly attempt to connect expectation driven suppression with this paradigm.

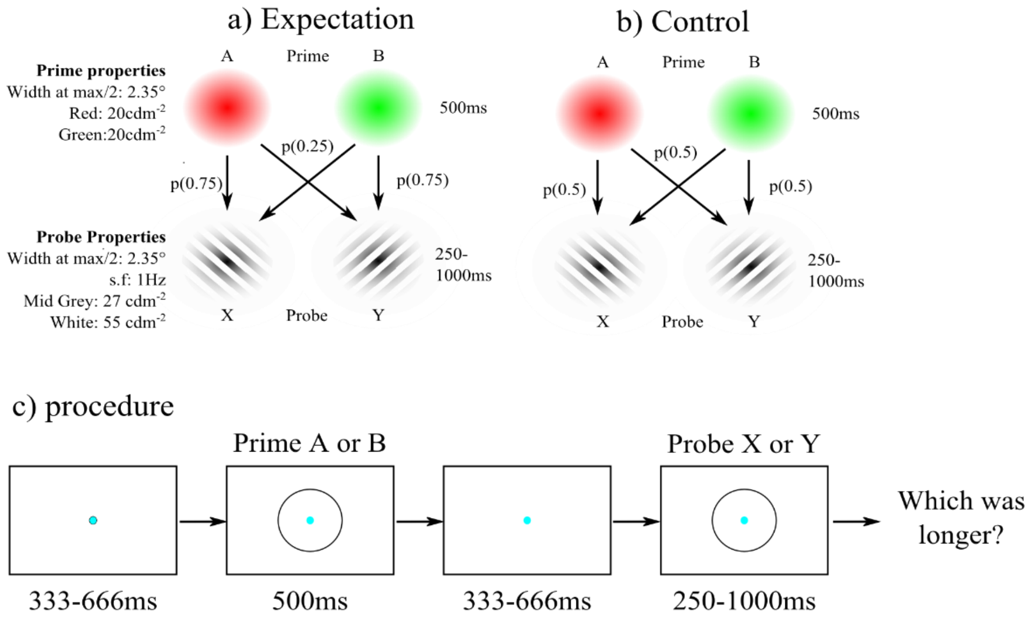


Figure 5-1 Shows the stimuli and their relationship in each experimental condition and the procedure for each trial. a) shows the probabilistic relationship between the prime and probe stimuli for the experimental condition. Each of the probe stimuli are more likely to appear following a particular prime. b) shows the control condition where both probes are equally likely to appear after each prime. c) shows the experimental procedure. There is a random delay between trials to allow the participant to fixate before the prime stimulus appears, either A or B chosen at random. There is another short, randomised delay before the probe stimulus appears for between 250 and 1000ms as defined by a staircase procedure. The participant indicates by button press, which lasts longer, the prime or probe.

5.5.1. MEASURING DURATION PERCEPTION

Six participants took part in this experiment (four naïve to the purpose of the experiment, three females). Participants sat with their head in a chinrest positioned 57cm in front of a linearized Sony Trinitron monitor in a darkened room using a resolution of 800x600 and refresh rate of 100Hz. Stimuli were displayed using PsychoPy v1.78 (Peirce, 2007). Data analysis performed in MATLAB 2011a and SPSS 21.0. Experimental stimuli and procedure are shown in Figure 5-1 .

Participants fixated upon a small (0.1° radius) blue 9.82cdm^{-2} dot positioned in the centre of the screen that was present throughout all the trials. The prime stimuli A and B consisted of green and red Gaussian patches, coloured respectively (20cdm^{2}), with a width of 2.35° at half maximum (1° standard deviation) appearing on a mid-grey (27cdm^{2}) background and appeared in the centre of the screen. The probe always appeared for a duration of 500ms. After prime offset there was a uniformly distributed, random delay of 333-666ms before probe onset. Probe stimuli X and Y consisted of a greyscale Gabor patch with a peak luminance of 55cdm^{-2}, spatial frequency of 1Hz and a standard deviation of 1°, positioned in the centre of the screen. The Gabor patch was orientated 45° clockwise or anticlockwise from vertical.

For half the participants probe X was clockwise and Y anticlockwise and the other half this was reversed to compensate for any bias in responses due to orientation. The probe stimulus duration varied by a standard staircase procedure between 250 and 1000ms. The participant indicated if the probe or the prime stimulus appeared for the longer duration by key press on a computer keyboard.

Two different experimental conditions were used for this experiment defined by the probabilities of each probe stimulus appearing after the prime. In the control, condition both probes X and Y appeared following each prime half the time. While in the experimental condition, Probe X had a 75% chance and Y a 25% chance of appearing after Probe A while this was reversed for Probe B. These ratios were chosen as the same ratios create a repetition suppression effect in Larsson and Smith (2012). This means for Probe A, Y acts as the oddball stimulus and for B, X is the oddball. Prime-Probe combinations were randomly interleaved for both blocks. Naïve participants were not informed of the relationships between stimuli in either the control or experimental conditions. All they knew, in addition to the experimental task, was simply that the aim of the experiment was to investigate the effects of visual event predictability on perceived duration.

The perceived duration for each probe was measured by concurrent standard staircases, one starting at the minimum 250ms duration and the other starting at the maximum duration 1000ms (+/- 1 octave of the prime duration). Each staircase consisted of a minimum of 30 trials. This means that in the control, each prime-probe combination was shown for a total of 60 repetitions and in the experimental condition oddball combinations (Prime A, Probe Y and Prime B, Probe X) appeared 60 times and the expected combination (Prime A, Probe X and Prime B, Probe Y) appeared 180 times. Staircase step size was 160, 80, 80, 40, 40, 20, 20ms for each reversal, in order for the first seven reversals and 10ms for any reversal thereon. Blocks were run on different days to minimise learning between each run and the order was reversed for each participant to counterbalance any remaining learning effects carried over from one block to another.

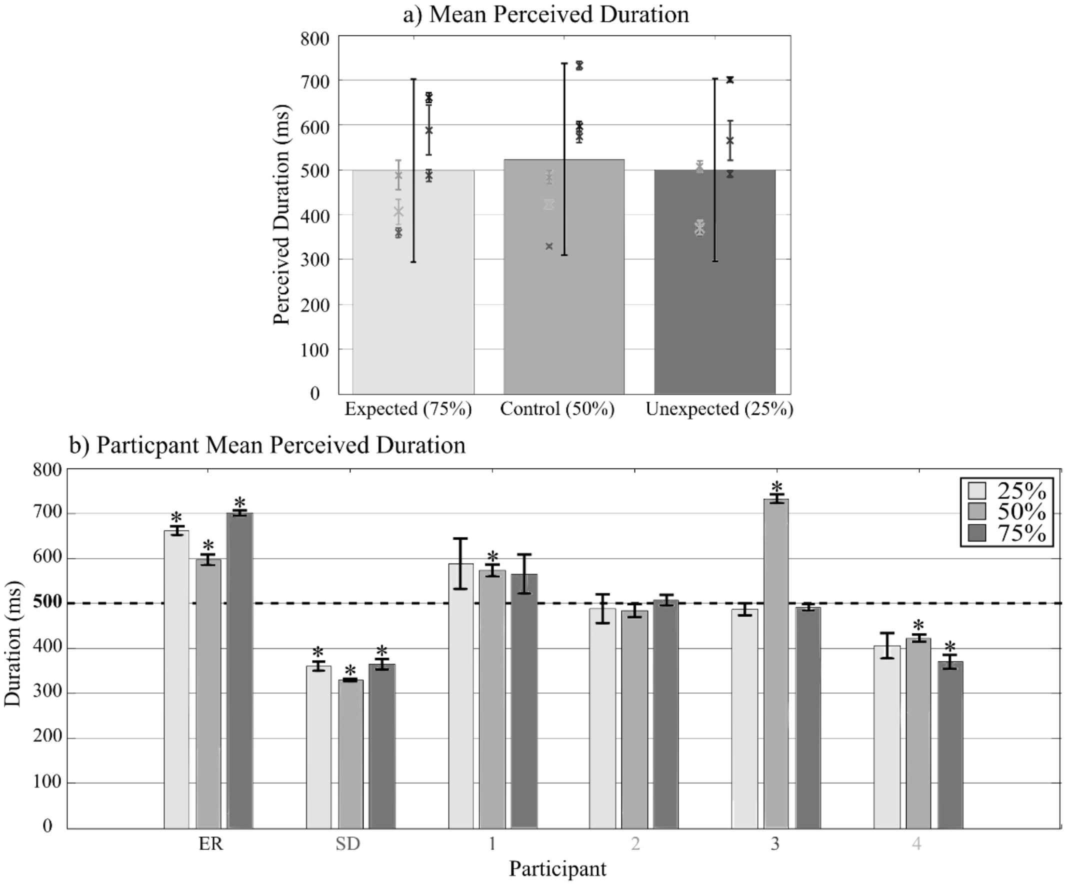


Figure 5-2: a) shows the mean perceived duration for each experimental condition across participants with error bars showing standard deviations (N=6). Shaded points are each individual participants' perceived duration with error bars showing standard deviation (N=4 for 25% and 75% conditions. N = 8 for 50% condition). There is no overall significant effect of stimulus predictability on perceived duration and there is no overall difference with the mean perceived duration across participants and actual stimulus duration (500ms) with any condition. b) shows each individual participant's mean for each condition with error bars indicating standard deviation (N=4 for 25% and 75% conditions. N = 8 for 50% condition). Some individuals show significantly different perceived durations from the 500ms stimulus duration (*, $p < 0.05$. dunn-sidak corrected for multiple comparisons) showing variability in perceived event duration and suggesting significant individual differences with stimulus timing.

As each stimulus pair had two staircases and each different probability condition had two different stimulus pairs (75%: A-X, B-Y, 25%: A-Y B-X), this gives four measures for each participant for the 75% and 25% probability conditions. These were averaged to give a PSE estimate and standard error. For the 50% control condition, there were eight measures as all four stimulus pairs have the same probability and each pair has two concurrent staircases. These where averaged to get a mean PSE and standard deviation. The behavioural results for duration perception are shown in Figure 5-2. The staircases for each participants' responses converged in all conditions, four typical staircases are show for the participant 2's unexpected (25%) condition, demonstrating that the issues discussed in Chapter 2 (specifically 2.4) regarding the problems encountered with measuring the Flash-Lag illusion with adaptive methods are not present with this paradigm.

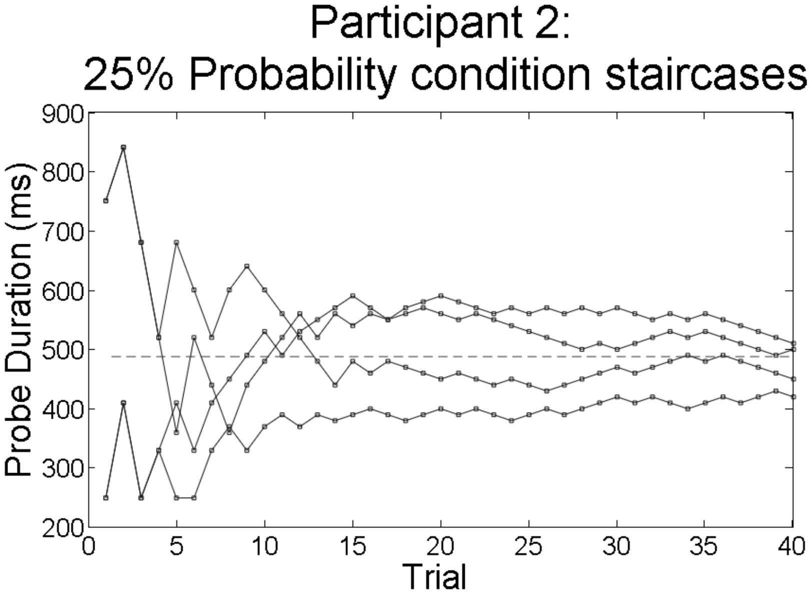


Figure 5-3 This shows staircases (solid) from a typical naïve participant for a single condition (25%/ unexpected condition). The four staircases converge on the mean stimulus duration estimate (dashed) of 487ms, which approximates the actual stimulus duration of 500ms.

The mean estimate of duration for each condition appears in Figure 5-2 a). For each condition there is no significant difference between the judgements and the probe duration (500ms) with one-sample t-test (Control: t_5= 0.394, p = 0.710. Predictable: t_5= -0.006, p = 0.995. Unpredictable t_5 = -0.36, p = 0.972), meaning on average participants' estimates of duration was accurate. There is no overall effect of expectation using repeated measures ANOVA ($F_{2, 10}$ = 0.25, p = 0.655 – Greenhouse-Geisser corrected) which is visible from the graph in Figure 5-2 as there is no clear trend in the results.

5.6. BEHAVIOURAL DISCUSSION

With no result coming remotely close to any significant effect, the experiment shows no temporal expansion effect due to expectation in our experimental paradigm. The complete lack of trend shown here suggests that the issue is not a lack of power, so adding more participants would be unlikely to show any significant trends.

Why is there no difference due to expectation? The most straightforward explanation is that temporal expansion effects are not due to differences in expectancy. This runs contrary to claims in literature citing expectation as creating the perceived increase in event duration (Pariyadath & Eagleman, 2007; Pariyadath & Eagleman, 2012). The low-level stimuli used might not be typically behaviourally relevant so not induce expectations, but oddball orientations have demonstrated temporal expansion (Pariyadath & Eagleman, 2012). It may be that previous temporal expansion effects have been strengthened by adaptation to low-level visual features, a factor we deliberately eliminated here, but reliable oddball effects have been found for cases where low level feauture adaptation is not happening or happens in a manner disassociable with expectation (Schindel et al., 2011; Pariyadath & Eagleman 2007). Increased attention to the oddball has been proposed as another alternative mechanism (Tse et al., 2004). Manipulating attention by using emotionally arousing stimuli does not result in a change in the temporal expansion effect (Pariyadath & Eagleman, 2007) suggesting attention is not the only factor creating the perceived increase in duration.

Similarly, perhaps what this experiment shows is that expectation alone is not the only factor in the temporal expansion effect. In the paradigm here, the ‘oddball’ is defined by a probabilistic conjunction between two stimuli and is expected to be learnt whilst performing the task without any explicit cue as to the relevance or even existence of the relationship. As this is more complex than the standard oddball, it is reasonable to suggest the patterns within the experiment were not salient so participants did not learn the relationship. The results cannot completely disprove the relationship between expectation and perceived duration but since it is probable an expectation did not develop that participants were conscious of it might mean that participants have to be aware of the expectation before it affects duration estimates. This is confirmed by the fact that when debriefing the naïve participants, not one mentioned they were aware of the relationship even when prompted. What this suggests is that when expectation is reduced by making the relationships between stimuli less overt to the point where participants are not aware of it, there is no temporal expansion effect, showing differences in expectation alone do not always create differences in perceived duration. Adjustments to the paradigm to create more obvious conjunctions could allow for experiments to test this hypothesis. Methods such as changing the probabilities of stimulus pairs to say 90%/10% instead of 75%/25% and/or having an initial learning period where one probe stimulus appears after one particular prime stimulus only, giving participants time to learn the relationship, could provide straightforward ways to alter the approach here.

The design of this experiment shares similarities with Summerfield et al., (2008) who show two faces in sequence which are either the of same or different people and creates an expectation as to what the second image will be depending on prior trials in the block. So it is interesting that in our similar paradigm (albeit with simpler stimuli), there is no difference in perceived durations suggesting expectation did not affect duration estimations. This would provide a test to see if this paradigm induces BOLD suppression using expectation and if apparent, would suggest expectation is not the only requirement for changes in duration as shown in the oddball paradigm. Since repetition suppression has been associated with various encoding mechanisms (Grill-Spector et al., 2006) it would inform thinking behind the mechanisms of duration perception.

5.7. FMRI METHODS

5.7.1. DATA ACQUISITION

Data were acquired using a 3T Siemens Trio MR scanner with a 32-channel array head coil. Functional images were acquired with a T_2*-weighted gradient-recalled echo-planar imaging (EPI) sequence (35 axial slices, TR 2500 ms, TE 31 ms, flip angle 85°, resolution 3 mm isotropic, echo spacing: 1.42 ms). Structural data were acquired using a T_1-weighted 3-D anatomical scan (MPRAGE, Siemens, TR 1830 ms, TE 3.3 ms, flip angle 11°, resolution 1 × 1 × 1).

5.7.2. MT+ COMPLEX LOCALISER

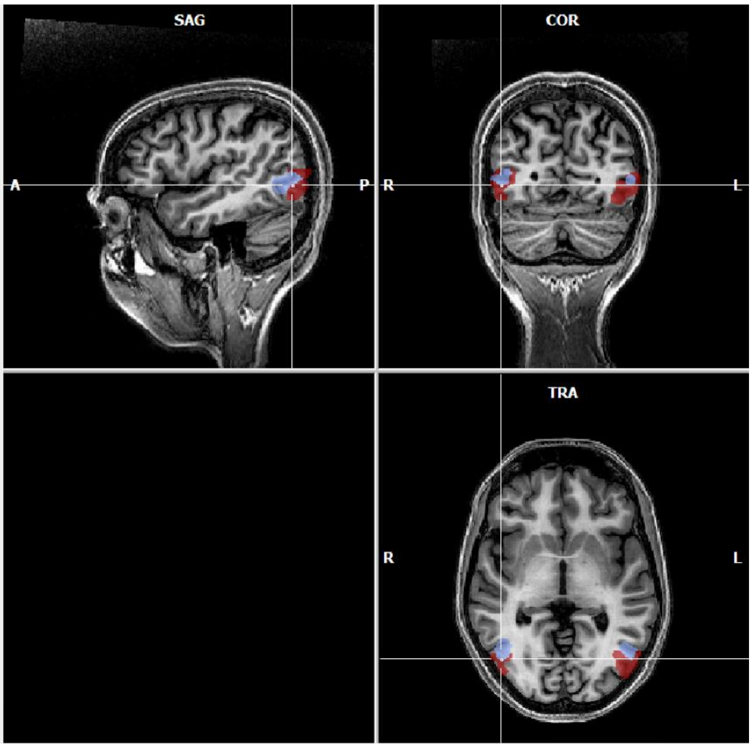


Figure 5-4: Shows MT (red) and MST (blue) making up MT+ as identified for a single participant.

The two regions of interest making up MT+ complex, MT and MST are defined in each of the participants using methods detailed in Huk, Dougherty, and Heeger (2002). The stimuli consisted of two circular dot clusters (radius 8°) with the centre positioned 10° from central fixation. The dots were ether static or moving divided into alternating 15s blocks. One run, consisting of 16 blocks, was presented with the stimuli on the left of fixation and another run with the stimuli on the right. Dot movement consists of alternating contracting and expanding motion where dots move inward and outward along the radial axes.

MT is localised as the contiguous voxels continuously active duration contralateral stimulation only. While MST is defined as voxels responding to both, ipsilateral and contralateral motion stimuli. MST is located anterior to MT (Huk et al., 2002), therefore voxels responding to only contralateral stimulation further anterior than the median values of MST on the axial plan are not included in the final MT ROI. A participant with MT and MST localised using this method is shown in Figure 5-4.

5.7.3. PRIMARY VISUAL CORTEX (V1) LOCALISER

A standard retinotopic procedure is used (Sereno et al., 1995). V1 is localised using an 8Hz counter-phase flickering checkerboard wedge rotating clockwise at 64s/cycle for a total of 8 cycles. Check size is scaled by eccentricity according to approximate cortical magnification factor (Radius-12° 24° Sector). Each voxel's temporal phase response to the rotating wedge is fitted using a model derived from the stimulus time series. Phase of BOLD response was superimposed on a segmented and flattened grey matter representation and is taken as a visual field position indicator with V1 boundary identified by eye.

5.7.4. FMRI STIMULI AND TASK

Seven adult human naive participants (four female) took part in the study. The stimuli are as described in the general methods section. Participants fixate on a small blue circle and the centre of the screen throughout the experiment. Each probe stimulus, X or Y, appears after a particular prime stimulus, A or B, 75% of the time respectively (Figure 5-5 a). Procedures for both tasks are shown in Figure 5-5 b) and c).

The prime stimulus always appears for 500ms with a random gap of 0.333 to 0.666s before the probe stimulus. The probe appears for either 250ms or 800ms duration (short or long), chosen as behavioural data indicated that these durations are judged to be longer or shorter the majority (90%) of the time by all participants. Before each trial is a mandatory 4s gap where participant response is recorded and a further random Poisson delay between trials of mean 2s and range 0-8s. There are 32 trials per block and eight blocks per run, with two runs, one for each task performed on separate days. The probe stimuli differ across two different properties: duration (long or short) and expectation/orientation (left or right). Each prime/probe combination makes up a single trial that is defined for the analysis as being 2.5s long, from the onset of the prime stimulus.

There are two tasks, one where participants respond by button press, indicating if the probe lasts a longer or shorter duration than the prime stimulus and another where participants indicate if the probe was orientated toward the left or right. The duration task will show if there is a relationship between BOLD and stimulus duration and if there is a suppression effect for more probable prime-probe combinations, which would demonstrate a dissociation between suppression and the temporal expansion effect. The orientation task is introduced to test if the experiment induces a suppression effect when the task is more relevant to the implicit relationship between the colour of the prime and orientation of the probe.

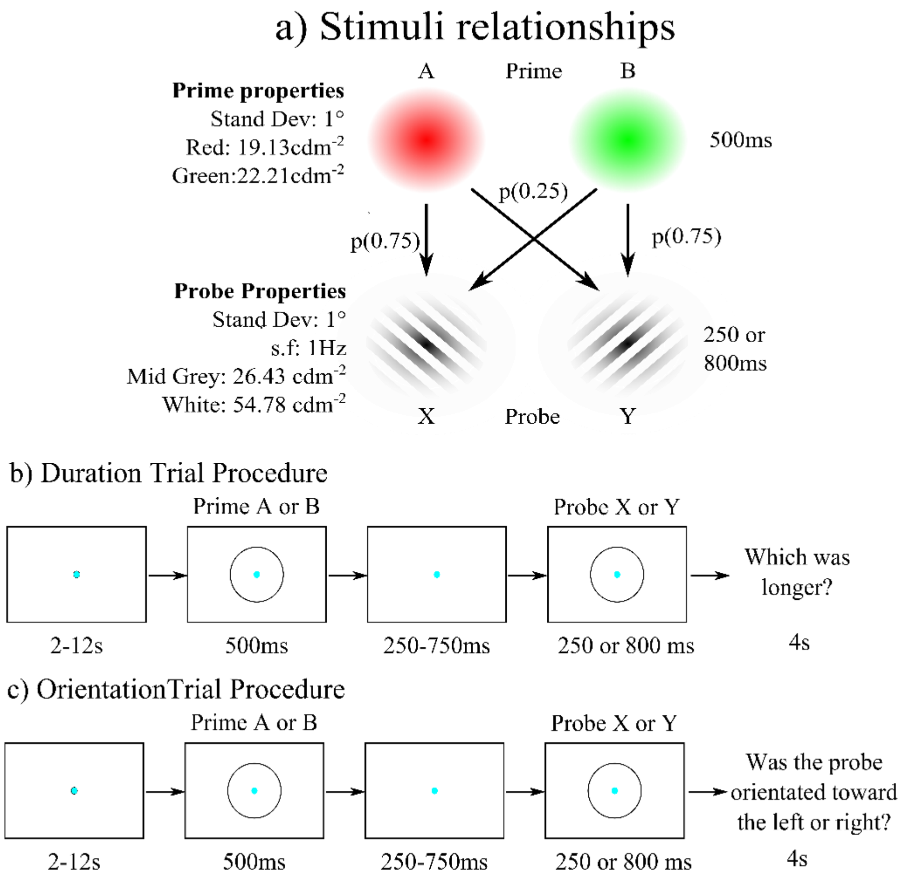


Figure 5-5: a) shows the stimulus properties and the probabilistic relationships inducing expectation. b) shows the duration trial procedure and c) shows the orientation trial procedure. In both there is an initial fixation alone period for 2-12s, mean 4s defined by a Poisson distribution. Prime is displayed for 500ms with a random delay before the probe stimulus appears. There is a period of 4s where responses are recorded.

5.7.5. ANALYSIS

Analysis was performed in Brain Voyager QX 1.4. Experimental effects are measured using Region of Interest analysis using a GLM with the two experimental tasks analysed separately. Before the data is pre-processed, the first four volumes of each block are discarded; three-dimensional motion and time slice correction was applied along with filtering the data through a 0.01Hz High pass filter. Functional and anatomical data is aligned in AC-PC space and GLM analysis performed for each individual participant. Each stimulus condition (A-X-Short, A-X-Long, A-Y-Short, A-Y-Long B-X-Short, B-X-Long, B-Y-Short, B-Y-Long) was modelled separately by convolving a haemodynamic response function with the stimulus time course, including head motion regressors.

For each stimulus condition the strength of response is given as mean percent signal change of all voxels in a particular ROI. Stimulus conditions are collapsed depending on the effect being measured for a particular experimental task, e.g. expectation effects involve contrasts between predictable and unpredictable trials given as Predictable: A-X-Short, A-X-Long, B-Y-Short and B-Y-Long. Unpredictable: A-Y-Short. A-Y-Long B-X-Short and B-X-Long.

5.8. RESULTS

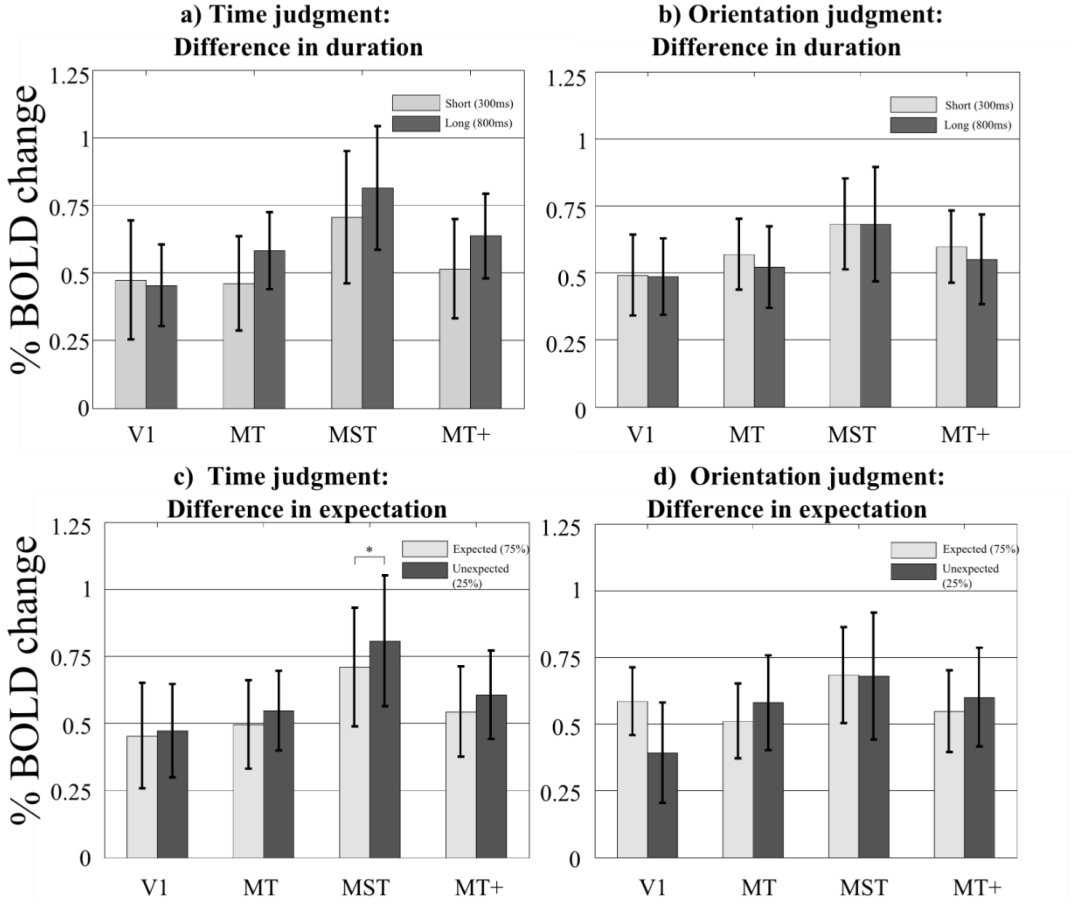


Figure 5-6: BOLD Response for different stimuli (rows) for the two experimental tasks (columns), error bars show standard errors (n = 7). Left graphs show results from time judgement experiments. Right show orientation judgements. Top shows differences in duration, bottom shows differences in expectation. All results except V1 short and expected durations in the time judgement task and V1 for long stimuli in the orientation task are significantly different from baseline. There appear to be consistent differences in medial temporal areas between long and short, expected and unexpected stimuli in the time but not orientation task.

Each measured variable for both expectation (expected, unexpected) and stimulus duration (long, short) is measured for each participant by first collapsing the appropriate trials and then averaging across all trials in the condition. Participants were able to distinguish short and long durations in a manner comparable to the behavioural data (~90% correct). These are shown in Figure 5-6. The majority of stimuli in both tasks show significant increases compared to the baseline (grey screen) across all areas.

In the duration task, both longer and unexpected durations show an increase in BOLD relative to shorter and expected durations respectively, except V1, which shows the opposite trend between longer and shorter stimuli. This is not repeated in the orientation task. Figure 5-7 shows this trend more clearly by displaying the differences in signal change between the two relevant stimuli (Short - Long and Expected – Unexpected) where MT and MST areas show the aforementioned trends in the duration task but not in the orientation task.

Two-tailed paired t-tests are used to look for differences in each condition across all participants. There are no significant effects in either experimental task in V1 for duration (Time: $t_6 = - 0.19$, $p = 0.859$. Orientation $t_6 = 0.14$, $p = 0.893$) or expectation (Time: $t_6 = - 0.24$, $p = 0.819$. Orientation: $t_6 = 1.27$, $p = 0.251$) or MT+ complex for duration (Time: $t_6 = - 1.58$, $p = 0.163$. Orientation: $t_6 = 0.16$, $p = 0.877$) or expectation (Time: $t_6 = - 2.08$, $p = 0.083$. Orientation: $t_6 = -0.26$, $p = 0.805$). While there is no significant difference in MT for either measure (Duration | Time: $t_6 = - 1.70$, $p = 0.141$. Orientation: $t_6 = 0.60$, $p = 0.574$. Expectation | Time: $t_6 = - 1.72$, $p = 0.135$. Orientation: $t_6 = -0.415$, $p = 0.693$),

MST shows a significant difference in activation between predictable and unpredictable stimuli in the duration task ($t_6 = - 3.08$, $p < 0.05$), an effect which does not carry over to differences in duration ($t_6 = - 1.21$, $p = 0.273$) or either contrast on the orientation task (Duration: $t_6 = - 0.28$, $p < 0.974$. Prediction: $t_6 = 0.14$, $p < 0.987$).

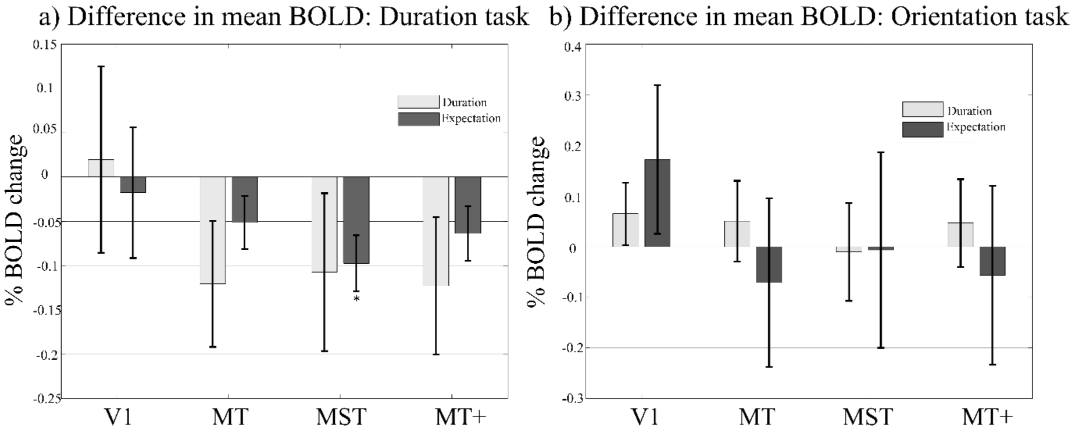


Figure 5-7 BOLD change in response to predictable and unpredictable stimuli and different durations, n = 7. Bars show short – long and expected – unexpected response, as these differences are expected to be in the same direction. Error bars show standard errors (N=7). a) shows results for the duration task. All visual areas show repetition suppression i.e. a reduction in BOLD for expected stimuli, however this effect is only significant in MST. There is a reduction across all but V1 with stimuli of different durations, i.e. stimuli that last longer show an increased BOLD signal, but again this is not significant. There are no significant effects in the orientation task and no non-significant trends either.

5.9. FMRI DISCUSSION

The fMRI data shows there is evidence of repetition suppression in MST in the duration judgement task, and the direction of the suppression effect is consistent across areas, although not significant. That this is not repeated in the orientation condition might seem at odds with previous results. Previous reports suggest that suppression associated with expectation is increased when the expected stimulus pattern is task relevant compared to when it is not (Kok et al., 2012a). Therefore, it would be sensible to hypothesise the opposite pattern to what is observed here. BOLD change induced by expectation would likely be observed in V1, as neurons in V1 encode orientation (Kok et al., 2012a). BOLD suppression due to expectation is reduced when attention is diverted (Larsson & Smith, 2012) and attention is suggested to modulate BOLD response, similar to stimulus onset in the visual system (Smith, Cotillion & Williams, 2006). This may provide an explanation as to why there is no effect in the orientation condition, despite the task relevant prime stimulus. In the duration task participants have to compare the duration of the prime to that of the probe stimulus meaning they have to attend to the stimulus. However in the orientation task, the participant is asked to judge the orientation of the probe with no comparison to the prime stimulus, therefore does not have to direct attention toward the prime stimulus (over the whole trial some attention is required, although less than for the duration judgment trial). As the duration task places greater attentional demands on the participant, there is an effect of expectation on BOLD because attention facilitates top-down repetition suppression so this result is compatible with previous findings.

The fact that only one ROI shows a significant effect here could also be important. Kok et al., (2012a) show significant repetition suppression in V1 only when guiding attention to orientation grating stimuli for which there is a selective response in V1 neurons. As this repetition suppression effect is observed in the duration task only, this suggests differences in duration drive MST neurons implicating MST in duration perception, reinforcing other findings (Sadeghi et al., 2011).

What is also apparent is a non-significant effect of stimulus duration in the fMRI data here, although there is a trend that longer durations cause greater activity in the motion processing visual areas when the task is duration specific. Overall, there is little correspondence between perceived duration and BOLD observable in this experiment, suggesting differences in event time do no relate to differences in BOLD signal in these visual areas. This suggests that duration is not encoded in sustained increases of firing in large numbers of neurons sufficient to drive changes in BOLD in these areas. There did not appear to be any consistent significant differences across participants in whole brain analysis. This does not exclude other encoding mechanisms using sparse populations, transient changes that are too fast to have any effect on BOLD or sub voxel resolution of selective responses to different durations.

5.10. CONCLUSION

There are two main effects in this study. First, that there is no temporal expansion effect observed with the experimental paradigm used here. Secondly, when attention is focussed on judging duration, repetition suppression due to expectation in MST occurs, despite the lack of a behavioural effect.

These two findings together suggest that not all forms of expectation contribute to the temporal expansion effects. This is problematic for proposals that perceived duration is related to expectations (Pariyadath & Eagleman, 2007) as with no behavioural effect on the perception of event duration it would be expected that their would be no corrisponding effect on BOLD signal, which is observed. This does not mean that expectation has no effect on perceived duration but does suggest that implicit relationships between stimuli are not enough on their own to drive differences in perceived duration. Since participants did not appear to notice the relationship between different stimuli it may be the case that participants need to be aware of the relationships for any effect of expectation on perceived duration to arise.

The lack of correspondence between BOLD signal and duration perception is further shown by the fact that a perceived temporal difference does not result in a difference in BOLD signal. Therefore, the relationship between neural energy, or at least its BOLD correlate and duration is not a straightforward one linking visual areas to duration of visual events (Eagleman & Pariyadath, 2009). There is also some suggestion that MST in particular might play a role in encoding duration, although it might be an attentional artefact that is not observed in the orientation task as it does not require as much attention to perform. The data exhibits interesting, though non-significant trends in the data showing reduction in BOLD of short compared to long stimuli in the duration identification task that might be due to representations of different stimulus durations but it is difficult to draw conclusions from this without further study.

Although participant numbers were small this is not atypical of tasks investigating repetition suppression using a similar analysis, e.g. Larsson and Smith (2012) use eight. Task difficulty could be the reason behind the differences in results between the two judgements as in the time judgement more attention is directed to the prime stimulus than in the orientation task. It is difficult to match exactly task difficulty and therefore attentional resources across two different judgments. An alternative method would be to introduce an easier duration and harder orientation judgment and see what effects are consistent within each task as such task difficulty manipulations have been used to show brain areas involved in timing before (Livesey et al., 2007).

Differences in expectation and duration might cause changes to stimulus representations that are encoded in sparse populations. MVPA has been used to show changes of this nature (Jiang et al., 2013; Kok et al., 2012a) so an alternative is to use multivariate techniques to investigate how representations change with expectation and stimulus duration. The number of trials is similar to Kok et al., (2012a) but further post-hoc analysis could be considered data peeking and to be avoided and participant numbers in these experiments where larger (>16). If MVPA analysis were desired, it would be better to redesign the experiment to match more closely other experiments that find significant MVPA effects to allow for comparisons between results and avoid data peeking.

6. CHAPTER SIX: DISCUSSION OF RESULTS

6.1. CHAPTER OUTLINE

This final chapter provides a summary of the findings reported in the previous chapters regarding how they relate to the literature and the three research questions identified in the introduction. These questions are: Do changes in perceived duration after adaptation have functional effects? How might duration be encoded in sensory systems? What is the relationship between repetition suppression, expectation and perceived duration?

Arising from this it is proposed where and how duration might be encoded in the visual system based on the simple model presented in Chapter 4, and general themes are expanded upon to suggest a general mechanism for encoding time across neural systems. Other models are discussed in relation to these claims as well as what this might mean for the conscious perception of time. Finally, some avenues for expanding upon the work here are detailed.

6.2. OVERVIEW OF FINDINGS

With the centralised clock not proving to be an ideal framework for interpreting results of duration perception (see Chapter 1) it is difficult to advance understanding of duration perception without developing a suitable alternative framework. Eagleman and Pariyadath (2009) suggest that the amount of neural energy associated with encoding a stimulus is proportional to its perceived duration. There are shortcomings with this; neural energy is loosely defined and does not provide a quantifiable mechanism meaning, as the authors state, this proposal is the starting point rather than a complete framework for understanding duration perception.

Chapter 4 details a model using increases in response to a stimulus to encode the duration of that event. This model demonstrates how duration can be encoded within neural systems using established properties in a manner compatible with the neural energy proposal. The model progresses the neural energy hypothesis by providing quantifiable predictions that match observations in literature (for more detail on this see sections 4.3.3, 4.3.6, 4.3.8, 4.3.9 and 4.4). Others have proposed similar models, showing how ramping activity can encode timing of action or the delay between two events using a single cell (Durstewitz, 2003) or a network (Reutimann, Yakovlev, Fusi, & Senn, 2004; Simen et al., 2011), so this concept is not new but the model demonstrates how this could apply to sensory systems. These other models also show how neural systems might create the type of response required by the SDD model, represented by the low-pass filters, on either a single cell or population level. There is also evidence of neurons in LIP exhibiting this type of ramping behaviour (Janssen & Shadlen, 2005; Leon & Shadlen, 2003).

Another issue that the model in Chapter 4 demonstrates is the necessity of controlling the input magnitude through a normalisation stage to avoid errors caused by variations in the input signal. Altering parameters in the normalisation stage can be considered analogous to mechanisms responsible for sensory adaptation and thus, give a possible explanation regarding why adaptation to sensory properties affect perceived duration (Ayhan et al., 2011; Bruno & Johnston, 2010; Curran & Benton, 2012; Johnston et al., 2006; Marinovic & Arnold, 2011). Adaptation to 'tune' sensory systems to encode optimally stimulus properties uses the same normalisation process that affects perceived duration, so any changes optimising sensory systems also affect duration estimates. While normalisation reduces effects of input magnitude on duration estimates, it does not eliminate it. This is in line with experimental evidence showing perceived duration of a visual stimulus correlates with arithmetic value (Alards-Tomalin et al., 2014), size (Alards-Tomalin et al., 2014; Ono & Kitazawa, 2011; Xuan et al., 2007), colour saturation (Alards-Tomalin et al., 2014) brightness (Brigner, 1986; Terao, Watanabe, Yagi, & Nishida, 2008), numerosity (Xuan et al., 2007), speed (Brown, 1995) and temporal frequency (Kanai, Paffen, Hogendoorn, & Verstraten, 2006).

We find suggestions of shared mechanisms of time and space in Chapter 3, which shows temporal frequency adaptation changes the Flash-Lag illusion in a way that is consistent with a reduction in the time component. This matches reports in other studies (Ayhan et al., 2009; Burr et al., 2007; Johnston et al., 2006) which use a similar adapting stimulus to show a compression of perceived event duration. The work here suggests a relationship between the perception of duration and the perception of space as this reduction of the time component is measured as a reduction in the illusory spatial offset observed in the Flash-Lag illusion. This relationship between apparent duration and space provides some advantages in that it reduces the Flash-Lag illusion meaning a more veridical perception of the stimuli. Sensory systems could be tuning their measure of duration to recalibrate sensory percepts to provide more useful information in a rapidly changing environment.

It has been shown that duration adaptation does not affect action timing, implying that there are separate timing mechanisms for perception and action (Marinovic & Arnold, 2011), so changes in perceived duration may be involved in recalibrating perceptual mechanisms only.

The result in Chapter 3 showing changes in duration appear to affect space in Flash-Lag is similar to research showing that both space (Ross, Morrone, Goldberg, & Burr, 2001) and time (Morrone et al., 2005) are compressed about the time of a saccade. This is significant as stimuli presented at the time of saccades show a reduction in contrast sensitivity of low spatial frequencies (Volkmann, Riggs, White, & Moore, 1978) suggesting that selective suppression of the Magnocellular pathway occurs about the time of saccades (Burr, Morrone, & Ross, 1994). A further interesting finding is the perisaccadic remapping of receptive fields. Macaque monkeys show this in LIP (Duhamel, Colby, & Goldberg, 1992), superior colliculus (Walker, Fitzgibbon, & Goldberg, 1995) and frontal eye field (FEF) (Umeno & Goldberg, 1997), suggesting common remapping mechanisms in areas involved in directing eye movements and attention. Further research shows this predictive remapping in the direction of the saccade is a convergence of receptive field positions toward the fixation target resulting in a compression of space (Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). This is of significance as LIP neurons are tuned to durations (Janssen & Shadlen, 2005; Leon & Shadlen, 2003), meaning LIP contains representations of time and space; as these are processed in the same spatial location this might mean manipulating one property also affects the other. The fact that neurons in LIP also exhibit predictive changes in their receptive fields further suggests that LIP is an area encoding time and space.

Walsh (2003) proposes a common magnitude system for encoding time, space and quantity, which there is some suggestion of in the results in Chapter 3, in regards to time and space. A feature of the SDD model is that the magnitude of the input, which could be used to encode other stimulus properties affect duration judgements. Such a link implies not only the use of common optimisation mechanisms, such as those shown by adaptation studies and the normalisation stage of the SDD model, but a common encoding mechanism as provided by the SDD population. Like neural energy, the model presented here could be considered to quantify the proposals outlined by Walsh (2003).

Results showing that expectancy is linked with perceived duration were one of the main findings motivating the neural energy proposal (Eagleman & Pariyadath, 2009). Chapter 5 aims to test the relationship between implicit expectation and perceived duration, finding no behavioural effect but a significant effect of expectation induced suppression in a duration task in MST. This suggests that whilst implicitly learnt temporal patterns can cause suppression induced by expectation whilst attending to duration, there is no corresponding behavioural effect on perceived duration.

This lack of an effect shows that the relationship between expectation, repetition suppression and perceived durations are not straightforward so this may have to be reconsidered in future theory. Since participants did not appear to be aware of the expectations in either the behavioural or the fMRI experiment, it is possible that the participants need to be consciously aware of the expectations before they have any effect on the perception of duration or that these types of expectation patterns do not drive this effect. As Chapter 5 shows expectation caused suppression of BOLD signal in MST when making a duration judgement, but not an orientation judgement and expectation induced suppression in the visual system is generally found in areas that are shown to encode the stimulus being displayed (Larsson & Smith, 2012; Jiang et al., 2013; Kok et al., 2012a), this finding hints that MST is involved in representing durations as well as areas like LIP.

The evidence presented here shows sensory systems appear to be encoding duration, using mechanisms common with other sensory properties. This evidence also supports the view that duration is encoded across distributed, hierarchical mechanisms typical of sensory systems. In particular there is evidence suggesting areas MST and LIP are responsible for duration perception, which form part of the dorsal/where pathway (Goodale & Milner, 1992; Goodale, Westwood, & Milner, 2004; Nassi & Callaway, 2009). The SDD model shows how measuring event duration could be performed by using the temporal response of neurons or populations of neurons and provides a candidate mechanism for the perception of duration across the brain. The next two sections expand upon these proposals and provide pathways for future investigation.

6.3. IS DURATION PERCEPTION COMPUTED IN THE DORSAL PATHWAY?

The evidence suggests that time perception is computed using mechanisms shared with processing other sensory properties which exist at multiple levels in the visual hierarchy. It has been proposed that sensory information used to measure event duration is initially processed in the magnocellular pathway where change in the contrast gain of M-cells (Solomon et al., 2004) causes a change in perceived event duration (Ayhan et al., 2009; Ayhan et al., 2011; Bruno & Johnston, 2010; Johnston et al., 2006). The magnocellular pathway makes up a large proportion of the input into areas in the dorsal or where pathway, thought of as being responsible for spatial vision (Mishkin, Ungerleider, & Macko, 1983) or more recently vision for action (Goodale & Milner, 1992; Goodale et al., 2004). The dichotomy between the dorsal/where/action and the ventral/what/perception pathway, including the degree of independence of the two pathways has been questioned (McIntosh & Schenk, 2009; Milner & Goodale, 2008). However, the idea that the visual system is organised into two different ways to process information for two different purposes provides a framework to understand the visual system. It must be recognised that with any individual task information is processed in networks within and across both pathways, depending on the demands of the task, i.e. there are no tasks where information is processed exclusively in the ventral or dorsal stream.

Adaptation to motion also can have a direction-specific compression effect on perceived duration (Curran & Benton, 2012) showing that adaptation in mid-level visual areas in the dorsal pathway that are sensitive to motion direction, such as MT (Kohn & Movshon, 2004), can also affect perceived time. This, along with Bruno, Ng, and Johnston (2013), provides evidence that adaptation at early and mid-level visual processing stages in the dorsal pathway changes perceived time. Areas in the dorsal pathway such as MT+ project to the parietal lobe (Nassi & Callaway, 2009) containing LIP, where neurons respond to event duration (Janssen & Shadlen, 2005; Leon & Shadlen, 2003).

Parietal areas have been theorised to encode various properties including, time as well as space and number in a common magnitude encoding system (Bueti & Walsh, 2009; Walsh, 2003). The right parietal lobe is implicated specifically in time perception, even to the point of being termed a third ‘when’ pathway (Battelli et al., 2007) in addition to the commonly identified what and where pathways.

The SDD model presented in Chapter 4 provides a quantitative mechanism showing how time can be encoded using normalisation and the temporal response of neural systems. Normalisation can be considered analogous to the adaptation stage(s) while the low-pass filters exhibit similar response to neurons in LIP. This means the two crucial components of the SDD model exist in the dorsal pathway. The problem with this proposal is that M-Cells are band pass (Hess & Snowdon, 1992). Output from M-Cells in response to a step function, representing the appearance of an object in vison as used in Section 4.2, is rapid increase then decay in spike rate toward the rest output at stimulus onset and a rapid reduction in spike output and decay toward rest at offset. At no point does the SDD model perform or require such a signal so initially it is difficult to see how the model is compatible with the proposal that duration perception is a function of the dorsal pathway. The band-pass characteristics of M-Cells mean they are sensitive to temporal change, e.g. flicker. In standard motion detection models (Borst & Egelhaff, 1989) M-Cells are analogous to the function of neurons in the second processing step, inputting to a third step with directionally sensitive neurons. In the visual system, cells in V1 are selective for spatial and temporal frequency (Priebe, Lisbeger & Mosvhon, 2006) and output to further along the dorsal stream, where in MT and MST cells are sensitive to speed and direction (Priebe et al, 2006). Output from MT or MST to a moving stimulus would more closely resemble the step input to the model. It is possible for mechanisms resembling the SDD model to exist along the dorsal stream but they need to exist in at the middle or higher visual system, a view that is proposed in Kaneko and Murakami (2009). This is compatible with aforementioned evidence suggesting MT, MST and LIP are involved in duration perception.

As a result, the SDD model explains experimental data using known neural properties, provides a quantitative model in line with current theories, and could plausibly exist along the dorsal pathway. This does not mean duration computed in the dorsal/action pathway of the visual system is used by actions directly and always, as Marinovic and Arnold (2011) show duration for perception and action are separable, but that visual duration is computed within the dorsal/action pathway regardless of if it is used for actions or not.

6.4. TEMPORAL RESPONSE OF NEURAL SYSTEMS PROVIDES A GENERAL MECHANISM FOR DISTRIBUTED ENCODING OF TIME IN THE BRAIN.

Visual perception is not the only system where duration may be useful. For example in timing an action, a duration estimate can also be crucial or in memory for recalling when, or how long for an event may occur. Neuroimaging evidence suggests that duration representation is distributed across the brain. The cerebellum (Jueptner et al., 1995; Mathiak et al., 2004), pre-supplementary motor and prefrontal areas (Coull et al., 2004; Macar, et al., 2006), basal ganglia and inferior parietal and pre-motor areas (Livesey et al., 2007; Rao et al., 2001) have all shown to be activated at various stages for tasks involving duration perception.

The SDD model uses the temporal response of neural systems to encode duration of a sensory event so there is no reason why similar mechanisms could not exist in other systems. In section 6.2 it is mentioned that neurons in LIP show ramping activity in response to durations. There is evidence of neurons in other areas varying firing rate according to durations such as decaying activity, opposite to ramping, shown in prefrontal neurons (Kojima & Goldman-Rakic, 1982). Other pre-frontal neurons also show ramping response to the duration of a stimulus (Brody, Hernández, Zainos, & Romo, 2003). Neurons within regions of the thalamus (lateral posterior nucleus and suprageniculate nucleus for visual cues, medial geniculate nucleus and the posterior intralaminar nucleus for auditory cues) show ramping increases in firing rate according to the expected time of reward (Komura et al., 2001). This evidence shows that in multiple areas there are neurons that vary their firing rate in either a monotonically increasing (ramping or climbing) or decreasing (decaying) in tasks that require a measure of duration. Essentially, the temporal dynamics of firing rates are used to measure time in multiple different areas and during different tasks, providing evidence that this is a potential common mechanism neural systems use to represent duration across the brain. Other models use the temporal response of neural systems in similar mechanisms to the SDD model here (Simen, Balci, deSouza, Cohen, & Holmes, 2011b; Zandbelt, Purcell, Palmeri, Logan, & Schall, 2014).

One interesting property of such mechanisms is that the neuron or population of neurons' output can perform another function as well as duration perception, such as encode a particular stimulus property or action so mechanisms that encode time in the brain can exist in parallel to other coding mechanisms within the same neural populations. Standage et al., (2013) provide an excellent example of how a population of neurons might do this using a population model of a type that is considered to represent cortical columns (Douglas & Martin, 2004; Wilson & Cowan, 1973). In this model, the firing rate of pyramidal cells in a population of pyramidal and inhibitory interneurons was used to encode time. This was achieved by varying the NMDA receptor conductance, which caused the excitatory population firing rate to increase with NMDA conductance, reaching threshold sooner. Thus, in this model NMDA concentration is inversely proportional to the duration encoded in the population.

This model holds many similarities (ramping outputs, thresholds) with the SDD model. What make it interesting is that the mean firing rate of the population is driven by the rapid spiking of a relatively small number of excitatory neurons. This mirrors how populations encode information, for example, a population encoding a motion direction for any particular motion direction, a small subset of the population will fire rapidly, but which neurons in the population that are firing rapidly will change depending on the direction of motion (Pouget, Dayan, & Zemel, 2000). By taking the mean firing rate across the population, the model presented by Standage et al., (2013) can encode time simultaneously with a particular stimulus property. As this is a standard population model, this means that such mechanisms can exist across the brain meaning that whenever 'something' is represented in the brain, be it a percept or action the duration associated with 'it' can be encoded within the same population providing a mechanism for a distributed sense of time.

Further evidence for distributed mechanisms comes from Critchley (1953), as reported in Walsh (2003), who notes that temporal abnormalities in perception occur with a corresponding spatial abnormality. Two more recent studies show that a patient suffering from hemispatial neglect in the left visual field reports overestimations of duration for stimuli presented in the afflicted part of the visual field compared to the other areas (Basso, Nichelli, Frassinetti, & di Pellegrino, 1996; Calabria et al., 2011). With a distributed mechanism, this can be explained as with a lesion there are fewer neurons processing stimuli in the left areas, this results in either a reduced stimulus drive associated with that event which would result in a reduced input to the integrating neurons (low-pass filters in the SDD model) that ramp-on slower, resulting in this reduced duration estimate.

A distributed mechanism has the benefit of being a highly efficient way to encode time as wherever a property is represented, its duration can be encoded without any additional metabolic cost. Having a distributed rather than a centralised timing mechanism also provides redundancies so that a complete loss of time perception across all modalities does not occur. But it does have inherent problems such as if the temporal response properties of the neurons are not known how is it possible to compare inputs from separate sources without errors?

There is some evidence for such errors occurring. Auditory durations are commonly reported to last longer than visual durations (Goldstone & Lhamon, 1974; Wearden et al., 1998; Wearden, Todd, & Jones, 2006), showing evidence of systematic errors, which could be due to a mismatch between modality specific coding mechanisms.

Another systematic bias is the central tendency effect (Vierordt's Law), where short durations are overestimated and longer durations are underestimated. This is discussed in Chapter 4 where, in the model the effect materialised because of the initially high normalised input causing detectors with fast filter time constants to ramp-on quickly causing the overestimation. Central tendency in the model is a problem of inaccurate labelling of detectors with slower or faster time constants. Lewis and Miall (2009) show that central tendency reduces with environmental feedback. Cicchini, Arrighi, Cecchetti, Giusti, and Burr (2012) find musicians show a more veridical perception of auditory time, i.e. a reduced central tendency, with percussionists showing this trend in the visual as well as auditory modalities. This shows that biases in duration estimates are reduced with feedback and learning, so it is possible that adjustments between independent timing mechanisms are made, and can be updated based upon environmental feedback and experience.

6.5. THE CONSCIOUS PERCEPTION OF TIME

In the previous section it has been argued that researchers in different areas are converging on a common mechanism using the temporal response of neurons that can be approximated as a linear slope function or low-pass filter to encode duration in a distributed fashion across the brain. A distributed mechanism reflects the multiple drafts (Dennett & Kinsbourne, 1992) or fame in the brain (Dennett, 2001). Time in the brain is perceived using different mechanisms in parallel that do not reflect a single frame of reference but one that is interpreted from multiple mechanisms and continuously revised. Under this framework, multiple representations of event time are computed in parallel as described in section 6.4, which produce multiple drafts that may be incompatible with one another and fluctuate over time in response to processes like attention and input from sensory organs. Each draft is competing with the others to become the 'strongest' or final draft that can change over time. This is in distinct opposition to the centralised timer measuring durations of all events and actions across modalities.

The centralised timer can be interpreted as a Cartesian approach to the problem of time perception (Section 1.2.5). So not only does the approach detailed in sections 6.3 and 6.4 argue that duration is measured using particular mechanisms it argues for a particular philosophical school of thought. This view has implications for some of the work presented. In Chapter 4, the SDD model uses a labelled line coding system to represent duration. To decode, or read out the information processed by the population, knowledge about each SDD's (the labelled line in the model) label needs is required. This is dangerously close to invoking a homunculus and a Cartesian explanation of duration. In the model, the labelled line coding system fulfils the purpose of demonstrating that information about event duration can exist in the system. Therefore, the purpose of the decoding scheme is to provide a proof of concept and is not deemed and essential property of the model. Alternatives to this coding scheme are discussed in Section 6.7.2 with the aim of reducing this problem.

6.6. OTHER MODELS OF DURATION PERCEPTION

6.6.1. CENTRAL CLOCK MODELS

There are two key differences where the proposals here differ from central clock modes. Firstly, there is a shift from a centralised, top down timing to a distributed, bottom up system, which it is argued more accurately represents the organisation of the brain, sensory systems in particular. Secondly the removal of a centralised timer, which is replaced by an input signal to the accumulator(s). The signal can be an external input such as in the SDD model or it could be an internal signal, such as preparatory activity encoding a motor plan for an action to be performed with a delay. This signal is passed through a neural system acting as an integrator that takes a specific time to reach threshold to delay the action and when threshold is reached the action performed.

Attention and arousal effects on timing have been a common topic of research providing evidence used to justify central clocks (Treisman et al., 1990), commonly showing an increase in perceived time with attention and arousal. Although little has been said on this topic in this work, these behavioural effects observed are compatible with the proposals here if attention and arousal are said to act as gain changes in a signal. An example of changing gain is described in Chapter 4, where it is demonstrated that a reduction in gain of the normalisation stage is shown to reduce duration estimates, therefore the reverse should increase duration estimates. Although the normalisation stage is not claimed to represent attention it shows that duration estimates should act in a way expected of them from literature. A possible extension to incorporate attention in the SDD model is described in section 6.7.2

6.6.2. CHANNEL CODING

Adaptation to duration, where a visual or audio stimulus of a particular duration is presented repeatedly, has been shown to have a repellent effect on duration estimates when the stimulus is shown for a different durations (Heron et al., 2012). This results in an effect where, after duration adaptation, longer or shorter stimulus durations than the adapting duration are perceived to be even shorter or longer. This effect is explained using a population model with neuronal output being described by Gaussian curves tuned to a peak duration (Heron et al., 2012). Adaptation is represented as a reduction in gain of a sub population resulting in a reduction of the peak in these neurons' tuning curves, resulting in the repellent effect on estimates.

In a further study (Heron, Hotchkiss, Aaen-Stockdale, Roach, & Whitaker, 2013) the duration of a visual test stimulus was distorted by an auditory distracting stimulus of a different duration presented at a time overlapping the test stimulus, causing distortions in duration estimation compared to estimates without the distractor. The duration adaptation effect was found to repel about a duration consistent with channel model estimates even when a distractor was presented showing that this cross-modal adaptation effect occurs before multisensory integration thus it is claimed it is an effect of sensory processing.

As has been mentioned previously, firing rate of LIP neurons increases as a function of elapsed time. However, this implies a summation, rather than channel based coding system proposed by Heron et al., (2012). There is neurophysiological evidence of duration-tuned neurons existing in a number of vertebrate species (Sayegh, Aubie, and Faure, 2011). Initially thought to be used for echolocation in the auditory system in species like bats and dolphins, neurons that perform similar functions have been found in the cat primary and secondary visual cortex (Duysens, Schaafsma, & Orban, 1996) so they exist in different modalities in species that do not echolocate. So there is evidence for such a duration channel coding scheme but the location and how these channels would select which event(s) to encode the duration of and what range(s) they might exist over is an open question.

6.6.3. STATE DEPENDENT NETWORKS

Recurrent neural networks can encode event duration (Buonomano & Maass, 2009; Karmarkar & Buonomano, 2007). Within such a mechanism, time is encoded intrinsically because of neural dynamics that encode duration in the network state that evolves over time. As these networks can exist across the brain it means time can be encoded using this type of network in a distributed fashion. State dependent networks share commonalities with the proposals outlined in section 6.4. The main different between state dependent networks and using temporal dynamics (ramping or decaying neural activity) described earlier to encode time is that it is easier to conceptualise how duration can be encoded using temporal dynamics and a threshold and the simple model is more firmly rooted in a specific type of neural response to stimulus.

Ramping or decaying neural response provides an explicit encoding of duration and it provides clear predictions regarding what activity should be observed in neurons or networks when encoding duration. Whereas state dependent networks would produce complex, dynamic patterns of activity that would be harder to detect, though there is some evidence of this (Goel & Buonomano, 2014). Due to state dependent networks' ability to create and reproduce complex patterns, they are suited to encode complex temporal relationships. It is plausible that state dependent networks might exist as a separate encoding mechanism to that proposed in section 6.4 for encoding complex action that require precise timing, such as speech, playing a musical instrument or storing complex sequences of events. While the comparatively simpler temporal responses are used for encoding event durations, time to action could be encoded by ramping or decaying activity which is a view shared by Goel and Buonomano (2014).

6.7. FUTURE RESEARCH DIRECTIONS

6.7.1. FLASH-LAG

ADAPT BAR AND FLASH INDEPENDENTLY

The most obvious modification to the Flash-Lag experiments in Chapters 2 and 3 is modifying the stimulus so that only the area over bar or flash is adapted and measure the effect on the Flash-Lag illusion. Since high temporal frequency adaptation does appear to reduce the time component of Flash-Lag the results of such an experiment will provide insight as to what mechanisms are behind both duration processing and the Flash-Lag illusion.

Such a study could inform current thinking on the mechanisms behind Flash-Lag. Temporal integration (Krekelberg & Lappe, 2000a) relies on averaging the position of the moving object over a temporal window. This would predict that adapting the bar, not the flash would shrink the time component of the Flash-Lag. Latency delay (Whitney & Murakami, 1998) explains Flash-Lag in terms of a relative delay between processing the moving bar and flash as such makes no clear predictions regarding whether adapting the flash, bar or just both would change the Flash-Lag illusion, as all of these would fit in with latency delay.

Similar to latency delay, postdiction (Eagleman & Sejnowski, 2000) does not make any clear predictions regarding if the adapting the bar, flash or only adapting both would have an effect. If adapting the bar has an effect, postdiction would explain this in the same way as temporal integration. An effect of adapting the flash can be explained by the Flash occurring in an area of the visual field where rapid changes are to be expected, thus could be assumed to not cause the resetting of internal model that postdiction uses to explain Flash-Lag. Temporal integration makes a different prediction to the two other commonly used explanations for Flash-Lag so this experiment provides a test of the temporal integration hypothesis of Flash-Lag and would also reveal if the Flash is being advanced as the results of Bruno et al.,(2015) might suggest.

OCCLUDER TO HIDE BAR

In an experiment where a moving object is occluded for a portion of its trajectory and participants have to indicate if the object appears earlier or later than expected shows that when the moving object is delayed behind the occluder over time, healthy participants can adjust their expectations and no longer report the delayed objects as late (Roth, Synofzik, & Lindner, 2013). It is possible to apply this paradigm in a similar set-up to the Flash-Lag illusion. Instead of having the bar visible throughout the trial, the bar is occluded about the position of the flash. Participants are judging where they think the bar would be at the time of the flash. If Flash-Lag were observed, this would indicate the Flash-Lag effect is due, at least in part to non-perceptual mechanisms, i.e. not directly a result of visual input, but that perceived duration can be adapted in the absence of visual input and this can affect prediction judgments. Regardless of whether or not there is an observed Flash-Lag effect with this paradigm, further experiments could be run with an adapting stimulus of 5 or 20Hz temporal frequency where the bar is occluded. This would have little effect on perceptual mechanisms of motion and position over these areas, as there is no stimulus to adapt. Any changes from participants' judgements observed in the 20Hz adaptation condition would be indicative of an effect on time and provide evidence suggesting a measure of duration is used in predictive perceptual models in the brain and that perceived duration can be adapted in a visual area where no visual stimulus is presented. This would require extending our model, which now only describes ways of detecting the duration of visual objects.

6.7.2. MODEL

ALTERNATIVE ENCODING METHODS TO LABELLED LINES

In section 6.5 some of the problems involved with using a labelled line coding are discussed. In the current scheme, the duration of the event is encoded by taking the label of the most recent detector to switch on. One alternative way to decode the event duration without changing the model, just the way it is decoded would be to take the number of on detectors as a measure of duration. This is effectively a switch between using a labelled line to a summation-coding scheme. This would preserve the properties of the model, as the components are the same, while reducing the prerequisite information required to estimate event duration and reduce the dependence on a homunculus. The parameters of the SDD population, such as the filter time constant (τ) and the threshold (T) do not have to be fixed as precisely as they are and these variables could vary within the population. This would still produce accurate duration estimates with a suitably large SDD population, as it does not matter which SDDs are on, just as long as there is variability as to when they switch on. Such a coding scheme would be more robust regarding internal noise in the detector population as a roughly equal number of faster (short labelled) SDDs would switch off as slower (longer labelled) would switch on. However, to know the exact effects this would have to be modelled and may depend on properties like the event duration and the distribution of τ and T values in the population.

MODELLING EFFECTS OF ATTENTION

The effect of attention on time perception has often been a subject of study (Coull, 2004; Mangels et al., 1998; Treisman et al., 1990; Tse et al., 2004). Currently the model does not incorporate attentional effects, so cannot make predictions regarding such experiments. Since the model already uses normalisation, one method to incorporate attention into this model would be to add an additional stage with multiplicative gain change before the normalisation stage in line with Reynolds and Heeger, (2009) so the model could then make predictions regarding attention. As attention would be modelled as a multiplicative gain on the input signal prior to normalisation, this means that its effects will likely be similar to changes in input magnitude. As the normalisation stage takes some time to normalise the signal fully this would mean the effects of attention would be more pronounced for shorter durations, which could provide some interesting experimental predictions.

6.7.3. INVESTIGATING THE EFFECTS OF EXPECTATION ON PERCEIVED DURATION

BEHAVIOURAL PARADIGM MODIFICATIONS

The paradigm used in Chapter 5 did not produce a behavioural effect of expectation on perceived duration whereas other paradigms do (Pariyadath & Eagleman, 2012; Schindel et al., 2011). One reason for this may be that the paradigm did not create salient relationships between the stimulus pairs. Modifications could make this stronger; the first would be simply to increase the ratios from 75%/25% to 90%/10%, making the unexpected conjunctions more surprising. Another method could be to split the experiment into two blocks: a training block where only the expected conjunction pairs are shown to build up expectations, then have a second test block where stimulus pairs are shown as before to include the unexpected conjunctions. Other changes could involve modifications of the stimuli themselves. While the Gabor patterns used here vary in orientation, which is a low-level stimulus property, they could be perceived as abstract. Stimuli like faces or places which have been used in previous studies to show the effect of repetition suppression on BOLD (Jiang et al., 2013; Summerfield et al., 2008) are more environmentally relevant and attract attention more. Thus, these could be more susceptible to learning effects. This would mean a shift away from investigating the effects of expectations in early cortical areas to higher areas in the hierarchy of the visual system, but the principle of learning another pattern than that of probability of repetition remains. It would be interesting to see if a behavioural effect emerges and if MST remains implicated.

A FURTHER STUDY USING MULTI-VOXEL PATTERN ANALYSIS OF FMRI DATA

The analysis carried out in Chapter 5 used a GLM applied to the mean BOLD response of voxels identified to be within a defined region of interest. While this is useful for identifying significant differences in average BOLD signal changes across regions this comes at the expense of spatial resolution that might contain fine activation patterns that are otherwise removed along with noise in the data. These patterns can contain relevant information produced by sparse population encoding that is a common mechanism for encoding information across the brain (Pouget et al., 2000). If duration information were represented in sparse population codes rather than in mean activations across a functionally derived ROI, then this would have been missed in the GLM. Using multivoxel pattern analysis (MVPA) can detect such patterns (Haynes & Rees, 2006). Support Vector Machines (SVM) are a commonly used classifier (Mitchell et al., 2004) and could be used in a within-subjects analysis, similar to the ROI GLM analysis performed. SVMs would perform a binary classification between two stimulus properties (long and short, unexpected and expected) in each ROI independently. If the classifier can reliably distinguish between the two different stimulus properties across participants it provides evidence suggesting that particular stimulus is encoded in a ROI.

MVPA classifications within a particular ROI are dependent on BOLD amplitude within the ROI (Smith, Kosillo & Williams, 2011), leading to potential issues with quantitatively comparing MVPA results from one ROI to another ROI and with the same ROI with different experimental designs. While Smith et al., (2011) do demonstrate how the MVPA results might be corrected using a BOLD amplitude measure any experiment where this is performed needs to be designed to do so from conception, so it lends itself to both univariate and multivariate analysis. One of the aims of the experiment in Chapter 5 was to investigate the link between duration perception and stimulus predictability by comparing results here to those found previously. This would also give the opportunity to change the paradigm to more closely follow similar studies (e.g. Kok et al., 2012a; Jiang et al., 2013) to allow for more direct comparisons or perhaps informed by further behavioural experiments discussed previously in this section.

6.8. SUMMARY

It is argued that duration perception is encoded in sensory systems as any other stimulus property and this measure of duration has functional roles in sensory systems. Duration is estimated using common systems shared by other perceptual mechanisms such as normalisation, explaining why adaptation to visual properties changes perceived duration. It is proposed duration is encoded using the temporal properties of neural systems responding to an input proposed to exist in the visual system along the dorsal pathway. This also provides a starting point for a framework of perceived duration across the brain that shows how duration might be encoded without using a centralised mechanism.

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8. ACKNOWLEDGMENTS

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