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Attention and Sensory Adaptation

by

Laura Kathryn Bartlett

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ABSTRACT

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ATTENTION AND SENSORY ADAPTATION

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The human sensory system features many dynamic and functional mechanisms that address processing capacity limitations and the complexity of sensory information available in the world. Attention allows the sensory system to prioritise the processing of relevant inputs and ignore those that are irrelevant, while adaptation provides individual neurons a greater sensitivity to a broad range of input. Aftereffects resulting from adaptation are a useful behavioural tool for probing the underlying mechanisms of adapted features, as well as the influence of attention. This thesis features a literature review, meta-analytic review and two empirical studies to explore the influence of attention on the visual motion aftereffect (MAE) and haptic curvature aftereffect (CAE).

Chapter 1 features an introduction to adaptation and attention and a review of the literature. *Chapter 2* demonstrates that attention affects the MAE, with stronger effects for translational than complex motion, and that this relationship is unaffected by adaptation duration or response bias. The meta-analysis of published research (*Chapter 3*) confirms these findings, revealing a substantial overall effect of attention on the MAE, predominantly driven by feature-based attention and not accounted for by response bias. *Chapter 4* reveals that haptic curvature adaptation is not modulated by visual or haptic attention.

The discussion (*Chapter 5*) combines these findings with the previous literature to conclude that visual motion adaptation is affected by attention, whereas haptic curvature adaptation operates independently of attention.

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Academic Thesis: Declaration Of Authorship

I, Laura Kathryn Bartlett declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

Title of thesis: Attention and Sensory Adaptation

I confirm that:

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Chapter 1 Review of sensory adaptation and attention

1.1 Adaptation and attention

1.1.1 What is adaptation?

Adaptation refers to the selective and temporary changes in perception and sensitivity that follow exposure to a new stimulus. Adaptation likely regulates a number of aspects of perception in the natural world - it is a beneficial mechanism that allows the sensory system to quickly and efficiently process and adjust to the huge amount of information present in the world.

Neurophysiological experiments in non-human animals have attributed the reduced sensitivity from adaptation to a contrast gain control mechanism, whereby adaptation decreases the gain of detectors tuned to the adapted stimulus contrast (Ohzawa et al., 1982). Adaptation is further characterised by a reduction of sensitivity for similar patterns to the adapted stimulus, but not for different stimuli (Movshon & Lennie, 1979). Adaptation tends to increase as neuronal responses to the adapting stimulus become stronger. Correspondingly, the magnitude of adaptation increases with the intensity of the adapter stimulus. For example, adaptation is increased for high-contrast adapters (Greenlee et al., 1991; Langley, 2002).

The effects of adaptation have been shown at multiple processing stages, including the retina, thalamus and sensory cortex (Clifford et al., 2007), and for both low-level features such as colour and motion and higher-level processes such as face adaptation (Webster, 2015). Variations in adaptation are also evident within a stimulus feature, for example different motion aftereffects (MAEs) are found for dynamic compared to static test patterns (e.g., Mather, Pavan, Campana, & Casco, 2008; though van Boxtel, van Ee, & Erkelens, 2006, argue that a single motion system can account for MAE differences). Adaptation is a pervasive feature of processing, integral to neural processing at all stages throughout the sensory system and consistently affects our perception of the world.

Neurons have a limited dynamic range for signalling differences and as the eye moves across an environment, adaptation mechanisms must adjust quickly with the substantial luminance and contrast differences within a scene (Webster, 2011). In particular, adaptation may recenter a cell’s operating range, or response curve, around the adapted input signal (Brenner et al., 2000; Gardner et al., 2005). This allows sensitivity to a wide range of contrasts despite the limited range of individual neurons. Using voxel-by-voxel functional magnetic resonance imaging (fMRI) analysis in human participants, Gardner et al. (2005) found evidence for this shift towards adaptation contrast in sensory areas V1, V2 and V3. The authors further revealed that V4 responded to any *changes* in contrast, suggesting a sensitivity to salient events. This is efficient as fewer metabolic resources are required for slowly changing contrast, whilst sensitivity to sudden changes is maintained.

Adaptation may also implicitly represent current expectations of the world, allowing perceptual systems to signal unexpected stimuli or errors in prediction more effectively (Webster, 2011). In this way, adaptation may be key for determining what captures attention. Adaptation may allow for error correction, and may also increase the saliency of novel features by minimising the processing of uninformative and predictable aspects of the environment. For example, adaptation may facilitate perceptual constancy when a stimulus changes (thus maintaining a steady perception) and filter out variations in the stimulus and context.

While adaptation is an essential and pervasive feature of the perceptual system, it has been exploited to gain understanding of the mechanisms of neural processing and perception. In particular, adaptation results in an *aftereffect* - a repulsive perceptual bias, where an opposite percept of a stimulus feature is generated once the stimulus is removed. The strength of this perceptual bias can be measured behaviourally, revealing the degree of neuronal adaptation. For example, the motion aftereffect (MAE), the illusory perception of motion opposite to that of a previously viewed motion stimulus (e.g., a stationary scene will be perceived as moving upwards after watching downwards motion), has been vital for extending our understanding of motion processing. Through measurement of the MAE under different experimental conditions, researchers have gained insight into the behaviour of motion-sensitive neurons and the mechanisms underlying motion processing. Similarly, the haptic curvature aftereffect (CAE), the altered perception of curvature following a period of tactile exposure to a curved surface (e.g., moving a finger across a concave surface for an extended period will cause a flat surface to be perceived as convex), has been a useful tool for understanding haptic processing. Analysing the CAE and the conditions affecting it has extended our understanding of curvature perception and the neural dynamics of haptic processing.

Inducing an aftereffect is an easy and quick procedure that modifies the sensory system and allows measurement of the resulting changes. As such, it has been used as a method for probing the nature, and neuronal sites, of attention. The research outlined in *Chapters 2 – 4* further our understanding of adaptation in both vision and haptics and determine the modulatory role of attention on visual motion and haptic curvature perception.

1.1.2 What is attention?

An additional important feature of sensory processing is attention. Attention is a selective process. It allows prioritised processing of relevant features in the world and inhibition of irrelevant information. Due to cognitive and neural resource limitations, attention allows the optimisation of performance despite the vast amount of information we receive about the world (Carrasco, 2011).

Attention can be captured automatically by a stimulus (exogenous attention) or voluntarily directed (endogenous attention) either overtly (dictated by eye movements) or covertly (oriented toward the relevant location in the absence of eye movement). Covert attention is thought to affect perception through signal enhancement of the attended location, where the representation of the stimulus is improved in quality and signal gain is increased. Attention is also thought to reduce external noise by changing perceptual filter properties, and by suppressing the representation strength of distractors (see Carrasco, 2011 for a review). Multiple types of attention have been identified. Feature-based attention refers to the allocation of attention towards a particular feature of a stimulus, either across stimulus dimensions (e.g., directing attention to motion or colour) or within a stimulus dimension (e.g., directing attention to a specific motion direction). Attention can also be focused towards a particular location (spatial attention) or a particular surface or object formed from perceptually grouping certain elements (surface/object-based attention). A considerable amount of research has been conducted for each of these variants in order to understand the behavioural effects and underlying mechanisms of attention.

Psychophysical and neurophysiological studies suggest that attention may act as an amplification of *contrast gain* in cortical neurons (Martínez Trujillo & Treue, 2002; Reynolds et al., 2000), such that neurons respond as if the contrast of an attended stimulus were increased. Alternatively, attention may amplify neuronal *response gain*, increasing a neuron’s firing rate (see Carrasco, 2011 for an overview). Attention has been likened to an increase in contrast sensitivity. In monkeys, attention has been estimated to increase perceived contrast by 51% (Reynolds et al., 2000). This finding is mirrored in humans: Carrasco, Ling and Read (2004) demonstrated that transient attention can increase the apparent contrast of a stimulus. Additional evidence has shown that transient and sustained covert attention enhances contrast sensitivity at a cued location, and impairs sensitivity at uncued locations (Ling & Carrasco, 2006a; Pestilli & Carrasco, 2005).

A wealth of research has shown the pervasiveness of attentional modulation throughout the visual system, with increasing amounts of attention required for sensory analysis at later processing stages (Treue, 2001). Even low-level striate processing can be modulated by attention, with increasing influence throughout the human cortical hierarchy (e.g., Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Liu, Pestilli, & Carrasco, 2005). For example, spatial attention appears to operate across all levels of the visual cortex, including the primary visual cortex (V1). As shown using fMRI, V1 responses differ when attention is alternated between spatially separate locations (Gandhi et al., 1999) and distinct V1 activation maps to the retinotopic representation of an attended location (Somers et al., 1999). Additionally, anticipation of a target modulates V1 responses (Silver et al., 2007). Similar results have been found for haptic perception, with both primary (SI) and secondary (SII) somatosensory areas of the brain affected by attention (Sambo & Forster, 2011).

A number of low-level sensory processes were initially thought to operate outside of attention (e.g., Treisman, 1985). However, psychophysical evidence has shown that low-level processes, such as contrast perception (for an overview see Carrasco, 2011) and orientation (Liu et al., 2005), can be altered by attention. As a result, some aspects of early perception could be revisited to determine whether a dichotomous theory of processes as pre-attentive or requiring attention holds true. The research in *Chapters 2 – 4* seek to evaluate the contribution of attention to basic visual and haptic processing.

1.1.3 How might attention affect adaptation?

Exploring the interplay between adaptation and attention is crucial for understanding sensory perception, as both intrinsically modify how the world is perceived. Adaptation is a general mechanism that allows the sensory system to adjust to the environment in an efficient and dynamic way. It is beneficial to sensory processing, serving as error correction, aiding perceptual constancy, and minimising metabolic resources in the detection of changes in the environment - which is important given that neurons are characterised by a limited dynamic range.

Adaptation and attention both dynamically alter neural processing. Adaptation reduces neuronal sensitivity to a stimulus feature following continued stimulus exposure, generating an aftereffect, while attention may affect processing through enhancing the signals of the attended stimuli and suppressing the processing of unattended stimuli. Ling and Carrasco (2006b) explored the effect of attention on contrast sensitivity using an adaptation paradigm. Contrast sensitivity was enhanced for a valid cue (i.e. a central line indicated the location of the target) and impaired for an invalid cue (i.e. a central line did not correctly indicate target location) relative to a baseline neutral cue following brief (300ms) adaptation. Conversely, after 6 s of adaptation the opposite was true: thresholds were highest for the valid cue and lowest following an invalid cue. Processing was enhanced by attention during longer adaptation periods, resulting in higher contrast thresholds and increased adaptation (akin to a higher-contrast adaptor). Additionally, suppressed processing at unattended locations led to reduced adaptation and lower contrast thresholds.

This research demonstrates that focusing attention towards an adaptation stimulus results in a stronger neuronal response, leading to increased neuronal adaptation (Ling & Carrasco, 2006b). Further, the processing of unattended stimuli is reduced, which may lead to a reduction in neuronal adaptation and the resultant aftereffect. While research has mostly focused on visual attention, this same pattern of activation and inhibition and its effects on adaptation may persist across all sensory domains. For example, focusing attention on a haptic location or feature increases processing (see Section 1.3.1), which may also increase neuronal adaptation while reducing responses for unattended stimuli. These possible effects of attention on haptic adaptation are explored in *Chapter 4*.

The load theory of attention (Lavie, 1995, 2005) provides an additional, complementary explanation of how attention may modulate adaptation. When perceptual processing capacity is reduced by an attentionally demanding ('high load') task, distractors and task irrelevant stimuli are less likely to be processed, whereas less demanding 'low load' tasks will leave more attentional resources available to process distractors. In terms of adaptation, a high load task would reduce processing of the irrelevant adaptation stimulus, which would also lead to a reduction in adaptation, compared to a low load task. Behavioural and neuroimaging evidence lend support to this explanation for motion adaptation (Rees et al., 1997), however the load theory has been criticised as lacking falsifiability and for having circular logic (Benoni & Tsal, 2013).

Adaptation is an easily measured behavioural phenomenon which can inform our knowledge of sensory processing in the brain. Coupled with evidence from neuroimaging, the interplay between adaptation and attention gives insight into the pervasiveness and effects of attention, and defines the cortical sites at which it exerts an effect. While extensive research has focused on low-level visual processing, for example revealing the hierarchical structure of processing features such as motion (e.g., Bex, Metha, & Makous, 1998), the influence of attention at different stages of processing warrants additional investigation. Further, different forms of attention, i.e., featural, spatial or object-based, may impact adaptation in different ways. These issues are addressed for the MAE in both *Chapters 2 & 3*. Exploring these nuances will further our understanding of the neuronal basis and influence of attention.

1.2 Does attention affect visual motion perception?

1.2.1 Attention and motion processing

The relationship between attention and motion processing has been studied by researchers for many years. In 1912, Wertheimer (1912/1961) reported a change in the perceived direction of ambiguous motion due to attention, a finding that has since been supported (Kohler et al., 2008). The identification of third order motion (i.e., the motion of marked important visual details within a salience map) provides strong evidence for the role of attention on motion processing, where attention can entirely drive the perception of motion (Cavanagh, 1992; Lu & Sperling, 1995). Attention also appears to control motion signal integration across space (Burr, Baldassi, Morrone, & Verghese, 2009).

These findings are consistent with the notion that the effects of attention increase throughout the processing hierarchy of the cortex (Treue, 2001). At the neuronal level, single-cell recordings in medial temporal (MT) and medial superior temporal (MST) areas of monkeys have demonstrated enhanced responses when attention is focused on a stimulus moving in the preferred direction within the receptive field, compared to attending a non-preferred motion direction or a motion stimulus outside of the receptive field (Treue & Maunsell, 1999). Neuroimaging studies provide support for the theory that attention modulates motion-related cortical activity. Attending to moving dots leads to increased activation in MT / MST areas compared to attending superimposed stationary dots (O'Craven et al., 1997). MT activation is also increased when either translating or expanding dots within the same stimulus are attended, compared to passive viewing (T. Watanabe et al., 1998). Rees et al. (1997) presented words at fixation and irrelevant motion in the periphery. They found increased activity in MT under low load conditions (detecting uppercase words), and baseline activity when participants engaged in the high load task (detecting bisyllabic words). Research has now also demonstrated that attention affects lower level visual processing stages (Saproo & Serences, 2014).

The prevailing counterargument against attentional effects on motion processing relies on the ubiquity of motion in everyday activity. Motion is crucial for fundamental tasks such as object segmentation, depth perception, judging distance and the guidance of self-motion, as well as survival critical tasks such as object avoidance (Nakayama, 1985). Many of these attributes of motion information processing suggest, and perhaps rely on, motion operating independently from current task demands, as suggested by Morgan (2011, 2012, 2013). Indeed, motion that is communicating threat is processed automatically and without attention (e.g., Lin, Murray, & Boynton, 2009). Additionally, motion shows strong pop out during visual search (Driver et al., 1992; Nakayama & Silverman, 1986), though these effects are well modelled as a function of target and distractor saliency rather than evidence for automatic motion processing (Rosenholz, 1999). Therefore, while evidence suggests a role for attention in higher level motion processes, the extent of this attentional modulation for low-level first order motion is unclear.

1.2.2 The motion aftereffect and attention

The motion adaptation paradigm is a popular approach for investigating attentional modulation of motion processing. The MAE refers to the perception of illusory motion following inspection of a moving stimulus. The MAE has a long history of study, with descriptions dating back to Aristotle. It was further popularised in the 19th Century as 'the waterfall effect' (Addams, 1834), because after watching a waterfall, the rocks to the side are perceived as moving upwards. Termed "the psychologist's microelectrode" (Frisby, 1979), adaptation is a useful tool for studying the visual system and the MAE allows the exploration of motion-sensitive mechanisms. The MAE reflects neuronal adaptation across many motion-selective visual cortical areas (see Mather et al., 2008, for a detailed overview). Often, the MAE is explained as a form of automatic gain control, such that unit responses are attenuated following continued stimulation (Mather et al., 2008; van de Grind et al., 2003) – for example, the spontaneous baseline activity of neurons tuned to the direction of adaptation motion will be reduced with continued exposure. Adaptation is also thought to lower the inhibition to preferred direction in those cells that respond selectively to the opposite direction to adaptation. As such, when adaptation is released motion is perceived in the opposite direction.

There are a number of different experimental techniques used to quantify the MAE in the laboratory. MAE duration is often measured to determine MAE strength (e.g., Chaudhuri, 1990; Rezec, Krekelberg, & Dobkins, 2004), where observers report the cessation of illusory motion of a static test stimulus. This is the most common method of analysing the MAE as it is easily implemented. However, it has been criticised as susceptible to response bias – it is hard to determine when illusory motion has fully stopped (Blake & Hiris, 1993) and participants may adjust their responses to meet perceived researcher aims (Morgan, 2012). For example, Sinha (1952) showed that providing participants with the previous mean MAE duration shifted participants responses towards this arbitrary value. More objective measures are also common, typically using test stimuli that contain motion. One such technique is to estimate the degree to which test motion direction is biased due to motion adaptation. If leftward motion is adapted, upwards test motion will be perceived as moving upwards and right; the degree that the motion is biased away from actual test motion allows an estimation of MAE strength (e.g., Alais & Blake, 1999; Bartlett, Graf, & Adams, 2018; Blaser, Papathomas, & Vidnyánszky, 2005). While less susceptible to bias than measuring MAE duration, response bias from experienced participants with an understanding of the MAE could influence results. A further technique is that of nulling, where dynamic noise test patterns are adjusted to perceptually null, or cancel out, the MAE. The motion coherence of the test stimulus, i.e., the number of dots moving oppositely to the adaptation motion, required to null the MAE gives an index of MAE strength (Blake & Hiris, 1993). These experiments typically use a two alternative forced choice (2AFC) design (e.g., Lankheet & Verstraten, 1995; Taya, Adams, Graf, & Lavie, 2009), where observers select one of two options in response to the test stimulus (e.g., whether it is moving up or down). 2AFC methods are considered robust to response bias, as participants are unable to bias responses in a consistent way.

Determining the effect of attention on the MAE allows inferences regarding the site of attentional modulation in the brain, as well as the resilience of motion mechanisms to attentional influence. When attention is diverted away from a motion stimulus during adaptation, MAEs would be reduced in strength if attention affects motion processing.

The influence of both feature-based and spatial attention on motion processing have been explored using the MAE. Feature-based attention consistently alters motion adaptation, shown using an attentional tracking paradigm. Observers are presented with two superimposed patterns moving in opposite directions and asked to attend one motion direction (see Figure 1.1b). Resultant MAEs are reported in the opposite direction to the attended motion patch (e.g., Lankheet & Verstraten, 1995). Using a variation of this design, Alais and Blake (1999) presented coherently moving dots, superimposed with randomly moving dots that were briefly coherent at random times during adaptation. Compared to passively viewing the stimulus, attention to these briefly coherent dots biased the MAE in a way consistent with the brief motion direction. Differences between feature-based and spatial attention suggest that evidence for one does not support an effect for the other; specifically, Morgan (2011) has argued that they may represent different processes. For example, focusing on one motion direction in an attentional tracking experiment may reduce the processing of mechanisms tuned to the other superimposed motion direction. This would generate an aftereffect consistent with the attended motion direction. This would not, however, reflect attentional modulation within a spatial attention distractor paradigm. While feature-based attention affects motion adaptation, evidence regarding spatial attention is inconsistent.

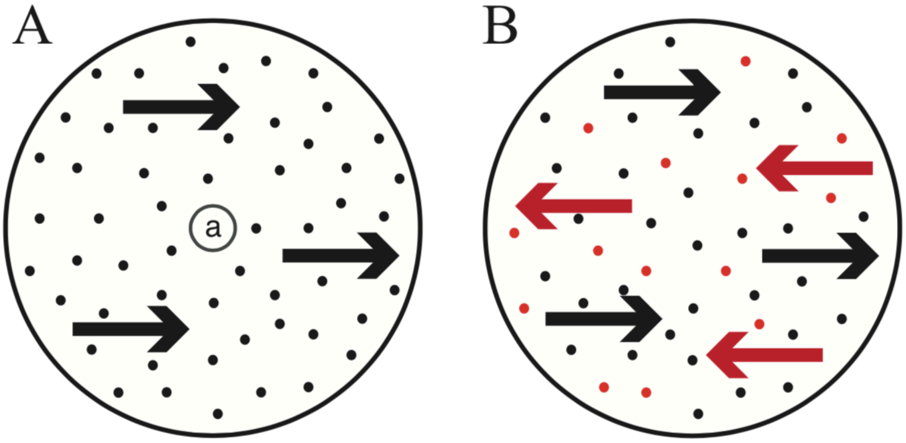

Figure 1.1 A schematic of typical paradigms used to measure the effect of covert attention on motion adaptation. (a) A moving stimulus is presented, as well as a central stimulus such as a stream of letters. (b) Two populations of dots (indicated here by different colours) each follow a different motion trajectory.

To investigate the effect of spatial attention on the MAE, typically participants adapt to a moving stimulus within an annulus in the periphery, while an alphanumeric stream is presented at fixation (see Figure 1.1a). This central, fixated stimulus is used to manipulate attention, where observers perform a difficult high load task (e.g., bisyllabic word detection), an easy low load task (e.g., detecting uppercase letters), or passively view the stimulus. As such, spatial attention is focused on the centre of the display rather than the peripheral motion stimulus. The first exhaustive investigation of the MAE, conducted by Wohlgemuth (1911), determined that attention did not alter MAE duration, resulting in an enduring notion that the mechanisms underlying the MAE are pre-attentive. However, an influential experiment by Chaudhuri (1990) found reduced MAE durations when attention was diverted compared to passive viewing of the stimulus. A number of studies have since reaffirmed this effect, for example Georgiades and Harris (2000a) found that diverting attention reduced both the duration and peak velocity of the MAE. Attention has been shown to modulate not only first-order motion adaptation (luminance driven, e.g., Nishida & Ashida, 2000), but also second order motion adaptation (defined by contrast, e.g., Nishida & Ashida, 2000), as well as motion in depth aftereffects (e.g., Shulman, 1991). Further, different factors affecting the attention MAE relationship have been explored, such as spatial extent

(Georgiades & Harris, 2000b; Takeuchi & Kita, 1994), interocular transfer (Nishida & Ashida, 2000), and awareness (Kaunitz et al., 2011). The research in *Chapters 2 & 3* seek to further explore the impact of a number of factors on the MAE-attention relationship.

1.2.3 Weaknesses and inconsistencies within the literature

Despite evidence suggesting a role for attention in motion adaptation, a number of studies have failed to find an effect (Morgan, 2011, 2012, 2013; Pavan & Greenlee, 2015), or found that the effect is inconsistent (e.g., Georgiades & Harris, 2002b; Takeuchi & Kita, 1994). As a result, explanations of attention's effect on the MAE have been called into question. While attention is commonly characterised as increasing the contrast of attended stimuli, Morgan (2011) found that attention did not affect the MAE when using a 2AFC design to determine contrast discrimination thresholds following adaptation. Further, the 'file drawer' effect, whereby nonsignificant results often go unpublished, may exacerbate the prevalence of attentional modulation in the literature (Morgan, 2011). As a result, researchers tend to frame negative findings as a consequence of differences between conditions.

To account for discrepant findings, Morgan (2011, 2012, 2013) proposed that previous positive findings might be driven by response bias. Observers may alter their responses in line with research aims, i.e., reporting that MAEs are weaker when attention is diverted during adaptation. MAE duration has frequently been used to measure MAE strength, and is particularly susceptible to bias (Blake & Hiris, 1993; Sinha, 1952). Indeed, Morgan (2012) found no attentional modulation of the MAE in naïve participants, measured via nulling and duration of MAEs. Nor was an effect found using a bias-reducing MAE paradigm (Morgan, 2013). In this paradigm, participants adapted to oppositely moving grating patches presented above and below fixation, either passively or while judging whether a central black square was smaller or larger than the average of all previously presented squares. Test stimuli were presented in the same spatial location as the adapting stimuli. When both test gratings moved in the same direction, one patch matched the direction of the adapting motion. The speed of this matching test stimulus should be perceived as slower relative to the non-matching stimulus as a result of motion adaptation. Observers reported which test grating was moving faster to indicate MAE strength; this did not differ across the attention conditions. A modified version of this paradigm is implemented in *Chapter 2*.

While response bias is a substantial concern for such experimental paradigms, this criticism fails to take into account previous findings of attentional modulation of MAE duration in naïve participants (e.g., Chaudhuri, 1990; Patterson et al., 2005), or using more stringent measures of the MAE such as 2AFC nulling (e.g., Taya et al., 2009). MAE responses must be altered in a systematic way; responses would need to be modified such that test motion is opposite to that of the adaptor, as well as increasing this effect when attention is focused on the motion. It is unclear how naïve participants would know to bias their responses in this way, especially with increasingly complex experimental designs. As such, a reasonable interpretation of the literature could be that variations in experimental design determine the strength of the effect.

1.3 Does attention affect haptic perception?

1.3.1 Attention and haptic processing

Whilst visual perception has arguably been a primary focus of sensory and attention research, a growing number of studies have explored the effects of attention on haptic, as well as cross-modal, perception. Haptic perception refers to both tactile cutaneous cues (mechanical deformations of the skin) and proprioceptive cues (muscle, joint and tendon deformations) during active exploration of objects. If we are to understand human perception as a whole, the process of selection must be understood for each of the senses.

Behavioural investigations into the effect of spatial attention on haptic perception have often used a cueing paradigm: response accuracy or reaction time are compared between targets that follow an accurate (valid) cue and those where the cue does not correctly indicate the target location (invalid). Using this paradigm, Spence and McGlone (2001) demonstrated an effect of exogenous spatial attention on tactile processing. They found that responses for a tactile discrimination task were quicker and more accurate when non-predictive tactile cues occurred on the same hand as the target stimulus. Significant cueing effects were also found by Chica, Sanabria, Lupiáñez and Spence (2007), when isolating the effect of endogenous haptic attention. Sathian and Burton (1991) also discovered that detection accuracy was improved when a spatial location cue (a tap on the top of one finger) was valid (80% of trials), rather than invalid, when observers were required to detect the *absence* of a texture change (i.e., the distractors had both smooth and rough sections, and the target had a continuous texture). This suggests attention can modulate processing at the individual finger level. Conversely, when the *presence* of a texture change was the target, attentional cueing had no effect on detection accuracy. Cueing a specific location for a haptic target leads to benefits in processing but this effect is reduced for less attentionally demanding tasks, in line with the load theory of attention (Lavie, 1995, 2005).

Numerous fMRI studies and those measuring event-related potentials (ERP) have demonstrated that sustained tactile-spatial attention enhances processing at attended locations, relative to unattended locations, with effects for both perceptual and decision-making processing stages (see Sambo & Forster, 2011 for a review). For example, Forster and Eimer (2005) demonstrated a reaction time and ERP-measured somatosensory processing benefit following a valid visual cue, and a substantial cost for invalid cueing, for detecting a weak target vibration. Regional cerebral blood flow (rCBF) for the location of an anticipated haptic stimulus has also been measured to explore tactile spatial attention. Anticipating a stimulus at the tip of the index finger increased blood flow by 25% in the somatosensory finger area contralateral to attended location (Roland, 1981). Further, Drevets et al. (1995) demonstrated bilateral decreases in blood flow in SII, and ipsilateral decreases in SI, for an expected stimulus to the big toe, and for an expected painful electrical stimulus to the fingers. While the findings from Roland (1981) imply an increase in blood flow to the relevant cortical areas, Drevets et al.'s (1995) findings suggest suppression of activation in areas where stimuli are not anticipated. More recently, using high-resolution fMRI, Puckett, Bollmann, Barth and Cunnington (2017) demonstrated somatotopic attentional modulation within SI for attention towards individual fingertips.

Monkey and human neuroimaging studies have further demonstrated the influence of attention on processing in SI and SII, comparing conditions that focus attention on the tactile stimulus with those diverting attention to a non-tactile task. Hsiao, O'Shaughnessy and Johnson (1993) examined neuronal discharge rates in the somatosensory cortex of monkeys while attention was switched between a tactile discrimination task (respond when the raised letter moving across a finger matched the letter presented on a screen) and a visual detection task (detecting when one of three illuminated squares dimmed). The two tasks resulted in significant differences; 50% of neurons in SI cortex increased in discharge rate, while 80% of SII neurons responded with attention, some increasing and some decreasing in rate. These results indicate a role for attention in brain areas linked to haptic processing. In human participants, positron emission tomography (PET) has shown higher cerebral blood flow responses in SI as a result of vibrotactile finger stimulation when attention was focused on the stimulus than when engaging in a distracting task simultaneously (Meyer et al., 1991). Further, increased SI activation with attention, and significantly greater attentional modulation in SI than SII, has been shown using fMRI (Sterr, Shen, Zaman, Roberts, & Szameitat, 2007). However, using magnetoencephalography (MEG) in human participants, Mima, Nagamine, Nakamura and Shibasaki (1998) demonstrated that active attention to an electric pulse, compared to passive viewing of a video, enhanced SII activity, but not SI responses. This paradigm can be criticised, as allocation of attention is uncontrolled without a task to divert attention, however similar results have been found comparing a tactile and auditory task (Fujiwara et al., 2002). Sterr et al. (2007) argued that the disparities in attentional modulation of somatosensory areas across experiments are driven by differing task characteristics.

The modulation evidenced in early ERP components may simply reflect sensory gain, while SII activation may reflect attentional influences (Sambo & Forster, 2011). Utilising both fMRI and electroencephalography (EEG), Schubert et al. (2008) found enhanced early processing in SI as a result of spatial attention, as well as delayed attentional enhancement, which likely represents a relay effect from higher cortical areas.

As well as spatial attention, evidence suggests that tactile perception is affected by feature-based attention (e.g., Burton et al., 1999; Metzger, Mueller, Fiehler, & Drewing, 2019; Sinclair, Kuo, & Burton, 2000). In a behavioural investigation, Sinclair et al. (2000) found a performance benefit for duration of stimulation (i.e., stimulus length), roughness and vibrotactile discrimination following valid cuing, and a deficit following invalid cueing. A recent experiment confirmed this effect with task instructions (shape or roughness discrimination) occurring after object exploration (Metzger et al., 2019), preventing participants from adjusting their exploratory movements across tasks.

In line with this research, focusing resources on a single feature, compared to multiple features simultaneously, is beneficial (Burton et al., 1999). Burton et al. (1999) found that directing attention to either roughness or duration of pairs of stimuli resulted in a significantly higher percentage of correct responses when identifying which grating was rougher/longer, than dividing attention between these features. Their PET findings implicated that regions in SI and SII are modulated by feature-based attention, with greater changes in blood flow in SII than SI. Processing changes were equivalent regardless of attended feature, suggesting that duration and roughness are modulated similarly. However, a more recent fMRI study found no differences between selective and divided attention in SI or SII; rather, specific regions showed differences between the control counting task and all attention conditions (Burton et al., 2008). The authors posited that attentional differences may be too subtle for detection by fMRI, a temporally insensitive measure. While these findings indicate that feature-based attention modulates tactile processing, it remains unclear where exactly in the brain it exerts an effect.

Despite neuroimaging and psychophysical evidence that attention modulates haptic processing, ‘pop out’ effects have been found for haptic search: quick reaction times, regardless of distractor count, are found when searching for a target differing in roughness from distractor items (Plaisier et al., 2008) and for a moveable ball among anchored balls (van Polanen et al., 2012). These effects indicate that processing of these haptic stimulus characteristics may occur automatically. Certain stimulus qualities must be identified when interacting with an object, for example roughness may dictate the grip type and force needed to move the object. As such, it would be reasonable for certain vital haptic characteristics to be processed independently of attention, to reduce the likelihood of failure. While neuroimaging experiments and behavioural discrimination and detection investigations have been used to explore the effect of attention on haptic perception, attentional modulation of haptic adaptation was previously unexplored. The research in *Chapter 4* implements an adaptation paradigm to further elucidate the role of attention on haptic perception.

1.3.2 The haptic curvature aftereffect

There are a number of haptic illusions, including aftereffects analogous to those found in vision and audition (see Kappers & Bergmann Tiest, 2016 for an overview). A wide variety of stimulus features, for example roughness, stimulus size, tactile motion and compliance (i.e., stimulus softness) adaptation, all result in negative aftereffects – an opposite percept of the adapted feature.

The haptic CAE is well-researched, and has proven to be a robust and reliable feature of haptic perception. Gibson (1933) first demonstrated that a straight edge was perceived as concave following three minutes of inspection of a convex object. Following this initial finding, evidence of the CAE suggests that it is persistent under increasingly minimal conditions: for example, following only 2 s of adaptation, with a 40 s interval between adaptation and test (Vogels, Kappers, & Koenderink, 1996), and when the stimulus is touched with a static finger (van der Horst, Duijndam, et al., 2008). Typically, the CAE is measured by varying test curvature per trial and asking participants to make a convex/concave 2AFC judgement. This allows researchers to determine the point of subjective 'flatness, or equality (PSE) for each adaptation stimulus (see Figure 4.3a for example data). Convex adaptation would cause a flat surface to be perceived as concave; as such, a convex PSE is expected. The opposite applies for concave adaptation. The CAE is thus typically quantified as the difference between the test curvature perceived as flat for convex and concave adaptation.

Researchers have investigated the effects of exploration mode (static or dynamic, passive or active) and the degree that curvature adaptation transfers between fingers and between hands. Static CAEs partially transfer, i.e., aftereffects are weaker when adaptation and test stimuli are touched with different fingers (van der Horst, Duijndam, et al., 2008), while the *dynamic* aftereffect transfers fully between hands (van der Horst, Willebrands, et al., 2008). As dynamic touch gives curvature information over time and combines knowledge of finger rotation and movement direction, the authors argued that dynamic touch is represented at a higher cortical level than static touch. In a review of CAE studies, Kappers (2011) found that the strength of the CAE did not differ between static and dynamic conditions. Rather, aftereffects were smaller when exploration was needed to perceive the stimulus curvature. Kappers (2011) suggested that two distinct aftereffects may exist, reflecting differential processing; weaker aftereffects but strong transfer across fingers is found when movement is necessary to perceive the curvature, whereas strong aftereffects but partial transfer is found when the entire stimulus is directly touched. Consistent with the notion of separate adaptation mechanisms, van Dam, Plaisier, Glowania and Ernst (2016) found that dynamic and static exploration of slanted surfaces resulted in independent haptic slant aftereffects that did not transfer between exploration modes. As such, attention may have distinct effects for the different modes of exploration.

Clearly sensory adaptation extends to the haptic modality and can provide important insights into the mechanisms underlying perception. While there are numerous examples of haptic aftereffects, the influence of attention has not yet been explicitly explored. Attention has been shown to affect tactile perception (see Section 1.3.1), suggesting that haptic adaptation will be similarly affected by attention. Whether focusing feature-based attention on a certain stimulus characteristic increases the aftereffect magnitude, decreases adaptation of unattended features, or both, is currently unknown. Additionally, distracting attention from an adaptation stimulus would reveal the influence of spatial attention on haptic curvature. My research sought to reveal how both feature-based and spatial endogenous attention can affect haptic perception using an adaptation paradigm.

1.4 Cross modal attention

1.4.1 Attention and crossmodal processing

Interactions between sensory modalities have gained attention over recent years, with research exploring when different sensory representations of the environment are recalibrated or integrated to form a coherent percept of the world. Multisensory effects are often successfully modelled with the maximum likelihood approach: signals are estimated for each sensory cue and weighted by their relative reliabilities. They are then optimally combined to give observers a best possible guess of what is in the world (Ernst & Bülthoff, 2004). In the real world, it is vital to coordinate attention across the senses, as each sense can give important information that can assist in selection (Driver & Spence, 1998). The research outlined in this section focuses on the interplay of attention across visual and haptic perception, two senses that are intrinsically linked by intentional motivations towards the external world (Gallese, 2016).

Attention in one modality affects the processing of a different modality. There is a cost for switching between modalities: when a target is in an unexpected modality (vision / tactile / audition), detection is slower (Spence et al., 2001). However, there are also benefits of cross-modal attention. For example, reaction times are reduced when both the target and the cue occur on the same side, regardless of their modality. This has been demonstrated for: (i) visual and tactile cue and target combinations (Butter et al., 1989; Chica et al., 2007; Forster & Eimer, 2005; Gray & Tan, 2002; Posner et al., 1978; Spence et al., 2000), (ii) auditory, visual and tactile cues for visual targets (Gray et al., 2009), (iii) visual and auditory cues on a tactile target (Spence et al., 1998), and (iv) a tactile cue for visual and auditory targets (Spence et al., 1998). Evidence suggests that this is not a hemispheric effect as the same pattern of results are found when the hands are crossed, where the opposite would be expected (see Driver & Spence, 1998, for a review).

Gray and Tan (2002) explored dynamic endogenous attention, finding that tactile motion along the forearm orients visual attention, with faster discriminations when a final pulse was aligned with the visual target at short interstimulus intervals (ISIs). Faster responses were also found at longer ISIs when the visual target was offset in a way consistent with the tactile motion direction, with slower discriminations when the offset visual target was in the direction opposite to tactile motion. This was also the case for predictive visual motion on tactile discriminations. While these findings suggest that tactile attention aligns with visual perception, this attention effect is confounded with one of integration – i.e., visual and haptic cues occurring in the same location at the same place may lead to the expectation that they represent one object. Integration may enhance responses in a way consistent with the observed effects, rather than attention driving the findings.

These behavioural cross-modal attention effects may relate to multimodal neural processing. Multimodal neurons respond more strongly to information presented in more than one sensory modality, and have been found behaviourally in cats following deactivation of the anterior ectosylvian sulcus input to the superior colliculus (Wilkinson et al., 1996) and at the single-cell level in the cat superior colliculus (Stein & Meredith, 1993), as well as in human cortical neurons (Andersen et al., 1997). Multimodal responses are enhanced by cross-modal stimulation at a particular location and supressed at alternative locations. These neurons have receptive fields that spatially coincide across modalities. For example, cells within MT have been shown to not only respond to complex visual motion, but also tactile motion (Hagen et al., 2002). The correspondence of visual and haptic processing is further implied with the discovery of mirror neurons: motor neurons that respond both when actions are made, and when others perform actions. Thus, they are activated by haptic *and* purely visual perception (Gallese, 2016).

The effects of cross-modal attention may originate from such multimodal neurons; however, evidence suggests that typically unimodal areas can also be affected by cross-modal attention. For example, *visual* cortical activity is inhibited during a *tactile* discrimination task (Kawashima et al., 1995). Further, MEG results have shown that responses in SII are enhanced during electrocutaneous stimulation by attending the location of either a visual or tactile stimulus (Kida et al., 2007). Parallel findings for the visual cortex have been shown using fMRI (Macaluso et al., 2000): activity in the visual cortex was enhanced by tactile stimulation when both occurred on the same side, perhaps as a result of feedback from multimodal areas in the parietal regions. This supports behavioural findings, however similar criticisms of whether the findings reflect exogenous attentional orienting, or the integration of sensory cues, have been made due to the simultaneous presentation of cue and target (McDonald et al., 2001).

A role for attention in multimodal processing has been shown across behavioural and neuroimaging studies. Multimodal attention may exert an influence at higher processing stages where multimodal neurons dominate but may also feedback to lower level unimodal areas. Using haptic adaptation to complement the current neuroimaging data allows a simple but compelling behavioural investigation into the origin and specifications of cross-modal attention (as detailed in *Chapter 4*).

1.4.2 Is attention modality-specific or supramodal?

An important question within the attention literature is whether attention is a single supramodal resource or modality specific – i.e., with separable attentional mechanisms and resources for each sensory modality. Attentional resources are limited, so it is important to understand whether depleting these resources in one modality will affect processing in another. Research has provided conflicting findings, with neuroimaging evidence for a supramodal model of attention (Eimer & van Velzen, 2002; Macaluso et al., 2002), and TMS evidence for the modality-specific model (Chambers et al., 2004).

A separable-but-linked model of attention has also been suggested (Spence et al., 2000) with promising supportive evidence (Gray et al., 2009; Mengotti et al., 2018; Spence et al., 2000). This model suggests that attention can be directed to tactile, visual and auditory space independently, as demonstrated in previous neuroimaging studies, but is also characterised by functional links between modalities. Spence et al. (2000) investigated endogenous spatial attention effects for visual and tactile perception. Targets in one modality (tactile or vision) were more common than the other, with opposite likely locations for targets in each modality. Attention shifted for both modalities towards the likely location of the more common target modality, suggesting that attention is not modality-specific. However, stronger spatial effects were found for the more common target modality, indicating that attention is not completely supramodal – if it were, attention effects would be equivalent across modality. Mengotti et al. (2018) extended these findings by fitting a Bayesian ideal observer model to their data. Cue predictabilities for each target modality were combined, consistent with supramodal attention. However, attention became more modality-specific when the target location was more certain, and when the cues for one modality were much more likely to be accurate than for the other modality. This research suggests that attention is likely to consist of independent resources for each sensory modality, with strong cross-modal links to ensure that attention can be oriented to the same location if needed.

1.4.3 Multisensory aftereffects

Alongside numerous single modality aftereffects, a handful of studies have shown that adapting to a stimulus in one modality can lead to an aftereffect in a different modality (e.g., Konkle, Wang, Hayward, & Moore, 2009; Krystallidou & Thompson, 2016; Matsumiya, 2013). These multisensory aftereffects suggest that neural processing occurs across the senses. As we receive considerable information about the world from multiple senses, investigating how adaptation in one sense affects the processing of another sense improves our knowledge of where representations lie, and of neural dynamics across sensory domains (Konkle & Moore, 2009).

Face adaptation transfers between vision and haptics. Matsumiya (2013) adapted participants to a haptically explored emotional face (happy or sad), which resulted in a visual face aftereffect. Control experiments indicated that this effect was not the result of mental imagery, nor local feature adaptation. Further, visual face adaptation caused a haptic face aftereffect. Face processing therefore seems to depend upon shared haptic and visual neural representations. Similarly, Krystallidou and Thompson (2016) found a haptic tilt aftereffect from visual tilt adaptation. They further explored the reference frame, finding that the effect persists when the head is tilted, such that the visual gratings were retinally vertical. Thus, high-level visual adaptation must induce the effect.

A comparable finding has been demonstrated for the MAE. Akin to vision, the tactile motion aftereffect refers to the perception of oppositely moving motion across the skin following exposure to a tactile motion stimulus. Evidence is conflicted regarding this effect (e.g., Lerner & Craig, 2002), suggesting a dependence on experimental design, at odds with the robust visual MAE. For example, J. Watanabe, Hayashi, Kajimoto, Tachi and Nishida (2007) have argued that the effect requires the same mechanoreceptors to be stimulated across adaptation and test phases. Nonetheless, Konkle et al. (2009) reported visual MAEs following adaptation to tactile motion, and vice versa. Observers adapted to visual or tactile motion for 10 s. Using a 2AFC task to null the MAE, participants reported the motion direction of a test stimulus in the other modality (i.e., adapt tactile, test vision). These cross modal aftereffects indicate that vision and haptics are processed to some extent in shared neural areas. Konkle and Moore (2009) have proposed an adaptive processing hypothesis, whereby all areas related to the processing of a stimulus are altered – the MAE is the result of multiple processing stages across the striate and extrastriate cortices, some of which respond to both visual and haptic motion (e.g., MT, Hagen et al., 2002).

Visual and haptic adaptation therefore seem to have shared neural substrates. Although these findings are consistent, they are also limited; it is necessary to explore additional multisensory adaptation effects to determine whether other aftereffects show a similar pattern.

1.5 Conclusion and hypotheses

Despite a wealth of research revealing the modulatory effect of attention on sensory processing the precise role of attention is still unclear. In the case of visual motion adaptation, evidence for and against a role of attention exists, while it is unexplored for haptic aftereffects. Investigating how attention affects both visual and haptic processing gives insight into the pervasiveness of attentional modulation within and between sensory modalities. In addition to understanding the role of attention for both visual and haptic adaptation, understanding how the two modalities interact allows us to extend our knowledge of human perception and cross-modal processing.

In *Chapter 2* I investigated attentional modulation of the MAE using a psychophysics paradigm. Using a bias-minimising task, I explored the time course of adaptation accumulation under conditions of focused and diverted attention, as well as the influence of motion type on the attention effect. In *Chapter 3* I conducted a meta-analytical review of the published MAE-attention literature. I determined whether the relevant research, when taken together, evidenced a modulatory role of attention on the MAE, as well as exploring numerous factors that may affect this relationship. Using an experimental paradigm, in *Chapter 4* I explored the effects of both haptic and visual attention on the CAE. Implications of the findings are discussed in *Chapter 5*.

I hypothesised that attention would significantly affect both visual motion adaptation and haptic curvature adaptation. I predicted that the MAE-attention relationship would be affected by a number of factors. Specifically, I predicted that a stronger attention effect would be seen for adaptation to translating motion, compared to complex motion patterns. I further hypothesised that the CAE would be affected by both haptic and visual attention.

Chapter 2 The Effects of Attention and Adaptation Duration on the Motion Aftereffect

This chapter investigates a number of potential factors that may explain discrepancies within the attention and MAE literature; namely, adaptation duration, type of motion and response bias. We reasoned that if attention affects the build-up of the MAE, the effect may be masked in those studies that allow adaptation to accumulate over trials. We further explored attentional modulation of simple (i.e., translating) and complex (e.g., rotating) motion. Additionally, we adapted a bias-reducing paradigm developed by (Morgan, 2013) to determine the role of response bias in previous research that found attentional modulation.

2.1 Contributions

Data analysis and coding of Experiment 2, and the write-up for publication, were completed by Laura Bartlett under the supervision of Wendy Adams and Erich Graf. Experiment 1 was created by Wendy Adams. For all Experiments Laura Bartlett collected the data and was responsible for coding the linear mixed modelling analysis using R.

2.2 Abstract

The motion aftereffect (MAE) is the perception of illusory motion following extended exposure to a moving stimulus. The MAE has been used to probe the role of attention in motion processing. Many studies have reported that MAEs are reduced if attention is diverted from the adaptation stimulus, but others have argued that motion adaptation is independent of attention. We explored several factors that might modulate the attention-adaptation relationship and therefore explain apparent inconsistencies, namely (a) adaptation duration, (b) motion type: translating versus complex, and (c) response bias. Participants viewed translating (Experiments 1a and 2) or rotating (Experiment 1b) random dot patterns while fixating a central letter stream. During adaptation, participants reported brief changes in the adaptor speed (attention-focused) or the presence of white vowels within the letter stream (attention-diverted). Trials consisted of multiple adaptation-test cycles, and the MAE was measured after each adaptation period. Across experiments, focused attention produced significantly larger MAEs than diverted attention (15% change, Cohen's $d = 0.41$). Attention affected the MAE asymptote, rather than its accumulation rate, and had larger effects for translational than for complex motion. The effect of attention remained evident after controlling for response bias. Our results suggest that attention affects multiple levels of the motion-processing hierarchy: not only higher-level motion processing, as seen with ambiguous apparent motion, but also low-level motion processing, as evidenced by the MAE.

Keywords: motion aftereffect, attention, adaptation

Public significance statement: "Attention allows one to prioritise important, or task-relevant, aspects of the visual world at the expense of others. The current study examines the extent to which motion processing is influenced by attention. Because motion processing occurs early in the visual pathway and is critical in guiding one's actions, it has been considered to be independent of attention. The current study uses the motion aftereffect – a well-studied illusion – to investigate how attention modulates motion processing and compares experimental paradigms to determine whether previous findings have been confounded by participant response biases. Understanding the interactions between attention and basic visual processing is key to understanding human perception and action."

2.3 Introduction

Attention refers to the selective processing of certain aspects of sensory information at the expense of others, an important and necessary operation given the vast array of sensory data available at any given time (Carrasco, 2011). *Spatial attention* refers to the allocation of attention to a particular location, for example a region of the visual field that might be relevant to a current goal. Alternatively, attention can be *feature-based*, such that an observer attends to a particular stimulus dimension (e.g., motion rather than colour; e.g., Liu, Slotnick, Serences, & Yantis, 2003; Taya et al., 2009), or to particular values within a dimension (e.g., upward, rather than downward motion; e.g., Lankheet & Verstraten, 1995). Finally, *surface-based*, or *object-based, attention* refers to the attentional selection of all elements that are perceptually grouped into a discrete surface or object (Scholl, 2001).

The effects of attention on perceptual processes have often been measured via covert attention manipulations (i.e., directing attention without a corresponding change in fixation), as in the classic Posner cueing paradigm (Posner, 1980). This has produced well-documented effects on performance in tasks such as detection and discrimination (see Carrasco, 2011 for a review). However, the effects of attention on motion processing and motion adaptation remain contentious. The influence of attention has been suggested to increase along the cortical processing hierarchy, and its effects are apparent on "higher level" motion processes. For example, the integration of motion signals across spatial locations appears to be under attentional control (Burr, Baldassi, Morrone, & Verghese, 2009), and attention affects the perceived direction of ambiguous apparent motion (Kohler et al., 2008; Wertheimer, 1912/1961) and of third-order motion (Lu & Sperling, 1995; see Burr & Thompson, 2011 for a review). It is less clear whether all aspects of motion processing are influenced by attention – in particular - adaptation to first order (luminance-defined) motion stimuli.

After prolonged exposure to a moving stimulus such as a waterfall, a subsequently viewed static stimulus is perceived to move in the opposite direction; this is the classic motion aftereffect (MAE; Addams, 1834; Anstis, Verstraten, & Mather, 1998). As “the psychologist’s microelectrode” (Frisby, 1979), aftereffects allow one to probe sensory processes, and the MAE provides an effective tool to investigate motion-sensitive mechanisms (Thompson & Burr, 2009). An influential early study of the MAE found that it was unaffected by attentional manipulations (Wohlgemuth, 1911), leading to a long-standing view that the mechanisms underlying motion adaptation are early and pre-attentive. Such a view was well aligned with findings from other studies that low-level, sensory adaptation was unaffected by suppression from awareness via binocular rivalry (Blake & Fox, 1974) or by crowding (He et al., 1996). Given the key role of motion processing in guiding action and detecting threat, one might expect motion signals to be processed automatically (Vuilleumier et al., 2001). Consistent with this notion, motion is a strong cue for pop-out during visual search (Driver et al., 1992; Nakayama & Silverman, 1986), and looming objects capture attention when they are on track to collide with the observer, despite being perceptually indistinguishable from objects on a “near miss” path (Lin et al., 2009).

Undeterred, researchers continued to explore interactions between attention and motion adaptation. In a commonly used paradigm, a moving adaptation stimulus is presented in the periphery (e.g., within an annulus; see Figure 2.1) and attention is manipulated by asking observers to perform a difficult (high load) task or an easy (low load) task. A high-load task might require observers to focus attention on a central, fixated stream of letters, counting the instances where a vowel is presented, whereas a low-load task might be to passively view the same stimulus. Under such conditions, Chaudhuri (1990) found that when attention was diverted to a high-load task, MAE durations were reduced, relative to passive viewing. Subsequently, other researchers have similarly found that directing attention away from a peripheral adaptor results in reduced adaptation, as measured via the magnitude (Mukai & Watanabe, 2001; Taya et al., 2009) or duration (Nishida & Ashida, 2000; Rezec et al., 2004) of the MAE. The attentional tracking paradigm has provided complementary findings: the MAE can be modulated by whichever one of two superimposed motion stimuli is attended during adaptation (e.g., Alais & Blake, 1999; Lankheet & Verstraten, 1995).

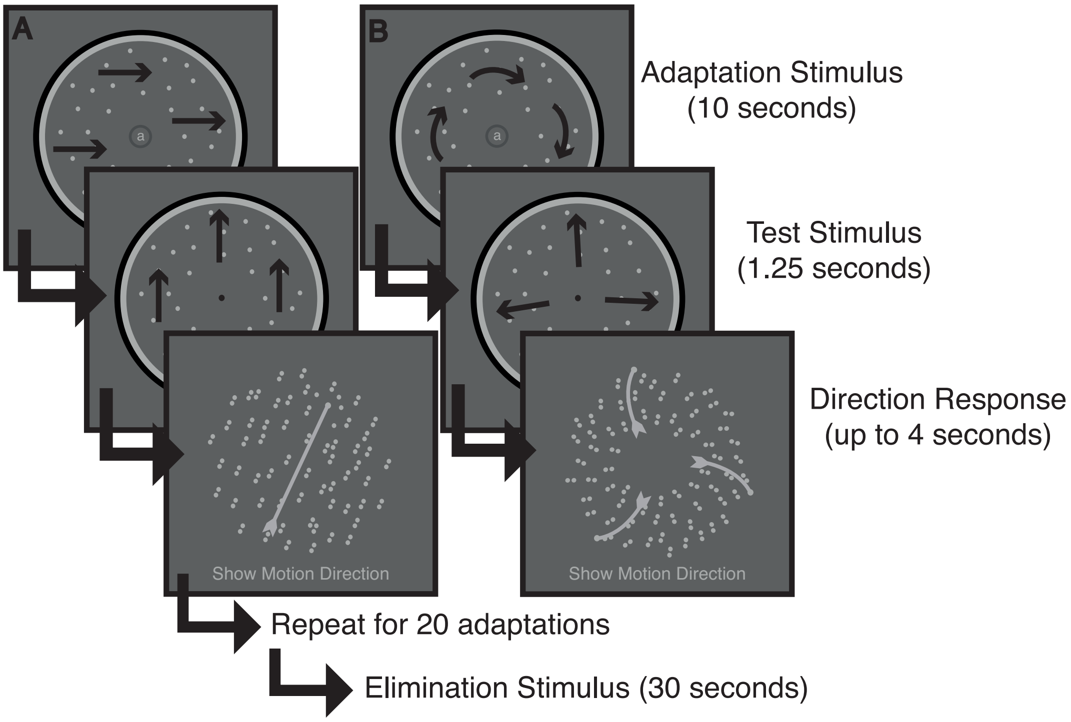

Figure 2.1 Schematic of a single trial. (a) Experiment 1a (translational motion) and (b) Experiment 1b (complex motion). Adaptation lasted 10 s while participants engaged in one of the two attentional tasks. The test stimulus was then presented for 1.25 s, followed by a Glass pattern that was adjusted to report the motion aftereffect. Each trial included 20 adaptation-test-response cycles, followed by a 30 s presentation of the elimination stimulus. Black arrows illustrate the direction of motion of adaptation and test stimuli (arrows were not present during the experiment).

Neuroimaging studies have provided further evidence that attention modulates motion-related neural activity. For example, attending to moving dots has resulted in significantly more activation in medial temporal (MT) and medial superior temporal (MST) areas than attending to stationary dots within the same stimulus (O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997). Attending to either the translational or expanding components of a transparent motion stimulus has resulted in increased MT activation, relative to passive viewing (T. Watanabe et al., 1998). The load theory of attention (Lavie, 2005) posits that when observers engage in a demanding task (e.g., a central letter task), other information within the visual array (e.g., peripheral motion stimuli) will receive limited processing resources. Accordingly, Rees et al. (1997) reported a reduction in MT activity and reduced MAE durations in high, relative to low attentional load conditions. These findings for motion are aligned with those of a broad array of studies that have now found attentional modulation of neural activity throughout the visual cortex, including the primary visual cortex (V1) – previously conceptualised as a "sensory" area and immune to such effects (see Hopf, Heinze, Schoenfeld, & Hillyard, 2009, for a review).

Recent behavioural studies, however, have failed to find an effect of attention on the MAE (Morgan, 2011, 2012, 2013; Pavan & Greenlee, 2015). Many previous findings have been attributed to response bias (Morgan, 2011, 2012), and it has been noted that the MAE *duration* measure, as used for example by Chaudhuri (1990), might be particularly prone to bias (Sinha, 1952) as observers struggle to determine when the MAE has fully dissipated (Blake & Hiris, 1993). However, a response bias account of attentional modulation of the MAE requires that observers' biases vary systematically across attention conditions, to selectively inflate the estimated MAE in conditions of low-load, relative to high-load, conditions. Such an explanation seems at odds with reports of attentional modulation within groups of naïve participants (e.g., Rezec et al., 2004). In addition, attentional modulation of the MAE has been shown using 2AFC categorisation of test direction, which is arguably less susceptible to bias as the true test stimulus characteristics will be unknown to the participant (e.g., Taya et al., 2009; see Experiment 3).

Here we focus on three factors that might affect the extent to which attention modulates motion adaptation and may thus explain apparent inconsistencies in the literature. In Experiments 1a and b, we consider (i) motion type (translational vs. complex) and (ii) adaptation duration. In Experiment 2, we revisit the issue of response bias, using a paradigm designed to eliminate it.

Why might motion type affect the attention-adaptation relationship? Translating and complex motion stimuli show different patterns of brain activation (Smith et al., 2006) and differ in the extent to which they recruit feature-based attention. When observers attend to a coherently translating stimulus, attention facilitates the representation of all stimulus elements. This can be explained by feature-based attention (all elements move in a common direction), spatial attention (the stimulus occupies only some of the visual field) and / or surface-based attention (all elements are perceptually grouped into a common surface). In contrast, when attending to a rotating stimulus, feature-based attention does not facilitate the representation of all surface elements: elements move in different, position-dependent directions. Thus, rotating / expanding motion patterns will successfully recruit only spatial and surface-based / object-based attention.

Spatial attention modulates motion–related activity in MT, via an overall response gain (Treue & Martínez Trujillo, 1999). However, substantial direction-specific effects of feature-based attention have now been found in V1 and MT (Saproo & Serences, 2014). These reflect both excitatory and inhibitory effects within neurons tuned to the attended, versus the opposing, motion direction (Treue & Martínez Trujillo, 1999; Treue & Maunsell, 1996). One might reasonably expect these direction-specific effects to be particularly important in modulating MAEs. Moreover, feature-based attention spreads across the visual field (Treue & Martínez Trujillo, 1999) and will thus have the largest effect when observers attend a coherently translating stimulus.

In contrast, complex motion patterns (i.e., expansion, rotation) consist of motion signals that vary as a function of position. Simple feature-based mechanisms will not, therefore, drive an enhancement of stimulus-related activity in V1/MT across the visual field. However, MSTd neurons with large receptive fields can be tuned to complex motion patterns including rotation and expansion/contraction (Smith et al., 2006; Tanaka et al., 1986). Moreover, there is now evidence of enhanced activation in V1/MT due to surface-based attention (Kamitani & Tong, 2006; Wannig et al., 2007), potentially driven by feedback from MSTd. By directly comparing adaptation to translating and rotating motion, one can start to understand the relative importance of these different attentional mechanisms. Previous functional magnetic resonance imaging (fMRI) work found little or no attentional modulation of V1 activity with complex motion patterns, in contrast to larger effects in MT/MST (Büchel et al., 1998; O'Craven et al., 1997; T. Watanabe et al., 1998), suggesting that effects of surface-based attention in V1 are weak. However, previous null effects in V1 may actually reflect pooling across substantial excitatory and inhibitory effects, as suggested by more sophisticated recent analyses of fMRI data (Saproo & Serences, 2014).

In the present study we also consider whether attentional effects vary across the adaptation period. For both translational and complex motion, MAEs increase quickly as adaptation duration increases until reaching an asymptotic saturation point at longer durations (Hershenson, 1993). Attention might affect the time course (i.e., the rate of accumulation), the asymptote, or both. If attention primarily affects the time course, attentional effects may not be detected in studies that use longer adaptation durations or those that employ designs including repeated adaptation periods with the same adaptor (e.g., Morgan, 2011, 2013) such that adaptation can accumulate over multiple trials. A similar argument has been proposed by Blake and colleagues with respect to luminance contrast: the effects of rivalry suppression on motion adaptation may be more easily detected for lower contrast adaptors than high, because saturation effects are avoided (Blake et al., 2006; Blake & Fox, 1974).

Experiments 1a and 1b directly compare adaptation to translational and complex motion, after multiple adaptation durations, under different attentional conditions. We hypothesised that, whereas MAEs would increase with adaptation duration, this accumulation may occur more quickly with greater attentional allocation. We also hypothesised that the effects of attention may be larger for simple translating motion patterns than for rotational motion, reasoning that translating motion will combine spatial, feature-based and surface-based attention to produce enhanced neuronal activation across motion-sensitive regions, whereas complex motion will not engage feature-based attention mechanisms.

2.4 Experiments 1a and 1b

2.4.1 Stimuli and Tasks

The experimental paradigm is shown in Figure 2.1. A single trial included 20 adaptation-test-response cycles. Each cycle began with a 10-s adaptation period. Adaptation stimuli consisted of 400 limited lifetime white dots displayed over a grey background. Each dot subtended 0.12° and had a maximum lifetime of 30 frames. Dots moved within an annulus defined by inner and outer radii of 2.7° and 6.7°, respectively. This region was enclosed by light and dark outer rings (see Figure 2.1) to enhance MAEs (Day & Strelow, 1971). In Experiment 1a, the dots drifted leftward or rightward at a rate of 4.8°/s. When a dot reached the annulus boundary it was replaced by a dot at the opposite side. In Experiment 1b, the dot pattern rotated either clockwise or anticlockwise, with a rotational speed of 58.79°/s; this rotation speed was chosen such that the median dot speed matched that of the translation experiment in terms of distance travelled per second.

During each adaptation period the adaptation stimulus would, at unpredictable time points, briefly move with increased speed (for 3 frames/50 ms). These motion changes were separated by random intervals within the range of 1.5 s to 6 s. In addition, a stream of light and dark letters was presented at fixation. On *attention-focused* trials, observers were asked to report each motion change (by pressing the space bar) within 1 s of its occurrence. On *attention-diverted* trials, they were required to report the appearance of light vowels in the central letter stream. Incorrect responses (false alarms) or missed events were followed by a tone. The magnitude of the motion changes and the duration of each letter presentation were controlled by an adaptive procedure (Quest: Watson & Pelli, 1983) driven by observers' responses in the corresponding tasks, such that performance was kept at 75% correct.

Test stimuli were presented for 1.25 s and matched the adaptation stimuli in terms of spatial extent and number of dots (see Figure 2.1). In Experiment 1a, the test stimulus drifted either upwards or downwards (determined pseudo randomly) at 0.12°/s. The perceived motion direction of the test stimulus provides a measure of the MAE (Blaser, Papathomas, & Vidnyánszky, 2005; Verstraten, Fredericksen, Grüsser, & Van De Grind, 1994); after adapting to a rightward stimulus, a test stimulus that moves upwards will be perceived as moving diagonally up and to the left, with the angular deviation from vertical providing a measure of the MAE. In Experiment 1b, the test stimulus either contracted or expanded at 0.12°/s. Adaptation to rotational motion caused this test stimulus to appear to move along a spiral path. After each test, observers reported the perceived motion direction of the test stimulus by manipulating a static Glass pattern comprised of 400 pairs of dots (Glass, 1969). Within each pair, one dot's position was fixed. In Experiment 1a, the vertical offset between the dots in each pair was fixed (±0.17° following upward or downward tests) and the observer adjusted the horizontal offset (using the mouse) until the orientation of the dot pair matched the perceived motion direction of the test. The response display also contained a line whose orientation matched the Glass pattern (see Figure 2.1). Similarly, in Experiment 1b, the radial offset within each dot pair was fixed at ±0.17° and the observer manipulated angular offset between dot pairs (and the shape of three lines) to match their perception of the motion direction of the preceding test. Observers had a 4-s window to complete this matching task, after which the next adaptation cycle began. The stimulus was removed once a response was given, but the fixed duration of 4 s until the next cycle began ensured that the adaptation time course was matched across observers and conditions, whilst providing sufficient time to respond (average response times were 1.99 s for Experiment 1a and 1.77 s for Experiment 1b). Any possible interference of the glass pattern would be equivalent across attention conditions, however interference is not expected as glass patterns do not contain motion. This matching task, used previously by Verstraten et al. (1994), allowed us to measure adaptation at frequent intervals and thus examine its timecourse.

At the end of each trial (i.e., 20 adapt-test-response cycles), a random dot motion stimulus (dots following independent random walk paths) was presented for 30 s to prevent adaptation effects from carrying over to the subsequent trial. Participants pressed the space bar when ready to begin the next trial.

2.4.2 Procedure

To ensure that participants understood the task and could accurately report the (perceived) motion direction of the test stimuli, they first completed practice trials without any motion adaptation. On each trial, a test stimulus was shown for 1.25 s, whose true motion varied from trial to trial to simulate the effects of adaptation. For the translational motion experiment (1a) the motion direction was varied, whereas for the complex motion experiment (1b) the rotational motion component varied, but the expansion / contraction component was held constant. Participants indicated the direction of test motion (as shown in Figure 2.1) and received visual feedback showing both the true test motion (as a Glass pattern, with a green arrow) and their response (an overlaid dark grey arrow if correct, red if incorrect). Responses within ±20° of the true motion direction for translational motion, and ±0.6°/s for rotational motion were classed as correct. Subsequent analyses revealed that correct responses within practice trials had mean absolute errors of 8.47° (*SD* = 5.47) and 0.26°/s (*SD* = 0.17), for Experiments 1a and 1b, respectively. Participants completed at least two blocks of 44 practice trials, and only participants performing at 75% or above were invited to complete the main experiment.

Participants then completed 4 practice trials with adaptation (2 for each attention task, each with 20 adaptation cycles), to determine initial stimulus levels for the attention-focused and attention-diverted tasks (i.e., the size of the motion changes and the presentation duration of the central letters, controlled by Quest).

Each experimental session included 4 trials: (2 attention conditions x 2 adaptation directions) and most participants completed 4 sessions (3 participants in Experiment 1a and 1 participant in Experiment 1b completed only 3 sessions, as determined by their availability). Trial number and the task instructions "Report speed changes" or "Report light vowels" were displayed prior to each trial. Experimental sessions were completed on different days.

Stimuli were presented using a 27-in. Apple iMac, with a nominal screen refresh rate of 60Hz and resolution of 2,560 x 1,440 pixels. A chin rest fixed the viewing distance at 54 cm. The experiment was run using MATLAB (MathWorks) and the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007). The display was viewed binocularly, in a quiet dark room.

2.4.3 Participants

To determine appropriate sample sizes, we estimated the effect sizes associated with (i) the effect of attention on the MAE following translating motion, (ii) the effect of attention on MAEs following complex motion, and (iii) the difference between the two. Using previous research that has also employed diverted attention paradigms, this revealed effect size estimates (Cohen's *d*) of 2.08 for translational motion (from: Rezec et al., 2004; Takeuchi & Kita, 1994), and 1.42 for complex motion (from: Kaunitz et al., 2011; Taya et al., 2009). Power analyses for one-tailed within-sample *t*-tests were conducted in G*Power (Faul et al., 2007) using an alpha of 0.05 and power of 0.80. These analyses suggested sample sizes of at least 4 participants for translational motion (Experiment 1a) and at least 5 participants for complex motion (Experiment 1b). At least 7 participants were required in each motion condition in order to detect a difference between the effects of attention on MAEs following adaptation to translational and complex motion.

Accordingly, twelve participants (aged 20-42 years) completed Experiment 1a and eleven participants (aged 20-42 years) completed Experiment 1b. All 3 authors participated in both experiments and all other participants were naïve, recruited from the University of Southampton through opportunity sampling. All participants had normal or corrected to normal vision. The University of Southampton granted ethical approval for all experiments and all participants provided informed consent. Data for all experiments are available from the University of Southampton Institutional Repository (doi:10.5258/SOTON/D0535).

2.4.4 Results

Figure 2.2 shows MAEs as a function of attention and adaptation duration for translating motion (Experiment 1a) and rotating motion (Experiment 1b). Data are collapsed across adaptation and test directions, as preliminary analyses confirmed that neither significantly affected the MAE. In order to compare the effect of attention across the two experiments (both for display, and subsequent analyses), we normalised data within each experiment by dividing by the overall mean MAE. This normalised MAE is indicated on the left y-axes, while the raw MAE responses can be inferred from the right-hand y-axes. Task difficulty was computed for the focused attention condition (average increase in motion speed; translating motion: *M* = 7.87˚/s, *SD* = 3.00; rotating motion: *M* = 84.57˚/s, *SD* = 21.31) and for the diverted attention condition (average duration of letter presentation; translating motion: *M* = 0.30 s, *SD* = 0.24; rotating motion: *M* = 0.19 s, *SD* = 0.05).

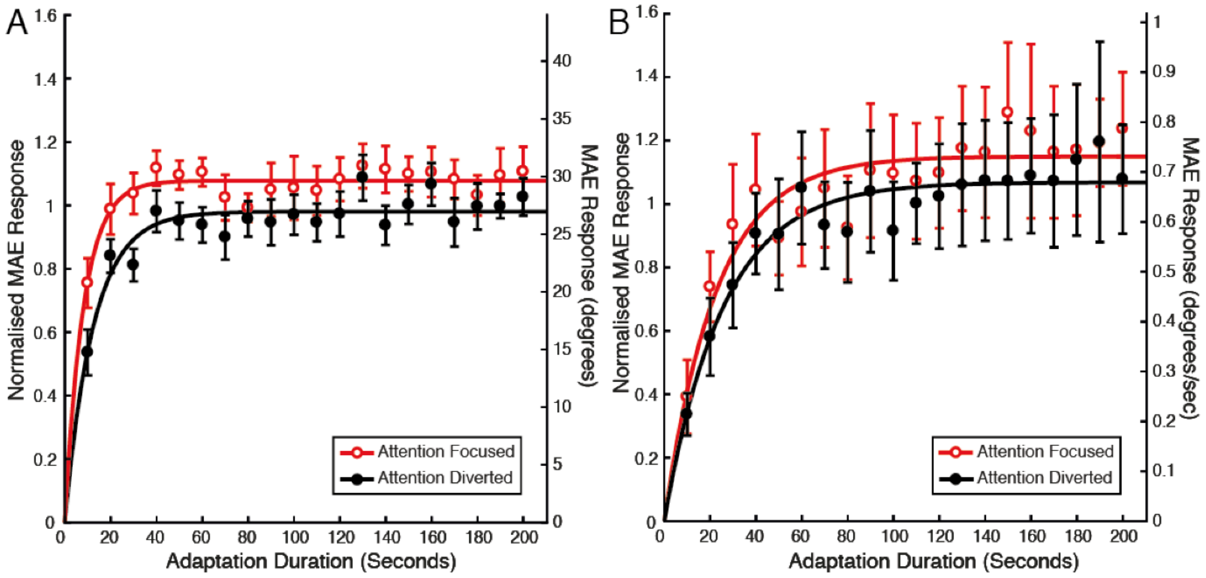

Figure 2.2 Measured motion aftereffects (MAEs) for Experiment 1. Panel A: Translating adaptor (Experiment 1a). Panel B: Expanding / contracting adaptor (Experiment 1b). Error bars represent standard error. Lines show exponential fits to the data.

Outliers (more than 2 standard deviations from the condition mean) and pre-emptive responses (those with a response time less than 0.5 s) were removed from the analyses (7% of responses) before a linear mixed-effects model (LMM) analysis, conducted in R (R Core Team, 2017; lmer4 package: Bates, Mächler, Bolker, & Walker, 2015).

To find a parsimonious model of our data, we followed the approach of Bates, Kliegl, et al. (2015) and Martin-Key, Graf, Adams and Fairchild (2017), starting with the most complex model supported by the data, followed by stepwise elimination to remove extraneous factors. The initial model included continuous factors of attention and adaptation duration, and the categorical factors motion type and participant naïveté, as fixed effects, in addition to their two-way interactions. Additional interactions were not specified in the model, as they were not theoretically justified and can lead to complex, uninterpretable models. LMM analysis treats every trial as a data point, allowing unbalanced data sets – as such, motion type, a partially within-subject and partially between-subjects factor, was included in the analysis. Participant and by-participant variation in the effects of attention and motion type were included as random effects. A full random structure was initially specified, however adaptation duration was removed due to an issue with singularity. A fixed effect was discarded if its removal did not significantly impair the model's goodness of fit (as determined by likelihood ratio tests). The final model is summarised in Table 2.1.

Table 2.1 Experiment 1. Fixed effects in LMM of MAEs.

Variable	*B*	*SE*	*df*	*t*	*p*
Attention	-0.15	0.02	14.04	-6.77	< .001
Adaptation duration	0.02	0.001	7206.93	16.73	< .001
Motion type	-0.17	0.16	11.73	-1.06	0.31
Participant naïveté	0.56	0.07	8.09	7.67	< .001
Attention x Participant naïveté	-0.22	0.04	10.34	-5.44	< .001
Adaptation duration x Motion type	0.02	0.002	7206.31	7.64	< .001

Motion adaptation was significantly modulated by attention; the attention-focused condition resulted in significantly larger MAEs ($M = 1.04$, $SD = 0.69$) than the attention diverted condition ($M = 0.96$, $SD = 0.69$). In addition, we hypothesised that attention may have a larger effect on adaptation to translating than rotating motion. Although the effect of attention was larger for translational (12.18% increase from diverted to focused attention) than complex (9.48% increase) motion, this interaction was not significant (and was removed from the final model).

As expected, adaptation increased significantly over time. It is interesting, and in contrast to our hypothesis, that adaptation duration and attention did not interact: the effect of attention was not significantly larger in, or confined to the early stages of, adaptation. Inspection of Figure 2.2 suggests that adaptation to translating motion saturates more quickly than adaptation to rotational motion. This was confirmed by a significant interaction between motion type and adaptation duration.

Naïve observers reported significantly smaller MAEs than non-naïve participants and the effect of attention on MAEs was significantly smaller across naïve observers than across the non-naïve authors. To examine this further, we re-analysed the data after excluding all non-naïve observers. This did not affect the *form* of the final model, i.e., the same fixed effects remained significant, including a significant effect of attention on MAE magnitude ($b = -0.04$), $t(5326.33) = -2.56$, $p = .010$.

Figure 2.2 also shows the best fitting exponentials: $MAE = -ae^{-bx} + a$. These were determined separately for each observer, attention condition and motion type (for Figure 2.2, they have been averaged across observers). In line with the LMM analyses, the asymptote, a, was significantly larger for the attention-focused than the attention-diverted task, $F(1, 21) = 10.88$, $p = .003$, $d =$

0.21; mean asymptote = 1.13 vs. 1.03. Attention did not significantly affect the time constant (*b*), *F*(1, 21) = 0.90, *p* = .354, *d* = -0.20. In line with the LMM analysis, the time constant was significantly different for translational versus complex motion, *F*(1, 21) = 11.70, *p* = .003, *d* = 1.23: adaptation accumulates more quickly for translating than rotating motion.

2.5 Experiment 2

Experiments 1a and b suggest that the MAE is modulated by attention when adapting to either translational or complex motion. Although motion adaptation followed a different time course for translating and rotating motion, we did not find an effect of attention on the time course of adaptation. In Experiment 2, we investigate the time course of adaptation with greater temporal resolution, by reducing each adaptation period from 10 s to 4 s. In addition, we seek to validate our findings by using a paradigm adapted from Morgan (2013) that is designed to be minimally susceptible to response bias. In this paradigm, observers adapt to translating random dot stimuli presented above and below a central fixation point and moving in opposite directions (see Figure 2.3).

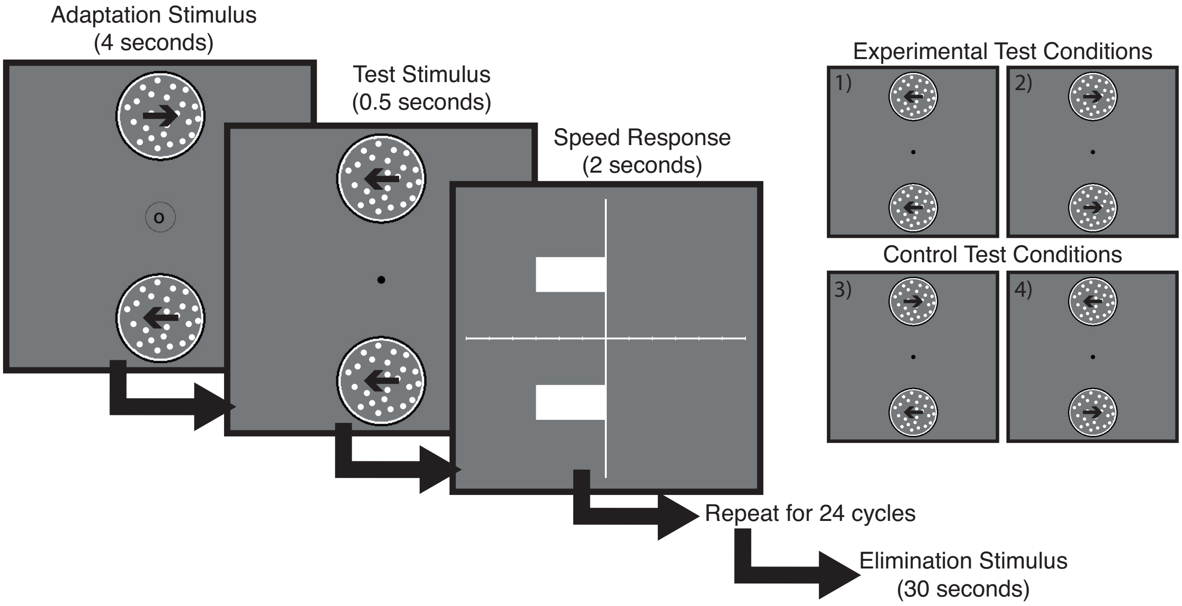

Figure 2.3 Schematic of a trial in Experiment 2. The four possible test conditions are shown on the right. Arrows illustrate the direction of motion (arrows were not present during the experiment).

After each adaptation period, test patches were presented at the two adaptation locations and the observer made a judgement about their relative speeds. Importantly, the paradigm includes four different randomly intermingled test conditions. In ‘experimental’ test conditions 1 and 2, both test stimuli move in the same direction, and adaptation will thus affect their relative perceived speeds. If, for example, the observer adapts to rightward motion above fixation and leftward motion below, as shown in Figure 2.3, then in test condition 1, (both patches move leftward) the lower patch should appear to move more slowly than the upper one. For the same adaptation condition, if test 2 is shown, the upper patch should appear to move slower. In contrast, in control test conditions 3 and 4, the two test patches move in opposite directions, and adaptation is therefore expected to have an equal effect on the perceived speeds of the upper and lower test patches (their perceived speeds should match, although the absolute perceived speed should differ between tests 3 and 4). Thus, to bias their responses in line with the attentional modulation hypothesis, observers should follow a complicated algorithm that depends on the combination of adaptation stimulus, test stimulus and attention condition.

2.5.1 Stimuli

Adaptation stimuli consisted of two disks (diameter 2.5˚, centred 4.38˚ above and below fixation) each containing 75 white dots (diameter 0.12°) with a limited lifetime of 30 frames (see Figure 2.3). Light and dark rings enclosed each disk. Dots in the upper and lower patches drifted in opposite directions, either leftwards or rightwards, for 4 s, at 3.12°/s. When reaching the disk edge, dots were reborn at the opposite side. Similar to the case in Experiment 1, dot speed could briefly increase during adaptation (for 50 ms), at random intervals in the range 1 s to 4 s. In addition, a stream of light and dark letters was presented at fixation. As in Experiment 1, the magnitude of the motion change and the duration of each letter were determined by an adaptive process according to participant responses. On attention-focused trials, observers were instructed to ‘detect motion changes’ and had to press the space bar within 1 s of the change. Similarly, on attention-diverted trials, they had 1 s to detect light vowels within the letter stream. A tone provided feedback following false alarms or missed events.

The test stimuli (0.5 s duration) matched the adaptation stimuli in spatial extent and number of dots. As shown in Figure 2.3, dots within the upper and lower patches could either drift leftward or rightward, to produce the four different test configurations. Test motion speeds were either (a) 2.74°/s and 3.19°/s or (b) 2.89°/s and 3.04°/s, randomly selected on each adaption-test-response cycle, so that the two patches differed in speed by either 0.44°/s or 0.15°/s; the location of the faster patch was randomised over each trial. Note that test speed did not vary significantly with attention condition, $F(1, 9) = 0.19$, $p = .677$; adaptation duration, $F(23, 207) = 1.04$, $p = .421$; or their interaction, $F(23, 207) = 1.10$, $p = 0.351$. Following the test, participants adjusted the length of two bars that represented the relative perceived speed of the two test patches. Upper and lower bar lengths were yoked such that their sum was constant - increasing the length of the upper bar decreased the size of the lower bar. However, the two bars always pointed in the direction of the true test motions; adaptation changed the perceived speed, but not the perceived direction of the tests. This response – which relied on reporting the relative (rather than absolute) speed of two stimuli – had two advantages: First, it made it difficult for observers to introduce response bias

(Morgan, 2013) and second, observers were not required to map their perception to an arbitrary response scale. Participants had 2 s to complete their response, after which the next adaption-test-response cycle began.

Each trial consisted of 24 adaptation-test-response cycles. Following each complete trial, random dot motion stimuli (dots following independent random paths) were presented in the same spatial locations as the adaptation and test stimuli, for 30 s, to prevent carryover effects across trials.

2.5.2 Procedure

Participants first completed 2 blocks of 48 training trials (without adaptation) to ensure that they could perform the relative speed judgement. For these training trials, test patches had absolute speeds in the range of 2.30° to 3.63°/s, and could be moving in the same or opposite directions. As in the main trials, observers adjusted the response bars to report the relative test speeds. As feedback, the response bar was displayed (showing the participant's response), with additional lines indicating the true relative speeds; green if the response was classed as correct (if within ±10% of the true values), red if not. Participants completed an additional block of training trials before each experimental session. All participants performed at over 75%. Following training, participants completed 4 practice trials with adaptation (2 attention conditions x 2 adaptation directions) to determine initial stimulus values for the two attentional tasks.

Each observer completed 4 experimental sessions consisting of 12 trials each (2 adaptation directions x 2 attention conditions x 3 repetitions). Test conditions were pseudo-randomly distributed within and across trials. Each trial featured 16 experimental tests (tests 1 and 2) and 8 control tests (tests 3 and 4). These were ordered such that across each session's trials, the same number of experimental and control tests appeared at each time point (i.e., at cycles 1 to 24), within each condition (adaptation direction x attentional task).

2.5.3 Participants

Twelve participants (aged 21-42), including 2 authors, completed the experiment. All had normal or corrected to normal vision. Two participants failed to consistently report MAEs in the expected direction and were therefore excluded from subsequent analyses.

2.5.4 Results

We quantify observers' MAEs as the difference between the true relative speeds of the test stimuli and their perceived relative speeds (as indicated by the relative bar lengths) in experimental test conditions 1 and 2 (see Figure 2.3). To provide an estimate of the MAE in absolute terms, we assume that adaptation has equal and opposite effects on the perceived speed of the two test patches (note that this assumption does not affect comparisons across experimental conditions).

Responses in the control test conditions were not significantly modulated by attentional task (*b* = -0.01, *SE* = 0.002), *t*(8.92) = -2.17, *p* = .059, nor adaptation duration (*b* = 0.00004, *SE* = 0.0001), *t*(3859.88) = -0.34, *p* = .730, as one would expect, in the absence of response bias. The analyses reported below include only the experimental test conditions. Outliers (responses more than 2 standard deviations from the condition mean) and pre-emptive responses (response times less than 0.5 s) were removed, corresponding to 8% of responses.

MAEs are shown in Figure 2.4 as a function of adaptation duration and attention condition. Similar to the case in Experiment 1, data were analysed via LMM. Data were collapsed across adaptation and test direction as preliminary analysis confirmed that neither variable significantly modulated MAE magnitude. Attention, adaptation duration, test speed and participant naïveté, as well as two-way interactions, were included as fixed effects. The random effects structure included participant, and per participant slopes for attention and test speed. Backward elimination using likelihood ratio tests determined the inclusion of fixed effects in the final model, which is summarised in Table 2.2.

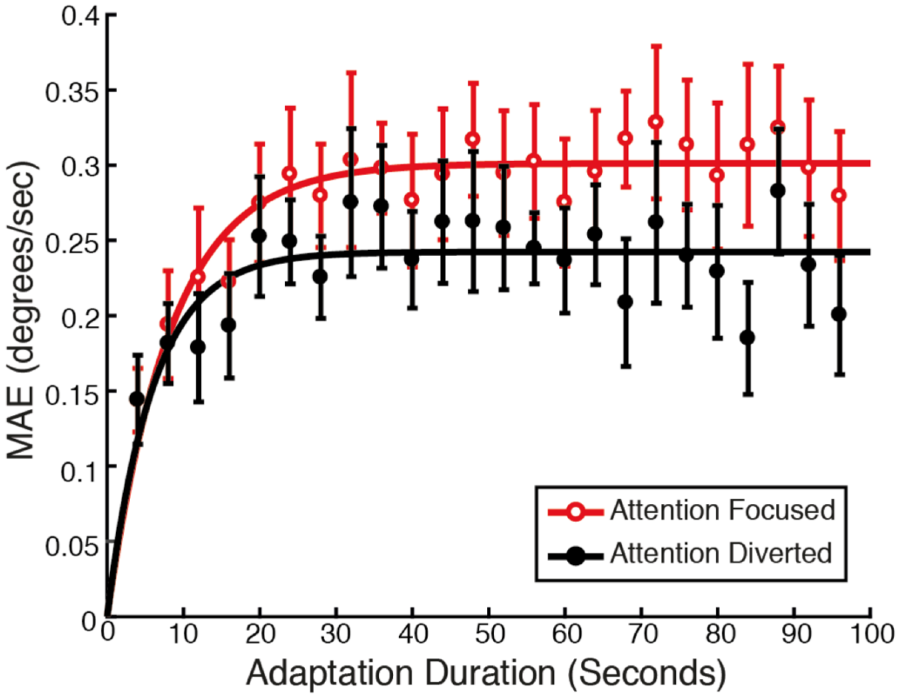

Figure 2.4 Motion aftereffects (MAEs) for Experiment 2. Error bars represent standard error. Lines show exponential fits to the data.

Table 2.2 Experiment 2: Fixed effects in LMM of MAEs.

Variable	*B*	*SE*	*df*	*t*	*p*
Attention	0.05	0.02	6328.67	2.15	.032
Adaptation duration	0.001	0.0003	213.53	4.41	<.001
Test speeds	0.30	0.07	6951.61	4.18	<.001
Attention x Duration	-0.001	0.0002	6940.62	-3.09	.002
Attention x Test speeds	-0.10	0.04	6951.70	-2.22	.026

Attention had a significant effect on motion adaptation; larger MAEs were found in the attention-focused task (*M* = 0.27, *SD* = 0.32) than the attention-diverted task (*M* = 0.22, *SD* = 0.33). As expected, the MAE also increased as a function of adaptation duration. In contrast to Experiment 1, there was a significant interaction between attention and adaptation duration: attention had a larger effect at longer adaptation durations.

The two groups of observers (authors vs. naïve participants) did not differ significantly in terms of MAE magnitude or attentional modulation of the MAE. Nonetheless, we explored the effect of excluding all authors from the analyses. This had little effect on the final model; the effect of attention was slightly larger and remained significant (*b* = 0.07, *SE* = 0.03), *t*(5048.23) = 2.60, *p* = .009), alongside a significant interaction between attention and duration (*b* = -0.001, *SE* = 0.0002), *t*(5559.16) = -2.92, *p* = .003.

Our analyses revealed a significant effect of test speed, and an interaction between test speed and attention. Examination of the form of these effects suggests that observers may have had a tendency to underestimate / underreport the difference in perceived speed of the two patches when this difference was large.

As in Experiment 1, exponentials were fit to the MAEs as a function of adaptation duration for each attentional condition. These fits (averaged across observers) can be seen in Figure 2.4. In line with the LMM, the fitted asymptotes differed significantly across the two attentional conditions (*t*(9) = 4.16, *p* = .003). However, the time constant did not (*t*(9) = 0.79, *p* = .450). Similar to the case in Experiment 1, therefore, data from Experiment 2 suggest that attention predominantly effects the asymptotic MAE, rather than the rate at which it builds up.

2.6 General Discussion

Our two experiments confirm that attention modulates the motion aftereffect. Directing attention toward moving adaptation stimuli increased adaptation to both translational and complex motion

(Experiment 1). In addition, we replicated the effect of attention on translational motion in Experiment 2 via a paradigm designed to minimise the possibility of response bias. Across all experiments, directing attention towards the adaptor, rather than diverting attention to a central task produced a 15% increase in MAE, quantified via fitted asymptotes. This corresponds to a medium effect size (Cohen's *d*) of 0.41.

Several previous studies have also reported an effect of attention on motion adaptation (e.g., Chaudhuri, 1990; Georgiades & Harris, 2000a; Takeuchi & Kita, 1994; Taya et al., 2009). The current study extends those findings by directly comparing translational and complex motion and employing different paradigms in order to measure the time course of adaptation, and to minimise the possibility of response bias.

Based on previous neurophysiological and fMRI evidence, we hypothesised that attention would have a larger effect on adaptation to translating than complex motion. This is because the former, but not the latter is likely to involve the effects of feature-based attention in V1 and MT. The magnitude of the attention-driven increase in MAE was larger for translational than for complex motion: complex motion: $d = 0.14$, 8.79% increase (Experiment 1b) versus translational motion: $d = 0.56$, 10.23% increase (Experiment 1a), and $d = 0.55$, 26.29% increase (Experiment 2). This finding, along with findings from our own meta-analysis (Bartlett, Hedger, Graf, & Adams, 2017) suggests that feature-based attention (exploited in the translating motion case) may be a substantial factor in driving the attention-adaptation relationship, and has a larger effect than does spatial and surface based attention.

We tested the hypothesis that attention primarily affects the *rate* of adaptation. Had this been the case, it might have explained some previous null findings (e.g., Morgan, 2011, 2013); that is, saturation of the MAE across multiple adaptation periods might have masked effects of attention during initial stages of adaptation. On the contrary, the effect of attention was mostly evident after longer adaptation durations, i.e., attention increases the asymptotic MAE.

Early descriptions of attentional load focus on the tasks that can be used to effectively divert attentional resources (Lavie, 1995, 2005). In studies of attention and the MAE, effective manipulation of attention is essential; if attention is not adequately diverted from the adapting motion stimulus, then firm conclusions regarding the impact of attention on the MAE cannot be reached. In our diverted attention conditions, we continuously monitored performance in the attentional task (detect light vowels) and provided feedback after incorrect responses, to maintain participants' vigilance. In addition, our diverted attention condition was compared to a condition in which attention was directed to the motion stimulus; it has been suggested that a comparison against passive viewing is ill-advised, because participants may be variably attending different features of the stimulus (Huk & Heeger, 2000). We did find a smaller effect of attention within naïve observers in Experiment 1 (although not in Experiment 2) and another possibility is that experienced observers are better able maintain attention on the required task. It remains possible that some apparent inconsistencies in the literature are due to differences in the effectiveness of the attention manipulations.

Several other factors may additionally modulate the effect of attention on motion adaptation. For example, Georgiades and Harris (2000b) suggest stronger attentional effects occur for stimuli closer to fixation. The spatial extent of the adapting stimulus may also play a role: Takeuchi and Kita (1994) found that the effect of attention decreased with increasing stimulus size (although see Georgiades & Harris, 2000b). Previous studies have also suggested that the measured effect of attention might depend on whether dynamic or static test stimuli are used (e.g., Verstraten, Fredericksen, Van Wezel, Lankheet, & Van De Grind, 1996).

The upsurge in research articles linking visual attention and perceptual processing (Carrasco, 2011) lies within a movement across cognitive psychology that seeks to re-evaluate dichotomous descriptions of cognitive processes as either pre-attentive or requiring attentional control (Moors & De Houwer, 2006). Within perception, tasks such as contrast discrimination, texture segmentation and visual acuity are no longer considered to be purely pre-attentive, and the present results add to a growing literature implicating attention in aspects of motion processing once deemed to be ‘automatic’. However, discrepancies remain in the literature; a comprehensive description of the attention/motion relationship and the many factors that affect it, may be best constructed via a meta-analysis (e.g., Bartlett et al., 2017), and further directed experimental efforts.

Chapter 3 Motion adaptation and attention: A critical review and meta-analysis

My psychophysical experiments revealed a clear modulatory role of attention on motion adaptation, which was affected by motion type and did not appear to be driven by response bias. However, the accumulation of motion adaptation was unaffected by the attention manipulation, rather affecting the MAE asymptote. As such, a number of questions remained. Most pertinently, it was still unclear what was causing a clear relationship between attention and the MAE in some experiments, and not in others. A whole range of stimulus and experimental features could be driving these differences, which had not previously been explored. To address these issues, my second paper aimed to provide a concise and analytical review of the published attention and MAE literature.

3.1 Contributions

The literature search was conducted by Laura Bartlett. Inclusion of experimental findings was determined by Laura Bartlett, Wendy Adams and Erich Graf. Analysis was conducted by Laura Bartlett with support from Nicholas Hedger. Write up was completed by Laura Bartlett under the supervision of Wendy Adams, Erich Graf and Nicholas Hedger.

3.2 Abstract

The motion aftereffect (MAE) provides a behavioural probe into the mechanisms underlying motion perception, and has been used to study the effects of attention on motion processing. Visual attention can enhance detection and discrimination of selected visual signals. However, the relationship between attention and motion processing remains contentious: not all studies find that attention increases MAEs. Our meta-analysis reveals several factors that explain superficially discrepant findings.

Across studies (37 independent samples, 76 effects) motion adaptation was significantly and substantially enhanced by attention (Cohen's $d = 1.12$, $p < .0001$). The effect more than doubled when adapting to translating (vs. expanding or rotating) motion. Other factors affecting the attention-MAE relationship included stimulus size, eccentricity and speed. By considering these behavioural analyses alongside neurophysiological work, we conclude that feature-based (rather than spatial, or object-based) attention is the biggest driver of sensory adaptation.

Comparisons between naïve and non-naïve observers, different response paradigms, and assessment of ‘file-drawer effects’ indicate that neither response bias nor publication bias are likely to have significantly inflated the estimated effect of attention.

Keywords: Attention, motion adaptation, motion aftereffect, systematic review, meta-analysis

3.3 Background

Attention refers to our ability to selectively process certain aspects of a visual scene, such that particular regions or features are enhanced, and irrelevant stimuli are inhibited (Carrasco, 2011). The effects of attention on perceptual processes are usually measured via manipulations of covert attention in which attention is directed independently of eye movements. This contrasts with overt attention, in which a redirection of attention is accompanied by an eye movement to fixate the attended region. Covert spatial attention enhances signals from the attended location, reducing noise, and changing decision criteria (see Carrasco, 2011 for an overview), and has been shown to operate at all levels of the visual hierarchy, even early visual areas previously believed to be pre-attentive and entirely sensory, i.e., the primary visual cortex (V1) (e.g., Silver et al., 2007; Somers et al., 1999). Whether such attentional effects generalize to motion processing, however, remains contentious. Here we consider evidence for the influence of covert attention on motion processing, as evidenced by effects of attention on motion adaptation.

The relationship between attention and visual motion processing has been studied since the early 20th century. Wertheimer (1912/1961) found that attention altered the perceived motion direction of ambiguous apparent motion, a finding supported by more recent work (Kohler et al., 2008). In addition, researchers have found that the perceived direction of third-order motion (the motion of important visual details, i.e., the ‘figure’ rather than the ‘ground’ within a salience map; Lu & Sperling, 2001) can be determined entirely by attention (Lu & Sperling, 1995). The observed effect of attention on higher-level motion processes is in keeping with the notion that attention exerts a greater influence in more advanced regions of the cortical visual hierarchy (Carrasco, 2011). However, the picture is less clear when we consider low-level (first-order/luminance-defined) motion.

The effect of attention on luminance-defined motion processing has been probed behaviourally via the motion after-effect (MAE): following prolonged inspection of a moving stimulus, illusory motion is perceived in the opposite direction. Descriptions of the MAE date back to Aristotle, and it was popularised by Addams (1834) as the ‘the waterfall effect’. After-effects have earned the label of the “psychologist’s microelectrode” (Frisby, 1979) and the MAE is viewed as a powerful research tool for probing motion-sensitive mechanisms (see Figure 3.1a).

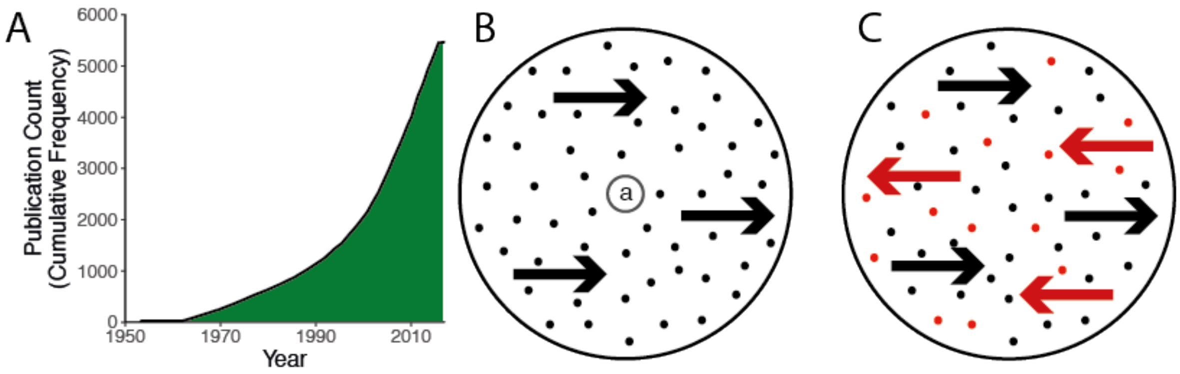

Figure 3.1 Publication count and attention-MAE paradigms. (a) Cumulative frequency of publications related to the motion aftereffect. A PubMed search (keywords: motion aftereffect OR motion adaptation) revealed 5470 publications since 1950. (b & c) A schematic of typical paradigms used to measure the effect of covert attention on motion adaptation. (b) A moving stimulus is presented within an annulus. To manipulate attention, a centrally presented stimulus such as a stream of letters is fixated, while observers perform either a difficult / high-load task (e.g., bisyllabic word detection), or an easy / low-load task (e.g., detecting uppercase letters), or passively view the stimulus. (c) The motion tracking paradigm: two populations of dots (indicated here by different colours) each follow a different motion trajectory. Observers attend to one of the two superimposed motion patterns.

If basic motion mechanisms are affected by spatial attention, we expect to find larger MAEs when attention is directed towards, rather than away from a moving adaptation stimulus. However, in an influential paper exploring the MAE, Wohlgemuth (1911) reported that diverting attention to a central rapid serial visual presentation (RSVP) task had no effect on adaptation to a spiral motion stimulus, leading to a long-held view that the mechanisms responsible for motion adaptation are pre-attentive. Indeed, some recent papers continue to endorse this view (Morgan, 2011, 2012, 2013). This suggestion – that motion adaptation is independent of attention - is aligned with previous reports that adaptation to other simple visual features (spatial frequency, orientation) is unaffected by attention or awareness (Blake & Fox, 1974; He et al., 1996).

A landmark study by Chaudhuri (1990) challenged this pervasive view. Observers viewed a large moving stimulus for 60 s. During this adaptation period, numbers and letters appeared within a small central aperture and observers either engaged in a demanding alphanumeric task, or passively viewed the stimulus (see Figure 3.1b). Observers subsequently viewed a static stimulus and reported the MAE duration. Attending to the central task caused a substantial reduction in the duration of the subsequent motion after-effect. Subsequently, multiple studies have similarly found that diverting attention away from a moving adaptor reduces the duration (e.g., Chaudhuri, 1990; Rezec et al., 2004) or velocity of the subsequent MAE (e.g., Georgiades & Harris, 2000a; Taya et al., 2009).

In broad agreement with this behavioural data, neuroimaging evidence suggests that, under similar attentional manipulations, motion-related activity in medial temporal (MT) / medial superior temporal (MST) areas is modulated by attention (Beauchamp et al., 1997; Rees et al., 1997). Load theory of selective attention suggests that during a demanding task, limited resources are available to process task-irrelevant information (such as a peripheral motion stimulus). Conversely, a low-load task requiring fewer resources leads to greater processing of task irrelevant stimuli (Lavie, 2005). Rees et al. (1997) presented irrelevant expanding motion in the periphery and words at fixation. In line with attentional load theory, a low load task (detect uppercase words) resulted in increased activation across several areas (MT, V1/V2 and the superior colliculus) and longer MAE durations, relative to a high-load task (detect bisyllabic words).

A clear consensus on whether (or under what conditions) attention increases motion adaptation is yet to emerge, however, due to null (Morgan, 2011, 2012, 2013; Pavan & Greenlee, 2015), or inconsistent findings (e.g., Georgiades & Harris, 2002b; Takeuchi & Kita, 1994). One might argue that, given the importance of motion for fundamental tasks such as segmentation (including breaking camouflage), depth perception and guiding self-motion (e.g., Gibson, 1958; Nakayama, 1985), it would be evolutionarily advantageous if motion were processed independently of attention. Certainly, motion is a powerful cue for pop-out in visual search (Driver et al., 1992; Nakayama & Silverman, 1986). If motion adaptation mechanisms are pre-attentive, why have many studies reported an effect of attention on MAEs? One suggestion is that affirmative findings reflect response bias: observers expect weaker MAEs to follow diverted-attention conditions and bias their responses accordingly. Measures of MAE duration (as used by Chaudhuri, 1990 and others) may be particularly susceptible to bias/criterion effects because observers struggle to determine the point at which the MAE has completely disappeared (Blake & Hiris, 1993; Morgan, 2012).

Other factors, such as the choice of stimuli and experimental paradigm almost certainly contribute to variability across the findings from different studies. Paradigms differ in the extent to which the attentional manipulations direct spatial, featural and surface/object-based attention. As reviewed below (see section 3.3.2.1.1), a coherently translating stimulus may recruit feature-based attention more effectively than complex (rotating and /or expanding) stimuli. Others have demonstrated that the eccentricity of the adaptor (Georgiades & Harris, 2000b, 2000a) and the type of test stimulus (static vs. dynamic; Culham, Verstraten, Ashida, & Cavanagh (2000) may modulate the effect of attention. Attentional tracking paradigms, in which observers attend one of two superimposed motion stimuli (e.g., Lankheet & Verstraten, 1995; Mukai & Watanabe, 2001; see Figure 3.1c) may reveal larger attentional effects than those that direct attention towards or away from the location of a single motion stimulus (Morgan, 2011). A meta-analysis allows us to evaluate all of these factors and others (as detailed in Section 3.3.2) such that we can better understand whether, and under what conditions, motion processing (and motion adaptation) is modulated by attention.

3.3.1 The current review: justification and objectives

In contrast to single empirical papers, or selective, narrative reviews (e.g., Burr & Thompson, 2011), our meta-analysis provides sufficient power to quantify the effects of multiple factors on the attention-motion relationship. We assess the effects of varying the adaptation stimulus (translation vs. complex motion, size, eccentricity, speed and duration), the test stimulus (static vs. dynamic), the experimental paradigm (MAE duration vs. strength/speed, 2AFC vs. matching, attentional tracking vs. distraction) and participant characteristics (naïve vs. non-naïve).

3.3.2 Factors that may affect the relationship between attention and motion processing

3.3.2.1 Characteristics of the adaptation stimulus

3.3.2.1.1 Type of motion

The effect of attention on neural responses to motion stimuli may depend on the type of motion being presented. Spatial attention has been shown to increase the overall response gain of MT neurons corresponding to the attended region (Treue & Martínez Trujillo, 1999). In contrast, feature-based attention has a substantial direction-specific effect, such that neurons in V1, MT and MST tuned to the attended motion direction show a response gain, while neurons tuned to the opposite direction are suppressed (Saproo & Serences, 2014; Treue & Martínez Trujillo, 1999; Treue & Maunsell, 1996). Importantly, this effect of feature-based attention spreads across the visual field, such that attending to leftward motion in one location will enhance processing of leftward motion across all retinal locations. One would expect this direction-specific modulation of neural activation to have a large role in the enhancement of MAEs. When observers attend to a large, coherently translating stimulus (vs. central letters, for example), spatial and feature-based attention will combine (Treue & Martínez Trujillo, 1999) to enhance the neural representation of the moving stimulus across multiple motion-sensitive cortical regions.

In contrast to translating stimuli, rotating or expanding motion patterns are composed of local motion signals whose directions vary as a function of position (Carrasco, 2011). Attending to these complex motion stimuli will not, therefore, enhance V1/MT activity via simple feature-based attention mechanisms. However, there is now evidence from neurophysiology (Wannig et al., 2007) and fMRI (Kamitani & Tong, 2006) that surface, or object-based attention can enhance V1 and MT activation as a function of both direction and position, when more complex motion patterns are attended. These effects could be driven by feedback from the dorsal section of MST (MSTd), an area known to have larger and more complex receptive fields that have been implicated in optic flow processing (Graziano et al., 1994; Saito et al., 1986; Tanaka & Saito, 1989).

Behavioural studies of attention and motion processing often assume, implicitly, that increased motion-related activation (due to attention) can be inferred from changes in adaptation. However, adaptation effects may vary across regions. Following prolonged activation, V1 neurons show substantial reductions in responsiveness and sensitivity to motion directions close to the adapted direction. However, reductions in responsivity in MT are much smaller (Kohn & Movshon, 2003, 2004). Thus, differences in adaptation across the cortex, in addition to variations in the effects of spatial, featural and surface-based attention on neural responses to translating vs. complex motion patterns, strongly suggest that the effect of attention on adaptation will depend on the type of motion stimulus.

3.3.2.1.2 Size of adaptation stimuli

Previous studies have asked whether stimulus size determines the extent of attentional modulation (Georgiades & Harris, 2000b; Takeuchi & Kita, 1994). If attentional effects are larger at higher-level cortical regions (at least for complex motion) then attentional modulation of MAEs might increase with stimulus size, given increasing receptive field size from V1 to MT and MST (Smith et al., 2001). On the other hand, it may be easier to shift spatial attention away from a smaller stimulus, particularly as its distance from the task-relevant stimulus increases.

3.3.2.1.3 Eccentricity of adaptation stimuli

Most paradigms used to explore the attention-motion relationship use an attentional task related to a central stimulus to draw attention away from a peripheral motion stimulus. One might expect that when the adaptation stimulus is close to the distracting stimulus, attentional resources may ‘spill over’ to the motion stimulus more easily. A key component of the load theory of attention is that the target and distractor must be spatially separated (Lavie, 2005). A demanding task at fixation may reduce the extent to which peripheral distractors are processed, by narrowing the window of spatial attention around the central, task relevant stimuli. Thus, more eccentric adaptation stimuli may reveal larger effects of attentional modulation. Conversely, there is some empirical evidence that attentional modulation is stronger for adaptation stimuli closer to fixation (Georgiades & Harris, 2000a, 2000b).

3.3.2.1.4 Speed of adaptation stimuli

Many studies have considered how motion adaptation varies as a function of adaptor speed, classically reported to follow an inverted U-shape (see Thompson, 1998 for an overview). In terms of attention, Georgiades and Harris (2002b) found that attention modulated motion adaptation for faster adaptation stimuli. However, for slower adaptation stimuli, the effect of attention decreased with decreasing spatial frequency. This suggests that diverting attention attenuates the processing of faster stimuli, whereas spatiotemporal filters (Adelson & Bergen, 1985) tuned to slow and coarse stimuli are less affected by attention. The relationship between speed, attention, and motion processing has rarely been examined within studies. However, the wide range of adaptation speeds used across different studies allows us to explore this in the current analysis.

3.3.2.1.5 Adaptation duration

As adaptation duration increases, MAEs increase (Hershenson, 1993). In previous work, we explored how the effects of attention vary across the adaptation period by measuring the MAE at regular intervals during an extended adaptation period (Bartlett et al., 2018). Attention affected the asymptotic MAE magnitude, but not the rate at which it accumulated (i.e., the time constant). This finding is broadly consistent with Takeuchi and Kita (1994), who found that diverted attention led to reduced MAEs across adaptation durations of 20, 40 and 80 s.

It could be argued, however, that diverting attention may reduce the rate of adaptation, without affecting the asymptotic point, i.e., at longer durations adaptation is saturated, and will not be further enhanced by attention. Such an effect could account for some null findings in the literature, and aligns with work by Blake and colleagues regarding perceptual awareness: after-effects in motion or spatial frequency are reduced under suppression or crowding for low contrast adaptors only – adaptation reaches saturation at higher contrasts, irrespective of awareness (Blake et al., 2006; Blake & Fox, 1974).

3.3.2.2 Test stimulus characteristics

3.3.2.2.1 Static vs. dynamic test stimuli

Motion adaptation can be quantified using static test stimuli (e.g., Chaudhuri, 1990) or dynamic tests, such as random dot motion patterns (e.g., Mukai & Watanabe, 2001; Taya et al., 2009) or counterphase flicker (e.g., Nishida & Ashida, 2000; Rezec et al., 2004). Nishida and Sato (1995) suggested that static test stimuli reflect adaptation to first order motion, whereas dynamic (flicker) tests reveal second order MAEs. Static and dynamic tests may also differ in terms of sensitivity to monocular vs. binocular motion mechanisms (e.g., Nishida & Ashida, 2000), adapting motion speed (van der Smagt, Verstraten & van de Grind, 1999) and storage effects (e.g., Verstraten et al., 1996). Using an attentional tracking paradigm (see Figure 3.1c), Culham et al. (2000) reported that attention modulated the MAE only when measured via a dynamic test. MAEs obtained from static and dynamic test stimuli may reflect different motion mechanisms that are differentially modulated by attention. Alternatively, van Boxtel et al. (2006) suggested that MAE differences between static and dynamic tests can be explained by a single motion system, however the influence of attention at different levels of this system are still unclear.

3.3.2.3 Experimental paradigm

3.3.2.3.1 MAE measurement and response

Many studies have quantified the effects of attention on motion adaptation by asking observers to report the cessation of the (illusory) motion of a static test stimulus, i.e., the MAE duration (Chaudhuri, 1990; Morgan, 2012; Rezec et al., 2004). As noted above, this reporting method has been criticised as susceptible to response bias. Alternatively, MAE magnitude has been quantified via velocity matching (Georgiades & Harris, 2000a). 2AFC designs have also been implemented, in which participants select one of two response options, such as the test stimulus' motion direction (e.g., Kaunitz et al., 2011; Taya et al., 2009) or which of two test stimuli was moving faster (Morgan, 2013). Some 2AFC paradigms use nulling techniques in which the percentage of test stimulus dots moving oppositely to the aftereffect (e.g., Blake & Hiris, 1993; Mukai & Watanabe, 2001) or the phase shift of the test (e.g., Culham et al., 2000) is adjusted to counteract the aftereffect. 2AFC / two interval forced choice (2IFC) designs have been considered preferable to duration or matching tasks in terms of minimising response bias (Morgan, 2013).

If our analyses reveal that the reported effects of attention on motion adaptation are larger when measured via duration estimation or velocity matching paradigms, this would suggest that some reported effects have been inflated by response bias.

3.3.2.3.2 Attentional manipulation

Two distinct methods of manipulating attention have been used in the context of motion adaptation. 'Distractor' paradigms involve diverting attention away from a moving adaptation stimulus – usually towards a centrally presented, difficult task (see Figure 3.1b). This condition is compared with one in which more attention is deployed to the adaptation stimulus, for example during passive viewing. This paradigm involves spatial attention (the moving adaptor and central task are spatially separated). Depending on the type of motion, it may also involve feature and / or surface-based attention, as discussed above. Some would also consider it to involve 'dimension' based attention, i.e., attention to motion rather than another visual dimension such as colour or shape, because the central task does not usually rely on motion. Reductions in motion-related activation in V1 and MT/MST have been found when attention is directed to the colour or luminance of a moving stimulus, rather than its motion (Beauchamp et al., 1997; Saproo & Serences, 2014), with corresponding changes in the resultant MAE also reported (Taya et al., 2009).

In contrast, 'attentional tracking' paradigms ask subjects to attend to one of two superimposed motion patterns (see Figure 3.1c). This relies on feature-based attention: i.e., attention is directed to one motion direction, at the expense of another motion direction. Studies that have used attentional tracking have fairly consistently demonstrated attentional modulation of motion adaptation (e.g., Alais & Blake, 1999; Culham et al., 2000; Lankheet & Verstraten, 1995). However, Morgan (2011) argued that attention to one motion direction may inhibit the processing of motion in the opposite direction, which would not account for attention effects with only one motion pattern (as in the distractor paradigm). Accordingly, it has been suggested that the two paradigms probe distinct attentional mechanisms that vary in their effects on motion processing (Morgan, 2011, 2012, 2013).

3.3.2.4 Participant characteristics

3.3.2.4.1 Participant naivety

It is often noted that the risk of response bias increases with certain paradigms (as discussed in Section 3.3.2.3.1), and also with non-naïve observers who may know the research hypotheses. As noted above, there have been claims that some reports of attentional modulation of motion adaptation are not just inflated by, but due to response bias (Morgan, 2012, 2013). Indeed, Morgan (2012) failed to find attentional modulation of motion adaptation with naïve observers. The overall picture, however, is less clear, with other studies finding significant effects within groups of naïve observers (e.g., Chaudhuri, 1990; Patterson et al., 2005).

3.4 Method

3.4.1 Inclusion and coding decisions

3.4.1.1 Inclusion criteria

All studies that met the following criteria were included in the present meta-analysis:

1. The study manipulated attention during motion adaptation and reported the subsequent behavioural motion aftereffect.
2. The stimuli did not differ across attentional manipulations.
3. The study was published in an English language journal on or before August 2016.
4. Participants were healthy human adults – studies using patient populations were excluded.
5. The study was not a re-analysis of existing data
6. Sufficient information was provided in order to estimate an effect size (see section 3.4.3).
7. Only within subject designs were included, due to well-known issues equating within subject and between subject effect size measurements (Lakens, 2013). This removed 7.32% of effects.

3.4.1.2 Other coding and inclusion decisions

1. If the study assessed both a low load and a no load (passive) condition, these data were pooled into a single ‘low load’ condition and compared against the high load condition.
2. If the study included a manipulation that was not pertinent to the research questions (e.g., different levels of contrast in the adapting stimulus; Rezec et al., 2004), data were pooled across this manipulation (see Appendix A for a full list).
3. In order to reduce un-modelled variability, data from conditions / experiments with atypical presentation conditions were excluded. For example, in studies investigating interocular transfer, only data from conditions in which adaptation and test stimuli were

presented to the same eye(s) were included (e.g., Nishida & Ashida, 2000). See Appendix A for a full list of included effects and details regarding excluded conditions.

4. If the study was investigating awareness, we only included the data from conditions where observers were aware of the adapter (e.g., Kaunitz et al., 2011).
5. Only visual manipulations of attention were included; auditory attention conditions were excluded (e.g., Houghton, Macken, & Jones, 2003).

3.4.2 General search and coding strategies

One of the authors (LB) conducted the search for relevant studies and coded the data, in consultation with all authors. A PubMed database search was first conducted. Subsequently, the reference sections of all relevant studies were examined to identify additional relevant papers. Next, articles citing any of the relevant studies were identified via Google Scholar, and the reference lists of all of these articles were then examined. A summary of the excluded articles and the database search terms are presented in Appendix B, according to the 'Preferred Reporting Items for Systematic reviews and Meta Analysis' guidelines (PRISMA: Moher, Liberati, Tetzlaff, Altman, & The PRISMA Group, 2009).

3.4.3 Methods

3.4.3.1 Effect size metric

Cohen's *d*, the standardised difference between means (Cohen, 1977), was used as the effect size index for all outcome measures. A positive value indicates a stronger motion aftereffect following passive or low-load adaptation than diverted or high-load attention during adaptation, or following motion-focused compared to passive viewing.

3.4.3.2 Standardisers for d

Our primary estimator (86.84% of included effects) of Cohen's *d* was d_{av}, the difference between means (M_{diff}) standardised by the averaged standard deviation (*SD*) of the measures (Lakens, 2013):

$$d_{av} = \frac{M_{diff}}{\frac{SD_1+SD_2}{2}}$$ Equation 3.1.

This formula is recommended for repeated measures designs where there is no pre-post distinction (e.g., before or after treatment). Because both SD measures are equally good estimators of population variability, averaging the two gives the best estimate (Cumming, 2012). In cases where standard deviations were only reported for multiple levels of an irrelevant experimental variable, these values were pooled to reflect the standard deviation collapsed across these levels (see Appendix C).

If means and standard deviations were not reported, effect sizes were computed from t, p or F values and the degrees of freedom to give d_{RM}, the difference between means standardised by the standard deviation of the difference scores (Lakens, 2013):

$$d_{RM} = \frac{t}{\sqrt{N}} \times \sqrt{2(1-r)} \qquad \text{Equation 3.2.}$$

In practice, few effect sizes were calculated using d_{RM} (13.16% of overall). As Equation 3.2 indicates, this estimate corrects for the paired correlation (r) between conditions. These correlations were calculated using equations reported by Morris and DeShon (2002), after first computing the variance of difference scores using reported N, M_{diff} and t values (see Appendix D). Paired correlations were estimated for the five effects for which the required data were available (Appendix F effect numbers: 5, 13, 16, 29 and 45), however one was removed (effect number 16) as it fell outside the possible range, leaving four correlations in total (M = 0. 81, SD = 0.31). The mean of these correlations was then assumed for the remaining calculations of d_{RM}.

The standard error of each effect size estimate was calculated via the formula:

$$SE = \sqrt{\frac{\frac{1}{N+d^2}}{2N}} \qquad \text{Equation 3.3.}$$

As in Equation 3.2, this SE formula was multiplied by $\sqrt{2(1-r)}$ to correct for the paired correlation between conditions.

When relevant statistics (e.g., t or F statistics) were not reported in the text, the effect size was estimated, where possible, using means and standard deviations estimated from published figures, via ‘GraphClick’ software (Arizona Software Inc., 2010). Finally, if insufficient information was available from any source, the study was excluded from analyses.

3.4.4 Model and analysis decisions

Effect size data were analysed in a random effects model. This model assumes that studies are estimating independent, randomly sampled values of the population parameters, and it is tolerant to heterogeneity across effect sizes (Cumming, 2012). Total effect size heterogeneity was estimated using the standardised measure Cochran’s Q, while I^2 was used to estimate additional heterogeneity beyond that expected in a fixed effects model (Cumming, 2012). Parameter estimates were derived via restricted maximum likelihood estimation to minimise bias (Viechtbauer, 2005).

To statistically assess model coefficients, Wald-type chi squared tests were computed. The pseudo-R^2 statistic was used to quantify the heterogeneity across effect sizes that was explained by moderators (see Appendix E). The unstandardized regression coefficient (b) indicated the direction and magnitude of effects. Likelihood ratio tests were used to compare models (whose parameters were derived via maximum likelihood estimation), in order to identify moderators that made a significant contribution to explained heterogeneity. All analyses were carried out in R, using the ‘metafor’ package (Viechtbauer, 2005).

3.4.5 Dependency among effect sizes

The number of included conditions (nested within samples) and the number of independent samples (nested within studies) were coded. Effects were treated independently (including those from the same authors and research laboratory) as listed in Appendix F. In some cases, samples were exposed to many conditions, resulting in multiple effect sizes from a single group of participants. Collapsing the data across these effects would ignore important information. However, the contribution of multiple effect sizes by a sample introduces dependency in the data; the results of the meta-analysis can become biased towards the (correlated) effect size estimates due to a single unrepresentative sample. The influence of dependency was examined by creating multi-level models (Cheung, 2014) where conditions (level 2) were nested within their samples (level 3). This allowed us to determine whether there was a significant effect size dependency (i.e., whether a 3-level model provides a better fit than a 2-level model). In addition, we investigated the influence of dependency by creating resampled data sets that included one effect size from each independent sample. This allows an examination of the data under conditions where dependency is eliminated (Greenhouse & Iyengar, 1994).

3.5 Results

3.5.1 Summary of included data

In total, 29 studies were analysed, involving 229 participants across 37 independent samples, yielding 76 effect size estimates. These effect size estimates, and the studies from which they originated are provided in Table 3.1. Detailed information about each effect is available in Appendix A. Two effect sizes were more than ± 3 SDs from the mean. However, removing these outliers reduced the overall effect size by only 0.04 and all significant moderators remained significant. They were therefore included in the main analysis. The coding for each moderator variable can be found in Table 3.2, and a summary of moderator coding for each effect can be found in Appendix F.

Table 3.1 Studies included in the meta-analysis.

Reference	Effect Size (Effect Number*)
Aghdaee & Zandvakili (2005)	0.64 (1)
Alais & Blake (1999)	2.62 (2)
Berman & Colby (2002)	2.13 (3)
Blaser & Shepard (2009)	2.04 (4)
Büchel et al. (1998)	0.98 (5)
Chaudhuri (1990)	3.29 (6)
Culham et al. (2000)	0.92 (7); 0.82 (8)
Dobkins, Rezec, & Krekelberg (2007)	1.11 (9); 0.44 (10)
Georgiades & Harris (2002a)	1.37 (11); 1.00 (12); 1.86 (13); 0.78 (14); 0.76 (15)
Georgiades & Harris (2002b)	10.97 (16); 1.04 (17)
Georgiades & Harris (2000a)	4.82 (18); 4.45 (19); 4.33 (20); 6.67 (21); 2.85 (22); 2.94 (23)
Georgiades & Harris (2000b)	7.92 (24); 6.08 (25); 4.39 (26); 1.95 (27); 1.81 (28)
Houghton et al. (2003)	1.61 (29)
Jung & Chong (2014)	2.31 (30); 0.58 (31)
Kaunitz et al. (2011)	0.74 (32); 1.09 (33)
Morgan (2013)	0.11 (34); 0.30 (35)
Morgan (2012)	0.22 (36); -0.16 (37)
Mukai & Watanabe (2001)	0.92 (38); 1.34 (39); 1.16 (40)
Nishida & Ashida (2000)	0.38 (41); -0.80 (42); 0.69 (43)
Patterson et al. (2005)	0.61 (44)
Rees, Frith, & Lavie (2001)	0.49 (45)
Rees et al. (1997)	0.49 (46)
Rezec et al. (2004)	1.27 (47); 1.38 (48)
Rose, Bradshaw, & Hibbard (2003)	0.83 (49)
Shioiri & Matsumiya (2009)	1.16 (50); 0.69 (51)
Shulman (1993)	0.76 (52); 0.71 (53); 1.51 (54); 1.41 (55)
Shulman (1991)	0.89 (56); 0.88 (57); 1.00 (58)
Takeuchi & Kita (1994)	2.54 (59); 1.11 (60); 1.78 (61); -0.23 (62); 0.01 (63); -0.18 (64); 0.20 (65); -0.03 (66); -0.13 (67); 2.02 (68); -0.73 (69); 2.77 (70); -1.94 (71); 0.03 (72); -0.11 (73); 0.16 (74); 0.16 (75)
Taya et al. (2009)	1.05 (76)

* Corresponds to the y-axis value in Figure. 3.2, and the *Effect Number* column in Appendix F

Table 3.2 Moderator coding.

Moderator	Type	Values	Description of variable	Descriptive Statistics*	Missing Cases
Characteristics of adaptation stimulus					
Type of motion (Section 3.3.2.1.1)	Categorical	1 = Translational motion 2 = Complex motion	The type of motion used for adaptation in the study. Complex motion refers to any case where motion direction varies across the stimulus (i.e., expansion, contraction, rotation and spiral motion.	k = 76 N_1 = 46 N_2 = 30	0
Adaptation stimulus area (Section 3.3.2.1.2)	Continuous	1.89°2 - 1256.39°^{2}	The total area (in degrees of visual angle^2) covered by the adaptation stimulus. Excluded those not reporting the size of a central blank square/ellipse, or if adapting stimulus shape was not clearly specified.	k = 64 μ = 158.87°^{2} σ = 277.50°^{2} Range = 1.89°^{2} - 1256.39°^{2}	12
Eccentricity of adaptation stimuli (Section 3.3.2.1.3)	Continuous	0.07° - 3.5°	The distance between fixation and the adaptation stimulus (in degrees of visual angle). Averaged across width and height of this space if they differed.	k = 55 μ = 1.03° σ = 1.08° Range = 0.07° - 3.5°	21
Speed of adaptation stimuli (Section 3.3.2.1.4)	Continuous	0.6°/s - 8°/s	The speed of the adaptation stimulus. Calculated tangential speed at average eccentricity for rotational motion.	k = 45 μ = 4.16°/s σ = 1.79°/s Range = 0.6°/s - 8°/s	31
Duration of adaptation (Section 3.3.2.1.5)	Continuous	1 s - 90 s	The duration of a single adaptation period within each trial.	k = 66 μ = 40.11 s σ = 21.40 s Range = 1 - 90 s	10
Test stimulus characteristics					

Moderator	Type	Values	Description of variable	Descriptive Statistics*	Missing Cases
Static vs. dynamic test stimuli (Section 3.3.2.2.1)	Categorical	1 = Static 2 = Dynamic	The type of test stimulus used to measure the MAE.	k = 76 $N_1 = 44$ $N_2 = 32$	0
Experimental paradigm					
MAE measurement (Section 3.3.2.3.1)	Categorical	1 = Duration 2 = Strength	The method of measuring the MAE. ‘Duration’ paradigms record the time until MAE cessation. The ‘strength’ category includes all other methods of MAE measurement (e.g., nulling, 2AFC).	k = 92 $N_1 = 51$ $N_2 = 25$	0
MAE response (Section 3.3.2.3.1)	Categorical	1 = Magnitude 2 = 2AFC	2AFC measures of the MAE require participants to select one response of two response options (e.g., test is moving left or rightward). All other methods are coded as ‘magnitude’ responses.	k = 76 $N_1 = 64$ $N_2 = 12$	0
Attentional manipulation (Section 3.3.2.3.2)	Categorical	1 = Distractor 2 = Tracking	The paradigm for manipulating attention. Distractor paradigms (see Figure 3.1b) divert attention from adapting motion with a centrally presented task. Attentional tracking (see Figure 3.1c) involves attending to one of two superimposed motion directions.	k = 76 $N_1 = 70$ $N_2 = 6$	0
<u>Participant characteristics</u>					
Participant naivety (Section 3.3.2.4.1)	Categorical	1 = Naïve 2 = Other	‘Naïve’ refers to a subject group composed only of observers naïve to the research hypotheses. The ‘other’ category includes experienced-only samples, as well as mixed naïve and experienced subject groups.	k = 69 $N_1 = 44$ $N_2 = 25$	7

* *k* refers to the number of effects; *N* indicates the number of effects for each condition

3.5.2 Overall effect size of attentional modulation of the MAE

Results of the meta-analyses are depicted in Figure 3.2. A large effect of attention was found (k = 76, N = 229, d_{RM} = 1.12, 95% CI [0.87, 1.38], $p < .001$). A number of analyses were conducted to explore potential file-drawer effects (in which null effects are sometimes unpublished). Rosenthal's (1991) fail-safe N indicated that 7,767 additional, null studies would be required to reduce the pooled effect size to non-significance. The actual number of unpublished (negative effect) studies was estimated to be 7, using the trim and fill method, based on the symmetry of the data (Duval & Tweedie, 2000a, 2000b). Attentional modulation of the MAE remained significant when these (simulated) effects were included, reducing the effect by only 0.18. When any single contributing effect was removed, the pooled effect remained significant (leave-one-out analysis, range [1.07, 1.15], $ps < .001$). See Appendix G for more details and figures.

Significant heterogeneity was found, $Q(75) = 244.06$, $p < .001$. The I^2 statistic revealed that 75.35% of the heterogeneity could not be accounted for by sampling variance. In order to explain this heterogeneity, moderators were examined.

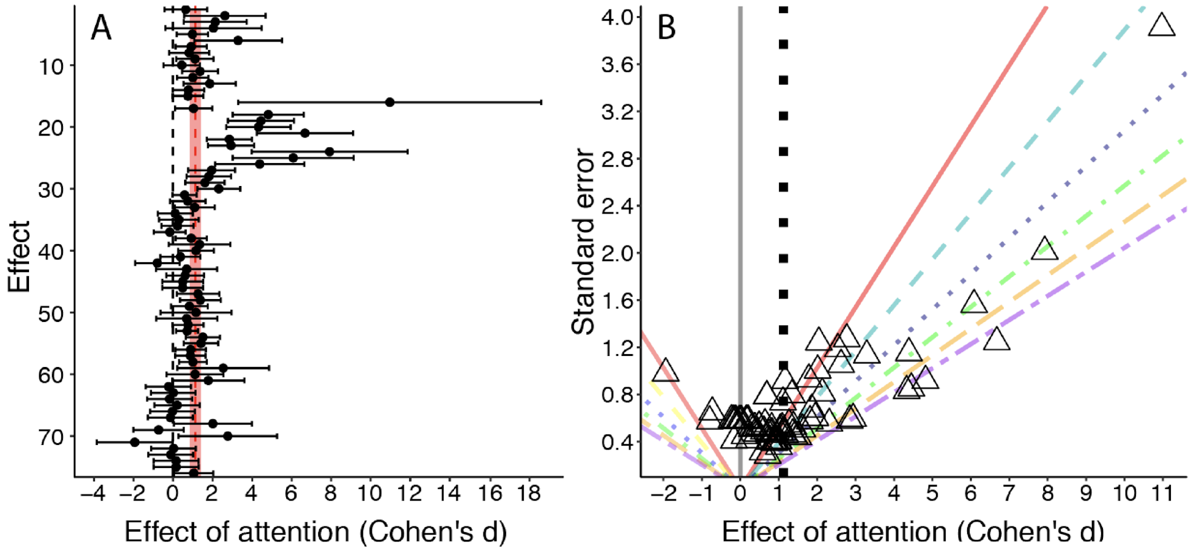

Figure 3.2 Summary of the effect of attention on the MAE. a) Forest plot of all 76 effect sizes. Error bars are 95% confidence intervals. Red dashed line indicates the pooled summary effect, surrounding shaded area depicts 95% CI. b) Funnel plot. Dashed line is the pooled effect size, coloured lines represent p values (Purple/Two-dash=.000001, Orange/Long-dash=.00001, Green/Dot-dash=.0001, Blue/Dotted=.001, Turquoise/Dashed=.01, Red/Solid=.05, Black=1).

3.5.3 Dependencies: overall analyses

A three-tiered model, nesting conditions within independent samples, was a better fit to the data than the two-tiered model $x^2(1) = 34.69$, $p < .001$. This indicates dependence in the data – i.e., there is an effect of study. To characterise the influence of dependency on our global outcomes, the random effects model was applied to 500 resampled data sets, each of which contained one randomly selected effect size from each of our independent samples, yielding a total of 37 effect sizes for each data set. All subsets revealed a significant pooled effect (mean $d = 1.01$, $SD = 0.05$), indicating a strong attention-MAE relationship regardless of dependency.

3.5.4 Regression models with one moderator

A table summarising all single moderator regression models can be found in Appendix H. Important moderators (those that were individually significant or contributed to the best multiple regression model) are shown in Figure 3.3. Motion type significantly affected the attentional modulation of the MAE ($Q(1) = 17.43$, $b = -0.99$, $p < .001$), accounting for 24.92% of the total heterogeneity: studies using translating motion stimuli reported significantly larger effects than those using complex motion, (see Figure 3.3a). However, attention had a significant effect on motion adaptation within the subset of studies using either translational motion, ($d = 1.54$, $p < .001$) or complex motion ($d = 0.56$, $p = .002$).

The size (area) of the adaptation stimulus significantly affected attentional modulation of the MAE, $Q(1) = 7.40$, $b = -0.002$, $p = .007$, accounting for 11.38% of the heterogeneity in the effect (see Figure 3.3b). As stimulus size increased, the magnitude of attentional modulation decreased. In addition, there was a significant effect of the eccentricity of the adapting stimulus, accounting for 8.59% of the total heterogeneity, $Q(1) = 4.05$, $b = 0.37$, $p = .044$ (see Figure 3.3c). The effect of attentional manipulations on the MAE was larger for stimuli that were further from fixation.

When considered alone, the speed of the adaptation stimulus was not significant, $Q(1) = 3.36$, $b = -0.14$, $p = .067$, accounting for 2.74% of total heterogeneity. However, motion speed did contribute to the final model (see below); slower stimuli resulted in stronger attentional effects (see Figure 3.3d).

Participant characteristics (i.e., naivety) did not significantly moderate the attention-MAE effect in a single moderator model ($Q(1) = 1.98$, $b = -0.43$, $p = .159$), but did contribute to the overall model, with larger effects reported for studies using naïve participants. (This was not driven by a relationship between sample size and sample type – see Appendix I). Significant effects of attention on motion adaptation were found within the subset of studies using naïve participants ($d = 1.33$, $p < .001$) and within those using experienced, or a mix of naïve and experienced, samples, ($d = 0.90$, $p < .001$; see Figure 3.3e).

The effect of test stimulus (static vs. dynamic) did not reach significance when considered alone ($Q(1) = 3.29$, $b = 0.46$, $p = .070$) but did contribute to the best complete model (see below). Using a static test stimulus to assess the MAE resulted in a weaker, though still significant, effect of attention ($d = 0.91$, $p < .001$) than using dynamic tests ($d = 1.37$, $p < .001$). This accounted for 7.12% of effect size heterogeneity (Figure 3.3f).

The response paradigm made little difference to the measured effect of attention on the MAE. The effect size was similar across studies that measured the MAE duration vs. its strength ($Q(1) = 0.49$, $b = 0.19$, $p = .485$) with studies employing either method reporting significant effects (MAE duration: $d = 1.06$, $p < .001$; MAE strength: $d = 1.24$, $p < .001$). Further, effect size was not significantly modulated by whether a 2AFC design was used vs. a magnitude estimation method ($Q(1) = 0.52$, $b = -0.25$, $p = .470$), although the stronger attentional modulation for magnitude designs compared to 2AFC designs contributed to the final model. Both subsets of studies produced significant effects of attention on the MAE (2AFC: $d = .93$, $p = .003$; magnitude estimation: $d = 1.17$, $p < .001$, see Figure 3.3g).

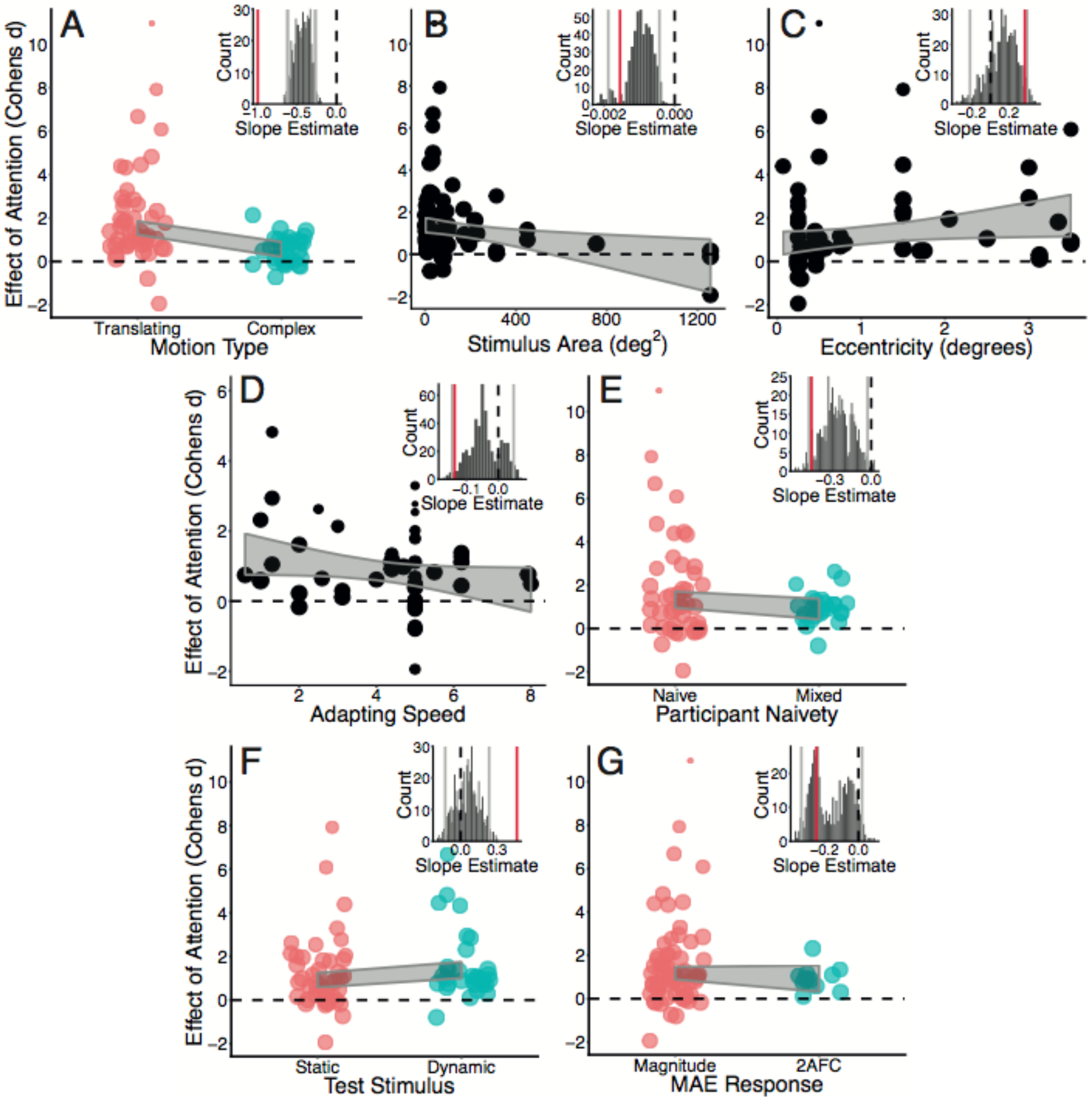

Figure 3.3 Effect size summary for significant moderators (a-c) and factors that significantly contributed to the final model when considered alongside other moderators (d-g). The effect of attention (a) was larger for translational than complex motion, (b) decreased as stimulus size increased, (c) increased with greater eccentricity, (d) reduced with increasing adaptation speed, (e) was greater for naïve than mixed participant groups, (f) was greater for dynamic vs. static test stimuli, and (g) smaller when using a 2AFC response. Larger points indicate smaller standard error. The shaded ribbon indicates the 95% CI from the full dataset. Inset histograms detail the estimated slope parameter for 500 randomly selected datasets with dependency eliminated (see dependency information); red lines indicate estimated slope from the full dataset; grey lines indicate the 95% CI determined by the resampled independent sample estimates; dashed black lines indicate the zero point.

The duration of the adaptation stimulus did not significantly affect the attention-adaptation relationship (see table in Appendix H). Finally, a significant effect of attention was reported within studies that used distractor paradigms (as depicted in Figure 3.1b: *d* = 1.12, *p* < .001) as well as those that used attentional tracking paradigms (Figure 3.1c; $d = 1.18$, $p = .010$). The effect size was similar across both (no significant effect of attention paradigm: $Q(1) = 0.01$, $b = 0.06$, $p = .904$).

As described above, the effect of dependencies was explored via resampling. The distribution of regression coefficients across the 500 resampled sets of independent data can be seen in inset histograms of Figure 3.3. Analysing these reduced datasets (with dependencies eliminated) reveals the same set of significant moderators. However, note that the regression coefficient for motion type (translational vs. complex) is larger when estimated from the complete data set than when estimated from reduced datasets. Some of the larger effect sizes for translational motion were produced from samples contributing multiple effects. Thus, we can be confident that studies with translating motion provide substantially larger effect sizes than those using complex motion, but the estimated magnitude of this difference may be inflated by dependencies across estimates from common subject groups.

Selected two-way interaction analyses were conducted (see Appendix J), however only one of these reached significance: the interaction between type of motion and stimulus area, $Q(1) = 4.29$, $p = .038$. While the effect of attention on complex motion adaptation remained constant with increasing stimulus area, smaller translating adaptation stimuli were more affected by attention than larger stimuli.

3.5.5 Multiple regression models

Multiple regression was used to determine the best-fitting model that incorporates multiple factors that contribute significantly to heterogeneity in effect size. A backward elimination strategy was implemented: starting from a model containing all complete effect moderators (those reported for every effect), moderators that did not significantly improve the model were eliminated in a step-wise fashion. We switched to Maximum Likelihood estimation to facilitate model comparison via likelihood ratio tests (*LRT*). Moderators were assessed in order of significance value, such that the moderator with the largest *p* value was considered first. Moderators were eliminated when their removal was associated with a non-significant decrease in the goodness of fit of the model, as determined by model comparison via *LRT*. Subsequently, reduced effect moderators (those reported for a subset of effects only) were considered individually and included only if they significantly improved the model. Those with the largest *N* were assessed first, to maximise the number of cases in the final model.

3.5.5.1 Complete effects

The initial model included all moderators for which values were available for all effects: type of motion (translation vs. complex), MAE measurement (duration vs. strength), MAE response (magnitude vs. 2AFC), test stimulus (static vs. dynamic) and attention paradigm (distractor vs.

tracking). Through backward elimination, the optimal complete effects model included motion type, MAE response and test stimulus as predictors. This model accounted for 42.05% of the heterogeneity of the effect of attention on motion adaptation.

3.5.5.2 Reduced effects

The complete effects model was significantly improved by adding four reduced effect moderators. The addition of each one decreases the number of effect sizes (*k*) included in the model. These reduced effects were participant naivety (*k* = 69), stimulus area (*k* = 57), eccentricity (*k* = 50) and adaptation speed (*k* = 31). The final model accounted for 63.18% of the heterogeneity of the effect; it is shown in Figure 3.4 and summarised in Appendix K.

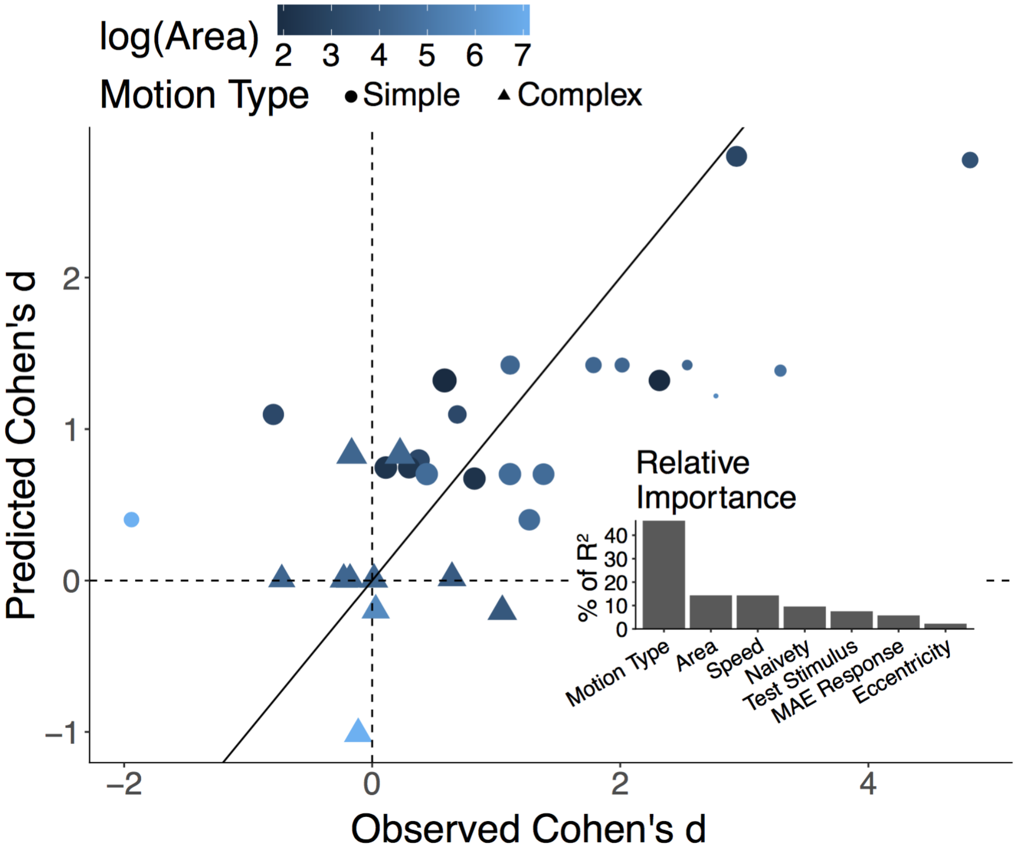

Figure 3.4 Predicted Cohen's d_{AV} values as a function of observed Cohen's d_{AV} for each effect size in final model. Size of the points indicates standard error; larger points have a smaller standard error. Inset: The relative importance of each factor in the final model. This is quantified by the pseudo R^2 statistic (see Appendix E), averaged across all possible orderings of regressor input (Lindeman et al., 1980).

3.6 Discussion

3.6.1 Summary of Findings

Attending to a moving stimulus significantly increases the resultant MAE. This effect of attention is modulated by various characteristics of the adaptation and test stimuli: larger attentional effects were found following adaptation to stimuli that were (i) translating (vs. those with complex motion trajectories) (ii) at a greater eccentricity and (iii) smaller in size. In addition, when considering multiple moderators simultaneously, stronger attentional modulation was reported in studies that employed dynamic, rather than static test stimuli, those using slowly moving adaptation stimuli, and those that used magnitude estimation, rather than 2AFC judgements to quantify the MAE. Further, greater attentional effects were reported in studies using exclusively naïve participants.

3.6.2 Discussion of adaptation and test stimulus characteristics

3.6.2.1 Type of motion

The effect of attention on motion adaptation was around twice as large for translating motion than for other motion patterns. This behavioural finding suggests that feature-based attention plays a substantial role in increasing motion adaptation. Although translational motion produced substantially stronger attentional effects, adaptation to complex motion was also significantly enhanced by attention. When considered alongside neurophysiology and fMRI evidence, the substantial difference between simple and complex motion suggests that surface-based attention may drive some attentional modulation of activity within V1 / MT, but that this effect is small compared to the effects of simple feature-based attention. In addition, we know that neurons in MST can be tuned to large field translating, rotating or expanding / contracting patterns (Smith et al., 2006; Wall et al., 2008). The relatively small effect of attention on adaptation to complex motion therefore also suggests that attentional effects on adaptation within MST are small compared to those in V1/MT.

Early fMRI studies reported a significant effect of attending to complex motion in MT/MST but found no significant effects of attention in V1 (Büchel et al., 1998; O'Craven et al., 1997; T. Watanabe et al., 1998). It is possible that the effects of surface-based attention in V1 are relatively weak and hard to detect. Alternatively, V1 facilitation in a subset of neurons may have been masked by suppressive effects within neurons tuned to unattended motion directions. Facilitatory and suppressive effects of attention (in response to translating stimuli) have recently been revealed in V1 using more sophisticated, voxel-based analyses (Saproo & Serences, 2014), consistent with our findings.

3.6.2.2 Stimulus size

Our analyses revealed a relationship between stimulus size and the effect of attention, with a smaller effect for larger adaptation stimuli, in line with Takeuchi and Kita (1994). They suggested that small vs. large (or whole field) stimuli are processed by separate motion mechanisms, with the former sensitive to object motion, and the latter sensitive to the optic flow generated by self-motion. Our analyses revealed smaller attentional effects for larger adaptation stimuli (which may be processed as optic flow), consistent with the idea that selective attention affects the processing of object, rather than self-motion (Takeuchi & Kita, 1994). These effects may also indicate the importance of receptive field size to stimulus size, as smaller neuronal receptive fields will overlap with larger adaptation stimuli closer to fixation. That translational motion was mostly driving this effect, with complex motion unaffected by stimulus size (demonstrated by the interaction between motion type and stimulus size), lends support to this suggestion.

We also considered whether the effect of stimulus size was driven by a confounding factor of eccentricity – smaller adaptation stimuli might, on average, be positioned further from fixation, allowing better control of spatial attention. Stimulus size was negatively correlated with eccentricity, but this did not reach significance ($r = -0.20$, $t(51) = -1.45$, $p = 0.15$). Moreover, both stimulus size and eccentricity contributed significantly to the final model, suggesting that both factors are important in attentional modulation.

3.6.2.3 Eccentricity

Larger effects of attention were found for adaptation stimuli presented at greater distances from fixation. One plausible explanation for this relationship relates to our ability to control spatial attention: when we attend to a central task, the processing of nearby stimuli may also be affected – attention is not perfectly focused on the central stimulus, but extends to proximal regions.

The positive relationship between eccentricity and the effect of attention on adaptation is in broad agreement with Lavie's (2005) load theory hypothesis - that an increase in load reduces the window of spatial attention.

3.6.2.4 Test stimuli

Some researchers have suggested that dynamic and static MAEs correspond to different motion mechanisms (e.g., Verstraten et al., 1996), which may differ in their susceptibility to attention. Our analyses show that attention affects MAEs measured with both dynamic and static test stimuli. Although larger effects were found with dynamic tests, this was a modest difference, that did not reach significance when considered alone and may be an artefact of dependencies within studies (see the resampling analyses in Figure 3.3f).

3.6.2.5 Adaptation speed

Our analyses provide some evidence that the speed of the adaptation stimulus affects attentional modulation of the MAE, with a trend for weaker attentional modulation for faster adaptation stimuli. One possibility is that fast-moving stimuli capture attention, and thus attempts to divert attention are less effective.

3.6.3 Factors related to response bias

3.6.3.1 Response type

We considered whether the effects of attention on the MAE might be driven by, or inflated by, response bias. Asking observers to estimate MAE duration is considered more vulnerable to response bias (Morgan, 2011, 2012, 2013), whereas 2AFC tasks are considered less prone to criterion and / or bias effects. However, reported effect size was not significantly moderated by these factors (when considered in single predictor models). In fact, measures of MAE magnitude produced slightly larger estimates of the attentional effect than studies that asked observers to report MAE duration. Although the choice of 2AFC vs. magnitude estimation was not significant when considered alone, it did contribute to the final model, providing some evidence that 2AFC paradigms produce slightly more conservative (but still significant) estimates of the attentional effect.

3.6.3.2 Participant characteristics

If response bias does inflate estimates of the effect of attention, one would expect this to be an issue predominantly amongst non-naïve observers, who understand the attention hypothesis: for response bias to modulate effect size, observers should not only bias their responses in accordance with motion adaptation, but to systematically vary this bias as a function of attention condition. On the contrary, participant naivety did not reach significance as a single moderator, and experiments using naïve subjects reported *larger* effects, with this effect contributing to the final model.

3.6.4 Nonsignificant moderators

A strong and significant effect of attention was found within both distractor and attentional tracking paradigms; both provide an effective manipulation of attention, and modulate the MAE to a similar extent. This contrasts with the suggestion that the two paradigms probe distinct attentional mechanisms, and that only attentional tracking paradigms modulate motion adaptation (Morgan, 2011, 2012). An alternative, supported by our analysis, is that attentional tracking paradigms have produced more consistent effects of attention because they tend to use translating motion stimuli (rather than expanding, or rotating motion).

Consistent with our previous research (Bartlett et al., 2018), adaptation duration did not significantly moderate attentional modulation of the MAE. Previously we examined whether attention affects the rate at which the MAE builds up, or the asymptotic MAE. We found that attention affects the MAE asymptote, rather than the timecourse of adaptation, and this finding is mirrored in our current analysis: comparable attentional modulation was discovered across the wide range of adaptation durations included in the surveyed literature.

Prior work has demonstrated that MAEs increase with adaptation duration (e.g., Bartlett et al., 2018). As discussed above, this duration-related increase in MAEs is not associated with increased attentional modulation. However, it is worth considering whether, more broadly, larger MAEs are associated with increased attentional modulation. Could it be that study designs that produce large MAEs (in terms of effect size) are more sensitive, and therefore also report greater effects of attentional modulation? Moreover, could MAE strength be a mediating variable that ‘explains’ the effects of some of our identified moderators? To investigate this, we quantified baseline MAE strength (in the passive, or low-load condition) using Cohen’s D. (Equation 3.1 reduces to the mean difference between a null result (i.e., no MAE) and the low-load / passive condition, divided by the low-load standard deviation). A small number of effects (12) were excluded from this analysis because an estimate of baseline MAE strength was not available. Within the remaining effects ($k = 64$), MAE strength was not substantially or significantly related to the effect of attention ($Q(1) = 0.20$, $b = -0.02$, $p = .655$). Further analyses confirmed that MAE strength did not significantly contribute to the final model, $LRT = 0.06$, $p = .800$ ($k = 57$). Thus, significant predictors of the modulatory effect of attention on motion adaptation (such as motion type, or stimulus size) cannot be ‘explained away’ via effects on baseline MAE strength.

3.6.5 Reconciling the literature

Attentional modulation of the MAE is a fairly robust effect: significant effects were found at each level of all categorical moderators. However, the strength of the attention effect is substantially moderated by a number of factors, with motion type (translating vs. complex) being the most important. Our multi-moderator model accounted for 63.18% of variation in effect size across studies.

Other, un-modelled factors will also contribute to apparent inconsistencies in the literature. For example, within the distractor paradigm, studies vary in how they manipulate attention; some ‘high load’ or ‘diverted’ attention conditions may be less effective than others in drawing attention away from the motion stimulus. However, this variability is hard to model, given the variety of tasks, and – in some studies – a lack of information about task difficulty / observer accuracy.

3.6.6 Relationship to neuroimaging

As described above, both monkey neurophysiology and human fMRI studies have provided evidence that attention modulates motion-related activity at multiple cortical regions, including V1, MT and MST. Although early work focused on spatial attention, many studies have revealed effects of feature-based attention, and surface-based attention. Some have suggested that a unified attention system exists that treats stimulus location (and possibly object identity) as stimulus ‘features’, alongside motion direction (see Maunsell & Treue, 2006), although recent work suggests that spatial and feature-based attention may, in part at least, rely on different underlying neural mechanisms (Xue et al., 2017). Our meta-analysis suggests that simple, feature-based attention has much stronger effects on motion adaptation than spatial attention, or higher-level ‘surface-based’ attention: the largest effects of attention are seen for coherently translating stimuli, that maximise the effects of feature-based attention. This suggests a larger role for V1 and MT in attentional modulation of motion processing.

Attentional modulation decreased for larger stimuli at smaller eccentricities, conditions that may increase the extent to which spatial attention ‘spills over’ from a central task, to a peripheral motion stimulus. This makes sense if spatial attention modulates neuronal activity according to the extent of overlap between a neuron’s receptive field and the spatial locus of attention (Maunsell & Treue, 2006). The decrease in attentional modulation for larger stimuli further suggests the importance of lower-level cortical regions, where neurons have smaller receptive fields, in driving the MAE attention relationship. Large-field stimuli will be particularly effective in driving activation in MSTd, where receptive fields are large and more will overlap with a central attended region of visual space.

We compared the effect of attention on MAEs measured with dynamic and static test stimuli. Previous authors have shown greater interocular transfer of the dynamic MAE (Nishida et al., 1994) and suggested that static MAEs predominantly reflect adaptation in V1, whereas dynamic MAEs also involve MT (Mather et al., 2008). Our findings are broadly consistent with this suggestion – the larger effect of attention on the dynamic MAE may reflect attentional modulation across V1 and MT/MST.

3.7 Conclusions

Our meta-analysis supports a number of conclusions. First, there is overwhelming evidence that motion adaptation is affected by attention. By analysing the effects of different paradigms, participant naivety and looking for evidence of the ‘file drawer’ effect, we can be confident that reported effects are not driven by response bias or publication bias. It seems that Wohlgemuth (1911) was wrong after all. More importantly, we identified several factors that modulate the effects of attention on motion adaptation, allowing us to explain some apparent inconsistencies in the literature. Our analyses suggest that the largest effects of attention on motion adaptation will be seen for studies that use translating motion stimuli, within either attentional tracking paradigms, or ‘distraction’ paradigms, particularly when the adaptation stimuli are some distance from fixation. These design choices are likely to exploit (direction-specific) feature-based attention, largely reflected in V1 and MT modulation that includes both facilitation and suppressive effects. However, some additional attentional modulation is likely to be driven by surface-based attention and (for ‘distraction’ paradigms) spatial attention.

Chapter 4 Attention and the haptic curvature aftereffect

My first two research papers provided strong evidence that attention has a modulatory effect on the MAE, which cannot be easily accounted for by response bias, and is affected by a number of factors. To extend my investigation into the effects of attention on adaptation, I chose to explore how attention may affect processing in another modality, specifically haptics. As my previous research demonstrated such a strong influence of attention on the MAE, I predicted a similar role of attention on haptic adaptation. While the effect of tactile attention has previously been explored both neurologically and behaviourally, no research has paralleled visual investigations into attention and the aftereffect. As such, a within-modality attention effect was explored for haptic adaptation. We extended this research further by investigating the cross-modal nature of attention for haptic adaptation, allowing a comparison between cross-modal and within modality attention effects.

4.1 Contributions

Experimental design, data collection and analysis and write up for publication were completed by Laura Bartlett under the supervision of Wendy Adams and Erich Graf. The stimuli were created by Erich Graf, and both experiments were created by Antony Wood.

4.2 Abstract

Attention allows us to preferentially process relevant aspects of the vast quantity of sensory information available. Attention has been shown to influence sensory processing in a number of ways. In visual motion adaptation experiments for example, decreasing attention to the motion stimulus via a secondary task weakens the motion aftereffect. Little is known about the effect of attention on haptic (touch) adaptation. We used the well-known haptic curvature after-effect (CAE) to probe the effects of attention on haptic processing. Participants actively explored virtual curved surfaces via a Phantom force-feedback device to induce a CAE. During adaptation, attention was either focused towards or diverted away from the adaptation surface via an additional *haptic* or *visual* task. Statistically significant CAEs were found under all conditions, confirming a substantial role for proprioception in curvature adaptation. However, the magnitude of the CAE was not significantly affected by either haptic or visual attentional modulations. These results suggest that curvature adaptation occurs independently of additional attentional demands.

Keywords: cross-modal attention, curvature aftereffect, attention, haptic adaptation

4.3 Introduction

Attention is the selective processing of particular locations (spatial attention), features (feature-based attention), or objects (object- / surface-based attention) from the extensive sensory world, at the expense of sensory information irrelevant to current task requirements (Carrasco, 2011). Attention has been shown to enhance sensory processing in behavioural (e.g., Posner et al., 1978) , neurophysiological (e.g., Treue, 2001) and fMRI studies (e.g., Gandhi et al., 1999), with most of this work constrained to the visual domain. However, attentional modulation has also been characterised in other modalities, including haptics (see Spence & Gallace, 2007 for a review), where attention has been found to enhance tactile processing while suppressing task-irrelevant information (e.g., Forster & Eimer, 2005; Schweisfurth, Schweizer, & Treue, 2014) .

Another question relates to the deployment of attention across modalities: Is a single resource shared across modalities, such that attention to visual stimuli degrades the processing of haptic information? Or, are attentional resources within the modalities independent? In two experiments we explore the effects of attention on haptic processing, as indexed by the haptic curvature after-effect. We compare within- and cross-modality attentional manipulations, to probe multisensory attentional deployment.

4.3.1 Attention and Visual Perception

As noted above, the majority of work investigating attentional modulation of perception has been done in the visual domain. Feature-based attention, where a particular stimulus feature (e.g., colour) is attended, has been shown to enhance processing for a number of visual features such as orientation, motion direction and colour (see Carrasco, 2011, for a review). Further, a wealth of research has provided evidence that visual spatial attention, i.e., attention directed toward a particular location, enhances processing for stimuli within the attended location (e.g., Luck et al., 1994; Posner et al., 1978).

Attentional effects have been demonstrated using detection and discrimination paradigms, whereby accuracy and/or response times are improved when attention is focused on the relevant feature/location (e.g., Posner et al., 1978). Additionally, adaptation designs have been employed to understand the effects of attention (e.g., Bartlett et al., 2018; Chaudhuri, 1990). The term ‘aftereffect’ refers to altered perception following prolonged exposure to an adaptation stimulus. For example, viewing leftward motion would cause a stationary scene to be perceived as moving rightward. Adaptation appears to be a fundamental characteristic of human perception and can provide vital insights into sensory processing. The aftereffect has long been heralded as a useful behavioural measure of neural activity (Frisby, 1979), and can act as a behavioural supplement to neuroimaging data (Konkle & Moore, 2009; Rees et al., 1997). As such, aftereffects are an established method for measuring attentional modulation of sensory processing – when attention is diverted away from an adaptation stimulus, a reduction in aftereffect magnitude indicates attentional modulation. For example, strong evidence for the effect of attention on motion processing has been revealed by measuring the motion aftereffect (MAE; e.g., Bartlett, Graf, Hedger, & Adams, 2019; Chaudhuri, 1990).

4.3.2 Attention and Haptic Perception

Several studies have now demonstrated that, within haptics (similarly to vision) feature-based attention modulates sensitivity within the attended dimension: discrimination of stimulus shape, duration, roughness and vibrotactile properties are all improved when attention is directed towards the relevant haptic dimension (Metzger et al., 2019; Sinclair et al., 2000). Similarly, discrimination of pairs of tactile stimuli with respect to roughness or duration is improved when attention is directed to the diagnostic feature, rather than spread across both features (Burton et al., 1999). However, using fMRI, (Burton et al., 2008) showed equivalent processing enhancements in primary and secondary somatosensory cortex (SI and SII, respectively) when attention was focused on a stimulus feature or divided across features. This suggests that divided attention does not significantly increase somatosensory brain activation compared to attending a particular stimulus feature.

Global feature-based attention in the tactile modality has also been demonstrated, mirroring findings within vision. For example, Schweisfurth et al. (2014) found faster responses in a tactile orientation detection task when the cue and target orientations matched, for both cued and uncued locations. Similarly, ERP correlates of feature-based attention are not affected by spatial attention (Forster & Eimer, 2004).

In addition to feature-based attention, attending to a specific location has been shown to affect haptic processing: stimuli within the attended location benefit from enhanced processing, whereas stimuli outside the locus of attention are inhibited (Spence & Gallace, 2007). In a series of experiments, Posner et al. (1978) revealed that cueing participants to attend to either the left or right hemifield enhanced processing at the attended location, while suppressing processing at the unattended location, for both visual and tactile stimuli. Forster and Eimer (2005) found a similar pattern of benefits and costs to RT, with correlated modulations of somatosensory processing measured via ERP: costs and benefits due to attention were present to a similar degree at early stages of tactile processing (in contrast to vision and audition; e.g., Luck et al., 1994), while at longer latencies attentional costs were mainly driving attention-based processing differences. Similar behavioural effects have been shown with tactile, rather than visual, cueing: Spence and McGlone (2001) showed that tactile discrimination was faster and more accurate when a nonpredictive tactile cue was presented to the same hand as the target stimulus, vs. the opposite hand. Further, Sathian and Burton (1991) found that accuracy was reduced for invalid tactile cueing to one of four fingers across two hands. However, accuracy was not reduced (compared to valid cueing) when the correct finger on the opposite hand was cued, suggesting a bilateral effect of attention. Exploring the effect of endogenous spatial attention on RTs for a tactile discrimination task, Chica et al. (2007) found significant attention effects for both visual and haptic cueing, with stronger effects for haptic cueing (i.e., within modality attention) at shorter cue-target latencies.

Neuroimaging techniques have further revealed the effect of spatial attention on somatosensory brain regions. Employing both EEG and fMRI, Schubert et al. (2008) demonstrated enhancements in evoked potentials in early and long-latency EEG signals due to spatial attention, with corresponding enhanced activity in contralateral somatosensory areas SI and SII. High-resolution fMRI has since been used to demonstrate that spatial attention towards individual fingertips modulates activity somatotopically within the primary somatosensory area (SI; Puckett et al., 2017). Furthermore, when tactile stimulation is anticipated, cerebral blood flow (rCBR) in related areas is increased (Roland, 1981), and suppressed in areas where stimuli are not anticipated (Drevets et al., 1995), compared to rest state recordings.

While attentional modulation of haptic processing has been assessed behaviourally via discrimination and detection experiments, the effect of attention on haptic adaptation is unknown. A number of robust haptic aftereffects have been documented that parallel those found in vision (see Kappers & Bergmann Tiest, 2016, for an overview). Investigating the effect of attention on haptic adaptation could provide a useful way to index haptic processing, as has been in the case in vision. If attention affects haptic and visual processing in a similar way, then diverting attention away from a haptic adaptation stimulus would reduce the strength of the aftereffect. Alternatively, if haptic adaptation is unaffected by attentional manipulations, this would suggest that attention may function differently across modalities.

4.3.3 Multisensory Processing and Attention

There is some evidence that attention can be directed to one modality at the expense of others: Target detection is slower when the target is not in the expected modality (audition / vision / touch), with a greater cost of shifting attention from or towards touch (Spence et al., 2001). Neurophysiological research has demonstrated a neuronal effect of switching between tactile and visual tasks in the somatosensory cortex. In monkeys, attending to tactile stimuli resulted in increased neuronal responses in both SI and SII compared to attending visual stimuli (Hsiao et al., 1993). Further, a suppressive effect of attention was shown in a number of SII neurons, with decreased impulse rates when attention was focused on the tactile stimulus. Using MEG in human participants, attention has similarly been found to enhance SII activity when attending a tactile task compared to passively viewing a video (Mima et al., 1998), however SI responses were not affected.

While this evidence suggests a processing and performance cost for tasks in an unattended modality, cross-modal attention may have some benefits. We receive important information from each of our senses, leading to integration or recalibration of sensory cues. Attention must be coordinated across the senses to aid our understanding of the world and guide action. Research has shown that a valid cue on one side of the body facilitates detection of a target on the cued side in a different modality (Butter et al., 1989; Driver & Spence, 1998; Gray et al., 2009; Spence et al., 1998, 2000). Further, a visual cue is able to orient tactile spatial attention, as outlined above (Chica et al., 2007; Forster & Eimer, 2005; Posner et al., 1978), and vice versa (Gray & Tan, 2002). MEG evidence has further shown that SII responses to tactile stimulation are enhanced by spatial attention at the stimulated location, regardless of the attended sensory modality (Kida et al., 2007).

It is well established that attentional resources are limited, however it is unclear whether these resources are independent of modality. Investigations of the neural basis of spatial attention have provided conflicting findings, with neuroimaging evidence suggesting that spatial attention is supramodal (Eimer & van Velzen, 2002; Macaluso et al., 2002) while TMS evidence has suggested that attention is modality-specific (Chambers et al., 2004). Spence et al. (2000) investigated the links between tactile and visual endogenous spatial attention in a series of behavioural experiments. Attention within both modalities was shifted towards the likely location of the more common target modality, even though the less common target modality was more likely to occur on the opposite side. While these findings suggest that attention is not independent of modality, attention is not completely shared across modality either as spatial effects were stronger for the more common target modality. Mengotti et al. (2018) confirmed these findings, altering the cue predictabilities for visual and tactile targets independently and fitting models to their data. They found that the modality-specific cue predictabilities were averaged (i.e., attention across the senses was combined, as in Spence et al., 2000). However, weighting of the separate cue predictabilities became increasingly separated (indicating separate attentional resources for vision and touch) with increasing divergence between cue predictabilities, i.e., the cue for one modality is much more likely to be correct compared to the cue for the other modality, and with higher cue predictability values for the target modality. This research suggests that while attention is linked across modalities, it is also flexible and separable under certain circumstances. The current experiments will extend these findings by investigating how attention within and across modalities affects haptic adaptation, to gain further insight into the mechanisms of attention in the haptic domain.

In parallel to the work done in vision with the MAE, we probe the effects of attention on haptic perception using a well-documented haptic after-effect: the haptic curvature aftereffect (CAE). First documented in 1933 (Gibson, 1933), haptic adaptation to a curved surface produces robust aftereffects, with aftereffects apparent following very brief adaptation (Vogels et al., 1996), and following both active exploration of curved surfaces and passive exposure to curvature with a static finger (van der Horst, Duijndam, et al., 2008).

In the current studies, observers actively adapted to a curved, virtual surface, presented via a PHANToM force-feedback device. The *haptic attention* condition investigated the effects of a within-modality manipulation: adaptation in an attention focused condition was compared to adaptation in a *haptic* attention diverted condition, where participants were required to monitor a spatially distinct haptic stimulus. The *visual attention* condition compared the same attention focused condition to a *visual* attention diverted condition in which participants were required to attend to a visual stimulus. Attention was oriented via visually presented instructions, and feedback was given as an auditory tone following incorrect responses, in order to maintain attention to the relevant task.

4.4 Methods

Participants adapted to a curved, virtual surface that was explored with one finger of their dominant hand. During adaptation, attention was either focused on the curved adaptation surface or diverted away from the stimulus, either towards a visually presented stream of letters (*visual attention* condition) or a stream of vibrations presented to the wrist of the non-dominant hand (*haptic attention* condition). We expected a smaller aftereffect when attention was diverted from the adapting stimulus. Such a reduction in the *haptic attention* condition would support psychophysical and neurological evidence for tactile spatial attention, and be consistent with previous attentional findings in the visual modality (Bartlett et al., 2019), suggesting that attention operates in a similar way across the two modalities. Further, if diverting *visual* attention reduces the magnitude of haptic adaptation, this would suggest that attention is a single resource shared across modalities.

4.4.1 Stimuli and Tasks

The experimental set-up is shown in Figure 4.1a. The haptic stimuli were curved surfaces created in Blender (Blender Foundation, https://www.blender.org/about/) and presented via a PHANToM force-feedback device (3D Systems Inc.). Although the curved adaptation surface (dashed lines, Figure 4.2a and 4.2b) and subsequent test stimuli were presented only within the haptic domain, the ground plane and initial position of the finger were visible, enabling the participant to locate the haptic stimuli at the start of each adaptation / test period. Visual stimuli were presented on a 20-in CRT monitor (with a resolution of 1,280 x 1,024 pixels) and viewed binocularly via a mirror, with a viewing distance of 56 cm, fixed with a chinrest. This mirror set-up allows the visual and haptic stimuli to be perceptually collocated. A vibrating plate was attached to the back of the participant's nondominant wrist with a strap. This device was controlled via an Arduino (Arduino, S.R.L.). The experiment was run using Unity (Unity Technologies, San Francisco, USA).

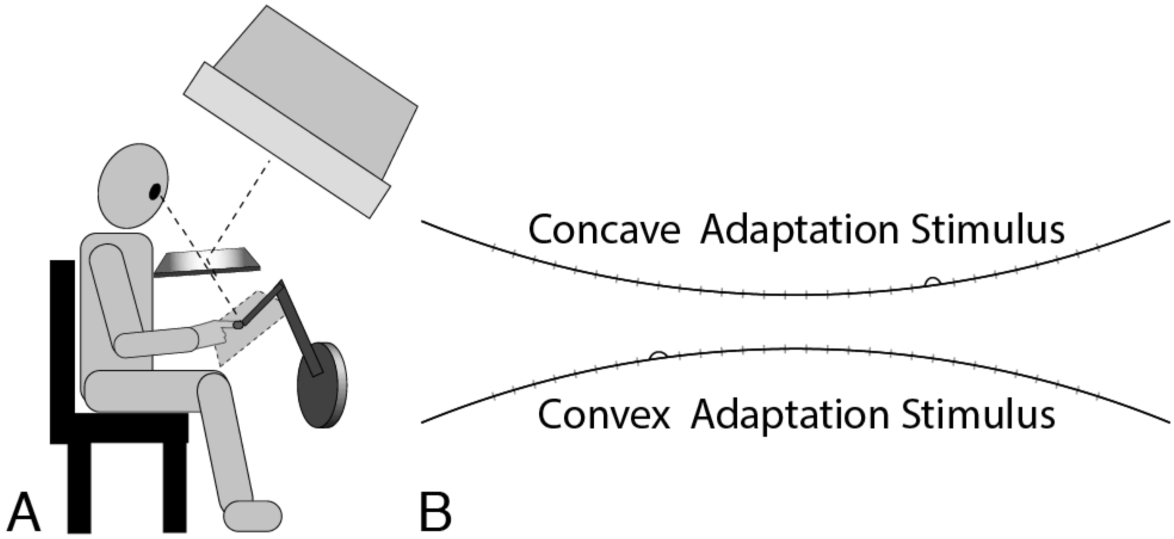

Figure 4.1 a) Experimental setup of the PHANToM force-feedback device. Participants were connected to the PHANToM device by placing a finger into a thimble. b) Representation of the convex and concave adaptation stimuli with vertical lines indicating possible locations of haptic ‘bumps’ that were detected in the attention focused condition. For each adaptation stimulus, one example bump is shown. To manipulate task difficulty, bump height was varied across trials (18 possible values). Central curser start position was the same for both adaptation curvatures.

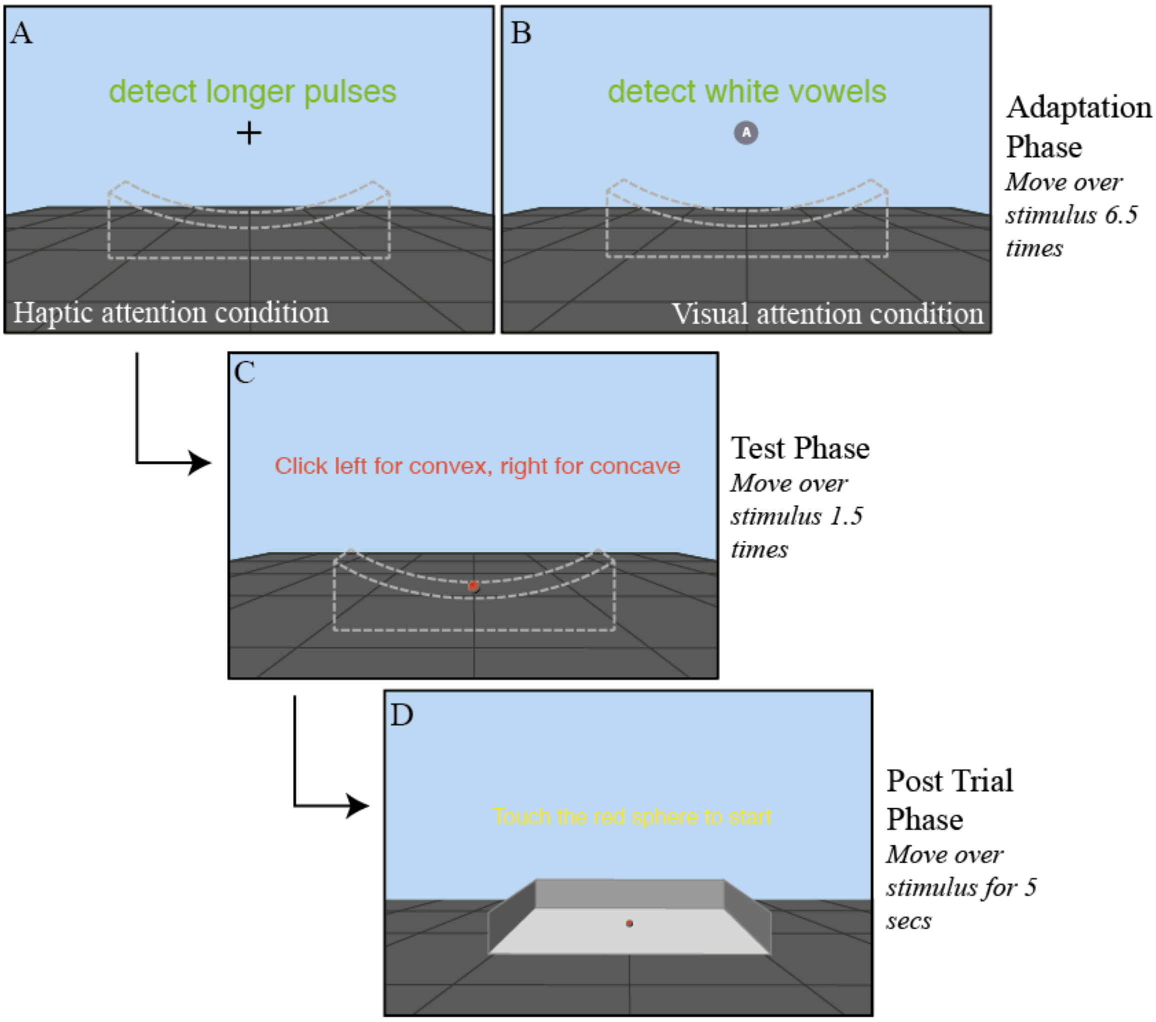

Figure 4.2 Schematic of a single trial. Participants moved their finger along the length of the adaptation stimulus 6.5 times, while attending the curved stimulus or either a series of vibrating pulses (a, *haptic attention* condition) or a visual stream of letters (b, *visual attention* condition). The test stimulus was then presented (c) and a 2AFC response was required (convex or concave), followed by 5 s of motion over a flat surface (d). Dashed lines are illustrative of the locations of haptically explored curved stimuli. All stimuli were presented in colour.

To ensure correct calibration of the PHANToM device between phases, participants were required to push through a visually and haptically presented cube (1.91° wide) at the centre of the display between each phase of the experiment (i.e., between adaptation and test, between test and post-test phases, and between trials). While pushing through the cube stimulus may affect the CAE (e.g., Vogels, Kappers, & Koenderink, 1997), any effects were minimal as this action was brief and required little force, and would be constant across attention conditions. Participants were guided visually towards the adaptation, test and post-test stimuli by the presence of a red sphere, positioned on the surface of the object. This sphere was removed upon contact, and haptic movement was constrained to the stimulus surface. A yellow sphere (0.51° in diameter) indicated the location of the fingertip in the virtual space. This cursor was removed upon contact with the red sphere (of the same size as the yellow sphere) on either the adaptation or test stimulus, and was visible again once the curved stimulus was removed. For the *haptic attention* condition, only these guiding squares and spheres, task instructions and information regarding invalid trials, and the post-trial stimulus were visible; adaptation and test stimuli were presented only haptically. A visual stream of light and dark letters was presented above the curved stimulus (see Figure 4.2) only for the *visual attention* condition.

Haptic adaptation stimuli were 20mm in width and 200mm in length, with a curvature of either -3.8m^{-1} or 3.8m^{-1}. Movement speed over the curved surface was guided by an audible metronome every 1.75 s, indicating when the stimulus edge should be reached. Small bumps were added within the central 80% (160mm) of the adaptation stimuli, at random times during adaptation. These bumps were ellipses that originated under the stimulus surface, offset by their circular radius (3mm) halved, and were oriented to the curvature of the surface (the 30 possible bump positions are shown in Figure 4.1b). The circumference of the ellipse bumps remained constant, but detection difficulty was altered by adjusting the ratio of major to minor axes. Task difficulty ranged between the most ‘squashed’ bump (i.e., the hardest to detect; 6mm in height and 6mm in width) and the most ‘peaked’ bump (elliptically elongated, i.e., the easiest to detect; 3.7mm in height and 2.3mm in width), in 18 steps. The first bump on each trial occurred 1 s after adaptation stimulus contact, with any value between 1.5 to 6 s between subsequent bumps. Bumps were removed from the surface within 0.5 s of contact with the bump.

We used an odd-one-out paradigm to divert haptic attention from the adaptation stimulus (Mima et al., 1998; Sterr et al., 2007). During adaptation, vibration pulses (frequency = 150Hz, vibration force = 0.5G) were presented to the back of the nondominant wrist, with a 0.5 s interval between presentations. The ‘standard’ vibrating pulse lasted 0.25 s, while the duration of the longer, odd-one-out target pulses was selected from the range 0.275 s (hardest to detect) to 0.8 s (easiest to detect) in 22 steps of 0.025 s.

In the *visual attention* condition, attention was diverted from the adaptation stimulus towards a visually presented stream of letters (each letter 0.73° in height). To alter task difficulty, the presentation speed of letters ranged between 0.1 s (hardest to detect) to 1 s (easiest to detect), in steps of 0.5 s.

During adaptation, *attention focused* trials required participants to detect and report haptic bumps on the adaptation surface, while *attention diverted* trials required detection of either longer vibrating pulses (*haptic attention* condition), or white vowels within the letter stream *(visual attention* condition), within 1 s of occurrence, using the left mouse button with their non-dominant hand. A tone provided feedback following missed targets or false alarms. Percentage correct was computed for each trial and incorporated into an overall percentage correct value for each attentional task. The shape of the haptic bumps, duration of target vibration pulses and letter presentation duration were adaptively controlled trial-by-trial via a one-up-one-down algorithm to maintain an overall average performance of 75% correct. Task instructions “detect bumps”, “detect longer pulses”, or “detect white vowels” were visually displayed prior to and during each trial.

Test stimuli matched the adaptation stimuli in width and length and ranged in curvature from -1.8m^{-1} to 1.8m^{-1} in steps of 0.4m^{-1}, creating 10 possible test stimuli. Participants made two-alternative-forced-choice (2AFC) convex or concave curvature judgements using mouse buttons. A flat surface was then presented both visually and haptically.

Trials were classed as invalid and repeated if participants moved their finger across the object either too slowly (> 18 s) or too quickly (< 7 s) during adaptation, or if the interval between adaptation and test exceeded 5 s. Text was displayed to inform the participant (e.g., “Task completed too slowly / quickly”, or “Please move faster between trials”). Invalid trials were only repeated once and not replaced, such that the participant would move onto the next trial if the repeated trial was also invalid.

4.4.2 Procedure

The *haptic attention* and *visual attention* conditions were run separately, with identical procedures. Each trial began with an adaptation period, during which participants had to engage in an attentional task whilst haptically exploring either a concave or convex surface (see Figure 4.2 trial schematic). Participants moved their finger over the curved stimulus, starting at the centre, for a total of 6.5 side-to-side movements. Participants then made 1.5 traversals across the subsequently presented test stimulus, after which the stimulus was removed, and a convex/concave response was required. After responding, participants were required to move their finger over a flat stimulus for 5 s, to minimise any carry over of adaptation to the next trial.

Participants first completed 10 blocks (10 test stimuli x 10 repetitions) of baseline trials (test and post-test stimuli only, without adaptation) to determine their pre-adaptation curvature perception. This allowed the range of test stimuli to be adjusted according to each participants’ perceived flatness. Feedback as to the true curvature of the test stimuli was not given at any point in the experiment. Participants then proceeded with 20 practice trials, 10 for each attention condition, to establish initial stimulus levels for each attention task – i.e., bump shape and either target vibration duration or letter presentation duration. Practice trials were identical to adaptation trials within the main experiment, and therefore allowed participants to get a feel for the speed they should move over the haptic stimulus, and to get comfortable with the experimental tasks.

For both the *haptic attention* and *visual attention* conditions, the main experiment consisted of 480 trials (2 attention conditions x 2 adaptation curvatures x 10 test curvatures x 12 repetitions). Each block consisted of 20 trials, featuring every combination of adaptation and test curvature for one attention task with random ordering of test curvature. Adaptation curvature was alternated between trials to reduce adaptation carry-over. Participants were invited to take a break between each block and advised that any other breaks should be taken before beginning a new trial. Each experimental condition was completed in a quiet room and lasted approximately 5 hr, spread over different days.

4.4.3 Participants

As the effect of attention on haptic adaptation has not previously been examined, appropriate sample size was determined from our meta-analysis of attentional modulation of the visual motion aftereffect (Bartlett et al., 2019). This reported an attentional effect size of 1.12, pooled over 76 effects. Using G*Power (Faul et al., 2007), a power analysis for two-tailed within-sample t-tests were conducted using an alpha of 0.05 and power of 0.80. This revealed a *minimum* sample size of 9 participants for each experimental condition. Across conditions, three participants' data were removed due to an aftereffect opposite to that expected, leaving a total of eleven participants (aged 18 – 28 years) in the *haptic attention* condition, and eleven participants (aged 19 – 30 years) who completed the *visual attention* condition. Four participants completed both conditions, one of whom was an author (LB). All other naïve participants were recruited through opportunity sampling from the University of Southampton. All participants had corrected to normal or normal vision. Ethical approval was granted by the University of Southampton. All participants gave informed consent before commencing the study and were debriefed following study completion.

4.5 Results

Data for individual participants are summarised in Figure 4.3, with group data shown in Figure 4.4 (*haptic attention* condition) and Figure 4.5 (*visual attention* condition). In total for the *haptic attention* condition, 7 trials were invalid (i.e. they remained invalid after repeating them once and were removed from the analysis), with 118 trials repeated. For the *visual attention* condition, 6 trials were invalid in total, with 112 trials repeated. As outlined in Section 4.4.1, task difficulty was adjusted to maintain a performance at 75% correct for both the haptic condition (focused attention: M = 10.49, SD = 2.70; diverted attention: M = 0.46 s, SD = 0.11) and for the visual condition (focused attention: M = 12.18, SD = 3.19; diverted attention: M = 0.13 s, SD = 0.05).

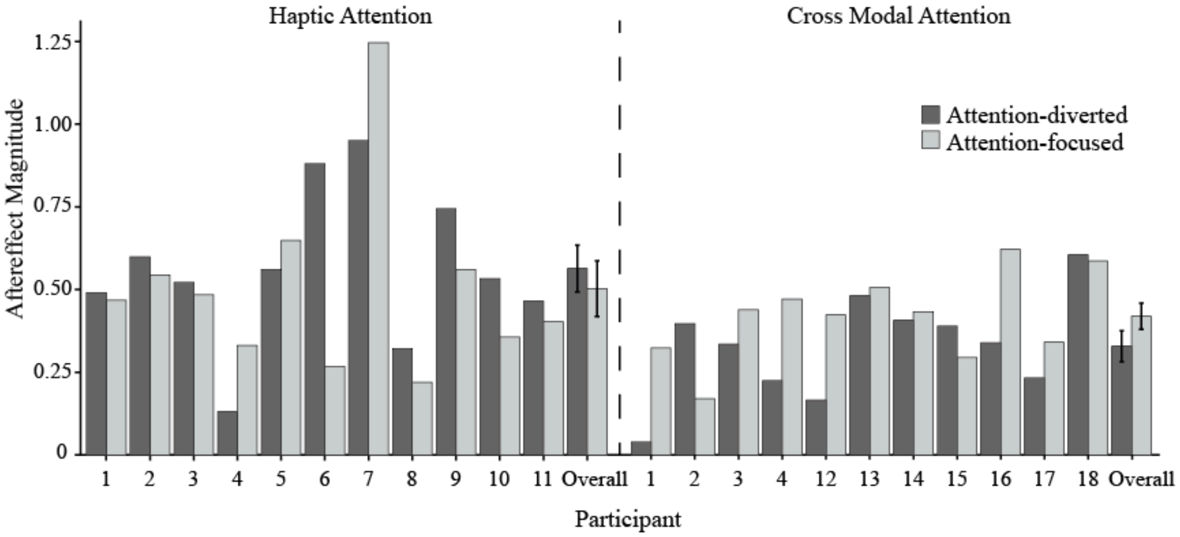

Figure 4.3. The magnitude of the haptic curvature aftereffect for each participant, and the averaged overall data, for each attention condition and attention manipulation. Aftereffect magnitude is defined as concave PSE subtracted from convex PSE. Error bars indicate ±1SE.

Separately for each attention condition, participant and attentional manipulation, the stimulus curvature that was perceived to be flat was estimated by fitting a cumulative Gaussian to their curvature responses and extracting the 50% threshold (equal probability of convex and concave responses). Aftereffect magnitude was quantified by comparing this threshold following adaptation to convex vs. concave stimuli. Model fitting was conducted using *fminsearch* in MATLAB version 2015b (MathWorks), to determine values for key parameters (mean, standard deviation, lapse rate) that maximised the likelihood of the participant's data. Data corresponding to the two adaptation curvatures were fit with a common lapse rate, but independent mean and standard deviation parameters, separately for each attention condition (haptic and visual) and manipulation (focused and diverted). Fitting was repeated 1,000 times with randomly selected initial parameter estimates, to avoid local minima.

For the within-modality *haptic attention* condition, a significant CAE was evident for both attention-focused ($t(10) = 5.98$, $p < .001$) and attention-diverted ($t(10) = 7.98$, $p < .001$) conditions, as indicated by one-sample t-tests against zero. However, the magnitude of this CAE was similar for the two attention manipulations (attention diverted: $M = 0.56$, $SD = 0.23$; attention focused: $M = 0.50$, $SD = 0.28$) with no significant difference between the two ($t(19.43) = -0.55$, $p = 0.587$, $d = -0.24$). This was also the case for the cross-modality *visual attention* condition, with significant CAEs for both attention focused adaptation, $t(10) = 10.59$, $p <.001$, and attention diverted adaptation, $t(10) = 6.97$, $p < .001$), and no significant difference in magnitude between the two, $t(10) = 1.78$, $p = .105$, $d = 0.63$ (attention diverted: $M = 0.33$, $SD = 0.16$; attention focused: $M = 0.42$, $SD = 0.13$).

These observations are confirmed by considering the pooled data for each attention condition separately (*haptic attention*: Figure 4.4, *visual attention*: Figure 4.5). Confidence limits for the fitted thresholds were derived via bootstrapping: data were resampled, with replacement, for each observer, before pooling the data and fitting cumulative Gaussians. This was repeated for 1,000 bootstrapped samples, and each sample was fit with 20 different initial parameters, to avoid local minima.

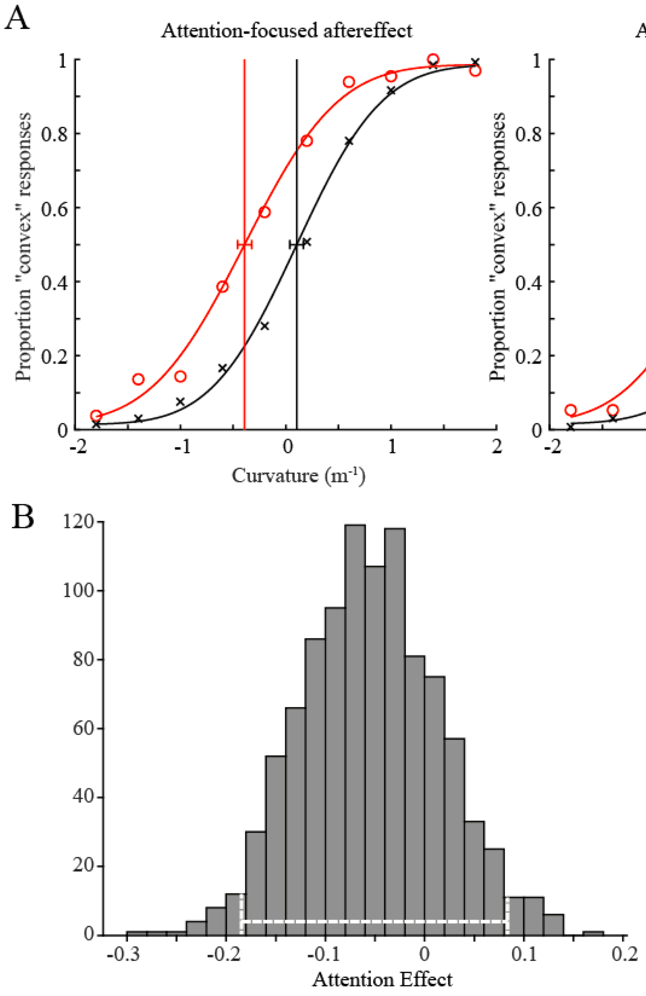

Figure 4.4 Data pooled across participants for the *haptic attention* condition. a) Cumulative gaussian fits for each adaptation and attention condition. Threshold values (PSEs) are indicated by vertical lines, with 95% CI for these thresholds shown by the horizontal error bars. b) Magnitude of the attention effect (attention diverted aftereffect subtracted from attention focused aftereffect) for each bootstrapped sample. Dashed line indicates the 95% CI.

For the *haptic attention* condition, within each of the attention manipulations, the test stimulus that appeared flat was significantly different following adaptation to convex vs. concave surfaces (see 95% CI from bootstrapping: Figure 4.4a). However, this adaptation did not significantly differ between attention manipulations: for each bootstrapped sample, the magnitude of the CAE was compared for attention-diverted vs. attention-focused conditions, with the distribution of this difference, i.e., the ‘attentional effect’ shown in Figure 4.4b. As can be seen, this attention effect is not significantly different from zero, and has a negative mean, indicating that adaptation was actually slightly greater in the attention diverted condition than in the attention focused condition, counter to expectation.

A similar pattern emerged for the *visual attention* condition. Within each attention manipulation, the test stimulus perceived as flat significantly differed between adaptation curvatures (see 95% CI derived from bootstrapping: Figure 4.5a). The CAE magnitude, however, did not significantly differ according to attention manipulation. Distribution of the bootstrapped ‘attentional effect’ is shown in Figure 4.5b, where it can be seen that the attention effect is not significantly different from zero. The positive mean indicates slightly greater CAEs when attention was focused on the adaptation stimulus than when diverted to a visual task, in line with predictions, but this did not reach significance.

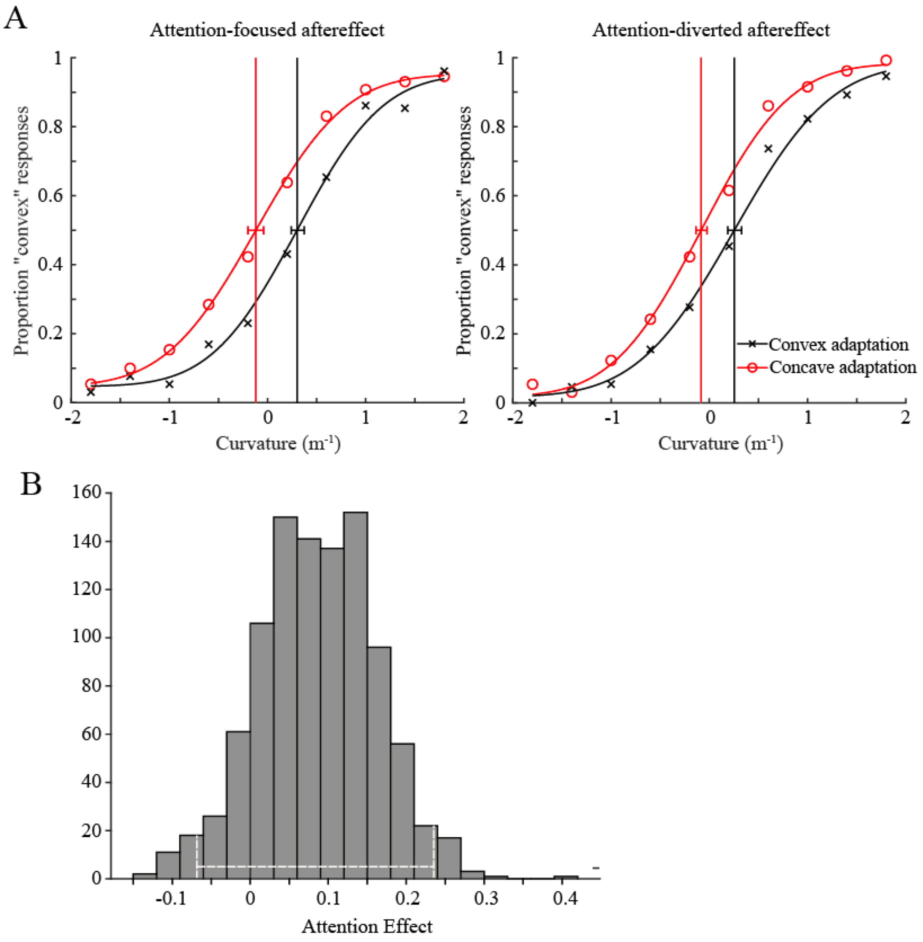

Figure 4.5 Data pooled across participants for the *visual attention* condition. a) Cumulative gaussian fits for each adaptation and attention condition. Threshold values (PSEs) are indicated by vertical lines, with 95% CI for these thresholds shown by the horizontal error bars. b) Magnitude of the attention effect (attention-diverted aftereffect subtracted from attention-focused aftereffect) for each bootstrapped sample. Dashed line indicates the 95% CI.

A between subjects t-test revealed a nonsignificant difference in the attention effect between *haptic* (M = -0.06, SD = 0.24) and *visual* (M = 0.09, SD = 0.17) attention conditions, t(18.11) = -1.73, p = .100, d = -0.75.

4.6 Discussion

A novel behavioural investigation into the modulatory role of attention on haptic adaptation was conducted. Attention was not found to significantly modulate the CAE: aftereffect magnitude was equivalent for diverted and focused attention conditions. This suggests that processing of haptic curvature may be independent of attentional manipulation and occurs at a low-level pre-attentive stage, conflicting with literature showing that basic haptic features are modulated by attention. This was the case regardless of distracting task modality (visual or haptic). However, the complexities shown in the attention / adaptation relationship within vision might guide interpretation of these findings.

The effect of attention on adaptation has been demonstrated for a number of visual aftereffects (e.g., the MAE, the tilt aftereffect). However, an adaptation design has not previously been used to investigate haptic attention. Based on behavioural (e.g., Metzger et al., 2019; Schweisfurth et al., 2014; Sinclair et al., 2000) and neurological (e.g., Puckett et al., 2017; Schubert et al., 2008) evidence, we predicted that attention would affect haptic adaptation in a similar way to visual adaptation. Our findings contradict this hypothesis: the haptic CAE was unaffected by both tactile and visual attention.

Physical objects are commonly used in CAE research (e.g., van der Horst, Duijndam, et al., 2008; van der Horst, Willebrands, et al., 2008; Vogels et al., 1996), whereas a virtual surface was used for adaptation in the current research. This may have influenced both the magnitude of adaptation and the possible influence of attention. Denisova, Kibbe, Cholewiak and Kim (2014) previously demonstrated that the CAE could be generated via a PHANToM stylus, using stimuli modelled on the real stimuli, with direct contact, used by van der Horst, Willebrands, et al. (2008). The use of a stylus held like a pen in the work of Denisova et al. (2014) engaged a number of fingers, whereas our experiments involved moving a single finger over the virtual surface. As the importance of hand posture has been shown for haptic slant adaptation (van Dam et al., 2016), adaptation differences between the experiments may be driven by more consistent hand posture when using a stylus. Despite these differences, clear CAEs were generated for all experiments in the current study, suggesting a strong role of proprioception over cutaneous factors. Our aftereffect magnitude and variability paralleled those generated with real objects (van der Horst, Willebrands, et al., 2008, with equivalent stimuli and experimental design), while Denisova et al. (2014) found stronger aftereffects and more variability using a phantom stylus (with slightly less curved adaptation and test stimuli). These findings suggest that curvature adaptation is not, in general, weaker for real than virtual presentation via a stylus / rigid thimble.

We aimed to contribute to the ongoing debate as to whether attention is a modality-specific resource, or one that extends across modalities, and establish the role of cross-modal attention in haptic perception. We found comparable CAEs whether attention was focused on the curved adaptation stimulus or diverted towards a visual task, suggesting that attention is modality-specific. However, the CAE was also unaffected by haptic attention. It could be the case that haptic curvature is processed at a pre-attentive stage. However, as this was the first investigation of its kind, the methodology may have affected this relationship. As has been shown for vision, the relationship between adaptation and attention may be affected by a number of factors. For example, the duration of adaptation and test exposure, size of the adaptation and test stimuli and the degree of adaptation curvature could all impact the attention-CAE relationship.

To allow conclusions regarding the influence of attention, it is essential that the attention manipulation is effective. Diverted and focused task performance was monitored throughout, and feedback was given following incorrect responses to sustain participants' attention. We also compared diverted attention to an attention focused condition rather than passive adaptation, where it is unclear what participants are attending to (Huk & Heeger, 2000). However, the additional attentional demands of the experimental paradigm may have limited the effects of our attentional manipulation. To guide motion during adaptation, an audible metronome indicated when participants should reach the edge of the stimulus. Attending to this, as well as actively moving the finger across the adapting surface, may have added to the attentional demands. Attention research has typically found that valid cues (i.e., those correctly predicting the target feature or location) result in faster RT's and improved accuracy when compared to neutral targets, where attention is presumably divided between features (Burton et al., 1999) and locations (Posner et al., 1978). Consequently, minimising additional demands may improve participants' focus towards the attentional tasks. Future research could present the adaptation stimuli passively, moving a curved stimulus under a stationary finger. This would reduce task irrelevant attentional demands, while maintaining a similar CAE magnitude: following passive adaptation, active test exploration has been shown to result in CAEs equal in magnitude to conditions where adapt and test are both actively explored (van der Horst, Willebrands, et al., 2008).

Previous cueing studies have demonstrated that task irrelevant, nonpredictive cues focus spatial attention on the cued location (e.g., Spence & McGlone, 2001). As such, it is possible that the vibrating stimulus in the *haptic attention* condition captured attention regardless of task, reducing attentional differences between the conditions. To investigate this, we compared the average task difficulty for the focused attention task (i.e., attending the adaptation stimulus) across the two experiments – the curvature focused task should be harder for participants in the *haptic attention* than *visual attention* condition if attention is distracted by the vibrations. Excluding those who participated in both experiments (to avoid order effects), focused task difficulty did not significantly differ between experiments, $t(11.73) = -1.48$, $p = .165$. It is therefore unlikely that task-irrelevant vibration captured attention, at least over and above the attention captured by the visual letter stream in the *visual attention* condition.

It is possible that attention exerts an influence on the accumulation of adaptation, rather than the asymptote. Movement across the adaptation surface was guided by a metronome so that adaptation would last 11.38 s; (*haptic attention* condition: $M = 11.14$ s, $SD = 0.98$; *visual attention* condition: $M = 11.02$ s, $SD = 0.95$). Previous research has shown that the CAE can be reliably measured following a very brief exposure to curved stimuli, and that the effect increases with adaptation duration, saturating after a few seconds (Vogels et al., 1996). Therefore, the current experiments likely measured the saturated CAE, which may have masked attentional modulation if accumulation rather than asymptotic CAE is affected by attention. Though, key differences between previous studies and our own (e.g., adaptation of a static, entire hand on a real object: Vogels et al., 1996) might give rise to different saturation points. Future research could investigate this, along with the relationship between curvature adaptation duration and attention.

Test duration differs across the literature. Vogels et al. (1996), Vogels, Kappers and Koenderink (1997, 2001) and van der Horst, Duijndam, et al. (2008) did not control for test exposure duration, rather a convex/concave response was given once a decision was made. Conversely, van der Horst, Willebrands, et al. (2008), Denisova et al. (2014), and the current experiments required at least one traversal of the test stimulus before a response was given. A longer test duration might increase variability in responses: if the CAE decays during test stimulus presentation, participants will have to decide whether their response reflects initial felt curvature (maximum CAE) or final curvature (once the CAE has started to decay). Adaptation to the test stimulus will further impact reported curvature. However, movement over the test surface was necessary to determine curvature in the current experiments, as cutaneous tactile cues were not available. Importantly, there would be no reason for participants to alter their response criterion between attention and adaptation conditions – if there is any effect of test duration on the CAE this should be equivalent across the experimental conditions. Finally, Vogels et al. (1997) found that statically touching a test stimulus, and taking more time to dynamically move over a test stimulus, resulted in CAEs of equivalent magnitude, suggesting that small variations in test duration do not substantially impact the CAE.

The current study was a novel investigation into the effects of attention on haptic adaptation, extending the existing literature regarding tactile attention and providing insight into the similarities and differences between haptic and visual adaptation. Haptic curvature adaptation was unaffected by either tactile or visual attention, suggesting that the CAE may occur independently of attention, though experimental characteristics may account for this null effect. This experiment provides a solid starting point for further investigations, which are needed to better understand the factors that may influence the interplay between haptic adaptation and attention.

Chapter 5 General Discussion

5.1 Research Motivation and Aims

The three previous chapters aimed to elucidate the effect of attention on sensory adaptation, in order to further our understanding of attentional mechanisms within both visual and haptic processing (see Table 5.1. for a detailed summary of research aims, hypotheses and findings).

Due to the wealth of sensory information available in the world and the limited capacity of human perceptual processing, attention is an efficient mechanism to selectively process relevant details at the expense of irrelevant information (Carrasco, 2011). Adaptation is an additional tool for efficient processing, given the narrow dynamic range of neurons. Following adaptation, strong perceptual aftereffects can be measured behaviourally. As such, adaptation has been utilised to understand how a multitude of features, such as tilt, motion and colour, are processed, as well as the effects of attention on this processing. Understanding both adaptation and attention mechanisms is vital for understanding how the sensory system works, as they are integral to human perception.

Chapter 1 reviewed the existing literature on attention and sensory adaptation within the visual and haptic modalities, identifying a number of weaknesses and gaps in current knowledge. Despite an extensive amount of research on the effect of attention on motion adaptation, inconsistent findings and weaknesses in experimental design complicate the conclusions that could be drawn from the literature. While the weight of evidence across a number of paradigms and numerous studies suggests that motion adaptation is affected by attention, a series of experiments were unable to find evidence of an effect (Morgan, 2011, 2012, 2013). *Chapters 2 & 3* address a key criticism of the MAE-attention literature drawn from these null findings: that previous positive findings can be attributed to response bias caused by inappropriate experimental designs (Morgan, 2011, 2012, 2013). Given the uncertainty about why some studies found the effect and others did not, minimising the influence of response bias is fundamental. To address this criticism, attentional modulation of the MAE was assessed using a modified version of Morgan's (2013) experimental design, where an influence of response bias was extremely unlikely due to experimental complexity (*Chapter 2*). Additionally, the meta-analysis reported in *Chapter 3* allowed a rigorous exploration of the influence of response bias across the literature. This was achieved by comparing the magnitude of the attention effect for measurement paradigms allowing more (i.e., MAE duration) or less (i.e., 2AFC paradigms) response bias. If bias was driving the effect, attentional modulation would be considerably reduced in bias-minimising paradigms. Participant naivety was also explored, comparing naïve and non-naïve participant populations experimentally in *Chapter 2* and via meta-analysis in *Chapter 3* – bias should be less of an issue for naïve participants, due to reduced understanding of the research goals.

Table 5.1 Summary of research aims, hypotheses and findings.

Research aims	Hypotheses	Findings
To determine whether attention modulates the MAE and explore the factors that affect the attention-MAE relationship.	Based on previous research it was predicted that attention would affect the MAE.	We found strong attentional modulation of the MAE, both psychophysically and via meta-analysis.
	Stronger attentional modulation was predicted for translating, compared to complex, motion adaptation.	In agreement with predictions, psychophysical results suggested that attentional modulation was strongest for simple translational motion adaptation. The meta-analysis further confirmed this, where attention effects for simple motion were approximately double those of complex motion.
	Motion adaptation duration was predicted to affect the strength of attentional modulation.	Adaptation duration did not affect the MAE attention relationship, either psychophysically or via meta-analysis.
	It was predicted that response bias would not account for positive findings in existing literature.	We found no evidence that response bias was driving the MAE-attention effect: strong modulation was still evident when bias-reducing paradigms were employed and when participants were naïve to researcher aims.
To investigate the effect of haptic attention on the CAE.	It was predicted that attention would affect the CAE in a similar way to the visual MAE.	The psychophysical investigation did not find any evidence for attentional modulation of haptic curvature adaptation.
To investigate the effect of visual attention on the CAE.	Visual attention was predicted to affect the CAE.	Evidence for cross-modal attentional modulation of the haptic CAE was not found.

An additional criticism of the MAE-attention literature is that experimental techniques differ considerably between studies, often without systematic investigation of the effect on results. For example, the complexity of motion during adaptation and test phases varies across studies, even though simple (translating) and complex (e.g., rotating, expanding) motion have distinct patterns of activation in the brain (Smith et al., 2006). The time scale for attentional modulation of the MAE was also previously unexplored. At what stage attention affects the MAE was identified as a potential factor driving disparities in the literature, determining whether attention affects the build-up of the MAE or the point at which it saturates. Null findings often result from paradigms with long adaptation periods (Morgan, 2012) or uncontrolled adaptation accumulation over trials (Morgan, 2013), and as such potentially only measure the effect of attention at maximum (asymptotic) MAE levels.

The psychophysics studies detailed in *Chapter 2* addressed these two potential moderating factors of the MAE-attention relationship, assessing attentional modulation as adaptation accumulates over trials and comparing simple and complex motion adaptation. For a more complete picture of attentional modulation of the MAE, the meta-analysis reported in *Chapter 3* allowed a comprehensive consideration of the literature as a whole. This was the first systematic statistical review of published MAE-attention research and allowed the investigation of numerous factors that vary across empirical experiments. It confirmed the effects of motion type and adaptation duration detailed in *Chapter 2*, and additionally explored the effects of attentional manipulation, the size, eccentricity and speed of adaptation stimuli, and compared static and dynamic test stimuli.

While the focus of perceptual research often centres around vision, it is important to consider the role of attention within and across different modalities. A number of behavioural experiments assessing detection and discrimination accuracy as well as RTs have shown that attention affects haptic processing (as detailed in *Chapter 1*). Even though numerous robust haptic aftereffects have been reported akin to vision (i.e., adaptation results in an opposite perception of the adapted feature), adaptation has not previously been used to probe the effect of attention on haptic processing. Given the parallels between adaptation in vision and haptics, the aftereffect paradigm would provide considerable insight into haptic attention. *Chapter 4* reports the first experiment to explore the influence of both haptic and visual attention on haptic curvature adaptation. This allowed a comparison between vision and haptics regarding the extent that within-modality attention modulates adaptation. Additionally, this paradigm allowed an exploration of cross-modal attention on haptic adaptation. Determining the influence of visual attention on the CAE contributes to the debate outlined in *Chapter 1* regarding attention as a single or shared resource across modalities.

5.2 Key Findings

5.2.1 Attention modulates visual motion adaptation.

A series of experiments (*Chapter 2*) and a comprehensive quantitative analysis of relevant published research (*Chapter 3*) provide powerful evidence that attention modulates the MAE.

The psychophysics studies detailed in *Chapter 2* reveal a significant effect of attention on the MAE, finding larger MAEs when attention was focused on a motion stimulus than diverted to a centrally presented stream of letters. The magnitude of motion adaptation was indexed in two ways: the degree that perceived test motion direction was biased from the objective motion direction (*Experiment 1*), and a relative speed judgement of test motion stimuli (*Experiment 2*). Significant attentional modulation was evident for both experimental paradigms, suggesting that it is a robust effect. This was further supported by the substantial effect of attention on the MAE found in the meta-analysis reported in *Chapter 3*, comprising of 76 effects across 37 independent samples.

A particular concern was the extent that evidence supporting attentional modulation of the MAE could be accounted for by response bias. Using a method that minimised bias (adapted from Morgan, 2013), a modulatory effect of attention on the MAE was found (*Chapter 2, Experiment 2*). In addition, the effect of attention persisted when only naïve participants were included in analyses across both experiments detailed in Chapter 2. The meta-analysis (*Chapter 3*) confirmed this: a strong attention effect was found for naïve participants and naivety was not a significant moderator. Though not significant, there was even a trend for stronger attentional modulation for naïve participants. Additionally, the meta-analysis revealed that response paradigms that are more susceptible to response bias (i.e., measuring MAE duration) report similar attentional modulation to those where bias is minimised (i.e., 2AFC).

Taken together, the evidence outlined in *Chapters 2 & 3* strongly indicates that attention modulates the MAE and that response bias is unlikely to account for this effect. This is consistent with previous research utilising different experimental paradigms. For example, attention has been shown to alter perceived motion direction (Kohler et al., 2008; Wertheimer, 1912/1961), control the integration of motion signals across space (Burr et al., 2009) and can drive the perception of motion altogether (Cavanagh, 1992; Lu & Sperling, 1995).

5.2.2 Attentional modulation of the MAE is affected by the characteristics of the adaptation stimuli.

To address inconsistencies in results across studies a number of potentially moderating factors were explored both psychophysically and via the meta-analysis. The influence of motion type and the effect of adaptation accumulation over a trial were investigated experimentally in *Chapter 2* and via the meta-analysis in *Chapter 3*. A number of additional factors were explored in the meta-analysis.

The type of motion stimuli used varies across studies, including both simple and complex motion patterns. Yet the effect of motion type has not previously been explicitly explored. While attention affected both simple and complex motion in *Chapters 2 & 3*, the magnitude of this effect was strongly influenced by motion type. In particular, attention affected adaptation substantially more when simple translational motion was adapted rather than complex motion patterns (i.e., rotation, expansion, contraction). This was a considerable effect when analysing the existing published MAE attention literature via meta-analysis.

As detailed in the critical review of the MAE-attention literature in *Chapter 3*, translating motion maximises the effects of both feature-based and spatial attention, while only object-based and spatial attention affects complex motion adaptation. As stronger modulation was found for translating motion, attentional modulation of the MAE is likely primarily driven by feature-based attention, with less influence from object-based attention. Additionally, as higher-level motion-related cortical regions (e.g., MST) are tuned to larger fields of complex motion (Smith et al., 2006; Tanaka et al., 1986) this finding suggests that attention affects low level primary areas (e.g., V1/MT) to a greater extent. The hierarchical nature of cortical processing has often demonstrated larger attentional affects with increasing processing levels (Liu et al., 2005); the research outlined in *Chapters 2 & 3* suggest this is not always the case for all stimulus features.

The meta-analysis reported in *Chapter 3* allowed a systematic investigation of the effect of various stimulus characteristics on the MAE-attention relationship. Both eccentricity (how far away the motion stimulus is from fixation) and spatial extent (size of the motion stimulus) affected attentional modulation. In particular when adaptation stimuli are presented further from fixation, attention has a greater effect. Additionally, as the size of an adaptation stimulus increases, attentional modulation decreases. The effects of attention may be reduced when stimuli are larger and closer to a central task as spatial attention may ‘spill over’ to the irrelevant peripheral motion.

A number of additional factors were found to *not* influence the MAE-attention relationship. For example, similar magnitudes of attentional modulation were found for both tracking and distractor paradigms (see Figure 3.1), despite suggestions that they tap into discrete mechanisms and that consistent effects are only found for tracking experiments (Morgan, 2011, 2012). As these experiments typically use translating motion, this may instead reflect stronger modulation for translating compared to complex motion. In addition, attention affected the absolute MAE, rather than the accumulation of adaptation. This revealed that adaptation accumulation could not account for inconsistencies in the literature. Following publication of the psychophysical experiment reported in *Chapter 2*, Morgan and Solomon (2018) sought to investigate how adaptation duration affects the MAE-attention relationship using a different experimental paradigm. They demonstrated evidence of adaptation accumulation (i.e., the MAE increases with adaptation duration), however attentional modulation was not found. It is worth noting, however, that the weight of evidence suggests that attention modulates the MAE, as outlined above, with most of the contrary findings coming from one group of researchers.

In sum, *Chapters 2 & 3* provide a more substantial characterisation of the influence of attention on motion adaptation than previously available. These findings should guide future research into attentional modulation of motion processing. The meta-analysis provides a succinct overview of the published literature; however, a number of potentially influential factors are yet to be explored. For example, future experiments could explore the effect of attentional tasks, as tasks vary considerably across the literature and could have a substantial impact on results and conclusions.

5.2.3 Attention and haptic curvature adaptation.

Despite commonalities between visual and haptic adaptation and attention, *Chapter 4* did not find an effect of attention on haptic curvature adaptation. In particular, aftereffect magnitude was equivalent whether attention was focused on the curved stimulus or diverted to a spatially separate haptic task. These findings could suggest that haptic curvature adaptation may be processed independently from attention, signalling differences between haptic and visual functioning, however experimental design likely influenced this result.

By investigating the influence of visual distraction during haptic adaptation, *Chapter 4* also extended and contributed to the cross-modal attention literature that has predominantly used cueing and neuroimaging methods. Diverting attention with a visual task, compared to focused attention on the curved adaptation stimulus, did not affect the magnitude of the CAE. However, this finding must be interpreted with caution as within-modality attention also did not affect the CAE.

These findings potentially suggest that haptic attention functions differently to visual attention. Indeed, some research has detailed differences between haptics and vision, for example Spence et al. (2001) found that switching attention from the tactile modality to another modality resulted in a greater cost than switching away from either vision or audition. Further, the processing time course of spatial attention may differ between vision and haptics (Schubert et al., 2008).

Alternatively, haptic curvature may be a low-level feature that is processed independently from attention. In other words, attention may modulate other tactile features, but not curvature processing. For example, previous haptic attention research has shown attentional modulation for roughness and stimulus size discrimination (Burton et al., 1999; Metzger et al., 2019; Sinclair et al., 2000). Future research could confirm these effects using an adaptation paradigm. However, the CAE has been shown to transfer across hands and fingers (van der Horst, Duijndam, et al., 2008; van der Horst, Willebrands, et al., 2008), implicating higher level bilateral neuronal involvement.

Additionally, even if curvature was processed at a lower level, the research discussed in *Chapter 1*, along with the MAE research outlined in *Chapters 2 & 3*, suggests that attention can certainly modulate low-level sensory regions. While haptic curvature perception may be ‘pre-attentive’, an alternative interpretation is that the CAE-attention relationship is affected by a number of factors, as was the case for the visual MAE.

The stimuli employed in the CAE experiment may have masked, or minimised, attentional effects. Previous research has shown that the CAE saturates following a few seconds of adaptation (Vogels et al., 1996), meaning the current experiment (with approximately 11 s of adaptation per trial) may have measured attentional modulation of the maximum CAE. While the rate of MAE accumulation was unaffected by attention (*Chapters 2 & 3*), exploration into the time course of attention for the CAE would provide further insight into the similarities and differences between visual and haptic adaptation. Similarly, the degree of adaptation curvature may have saturated the effect, as CAE magnitude increases with adapting curvature (Vogels et al., 1996). However, as the available CAE saturation information from the literature only concerns static adaptation, future investigation into dynamic CAE saturation could further inform the conclusions of *Chapter 4* and extend our understanding of proprioceptive contributions to the aftereffect.

As this was the first investigation into the effect of attention on haptic processing, features of the methodology may account for the null findings. For example, during adaptation a number of tasks may have been competing for participants’ attention: moving a finger over the adaptation stimulus, being mindful of the speed of this motion, and listening for various auditory tones (giving task feedback and guiding motion). Splitting attention across more than one task has been shown to reduce accuracy compared to focusing on one task (e.g., Burton et al., 1999; Wahn & König, 2015, 2016). Therefore, these additional tasks may have made the attentional tasks (i.e., detect vibrations / white vowels / bumps across the adaptation stimulus) harder and confounded the effect of attention by diverting both haptic and auditory attention. These additional demands were consistent across all conditions and may have masked or minimised the attention effect. Passive, rather than active adaptation (i.e., the finger remains stationary while the adaptation stimulus moves) could be used in future research to reduce these additional attentional demands.

Chapters 2 & 3 demonstrated that feature-based attention likely affects visual motion adaptation more substantially than spatial or object/surface-based attention. The same may be true for haptic adaptation. Rather than exploiting feature-based attentional mechanisms, the experiments of *Chapter 4* manipulated the spatial locus of attention (i.e., towards the adaptation stimulus, towards a vibrating motor on the opposite wrist, or towards a visual stream of letters positioned above the curved stimulus). Despite this, a wealth of research has shown a processing and behavioural effect of spatial attention on haptic perception. The results of *Chapter 4* reflect the first steps towards teasing out the conditions under which attention exerts an effect on haptic perception.

5.2.4 Implications for attention as a shared or separate resource.

Chapter 4 explored whether attention is a modality-specific or shared resource. However, as the CAE was unaffected by both visual and haptic attention, the conclusions that can be drawn are limited. While the literature regarding attention as a shared or separate resource across sensory modalities has predominantly focused on auditory and visual attention, some visual-haptic dual-task research has been conducted. Visual search task performance has been shown to be worse when a simultaneous localisation task was visual, rather than tactile (Wahn & König, 2016), suggesting that tactile distraction affects visual processing to a lesser extent than within-modality distraction. However, Wahn and König (2015) found task performance was worse when two tasks, rather than one, were engaged simultaneously, whether the tasks were both visual or visual and tactile.

The theory that attention is a separate resource is in line with a number of findings from visual MAE research. Rees et al. (2001) found equivalent MAE durations and similar amounts of activation in motion-related visual areas (revealed using PET) for high- and low-load *auditory* tasks, but significant reductions for high, compared to low, *visual* load. Similar effects have been found for auditory adaptation; for example, voice gender aftereffects are reduced when auditory attention is diverted, but unaffected by visual load (Zäske et al., 2013, 2016). Rees et al.'s (2001) finding has since been disputed however, by studies that found reductions in MAE magnitude when a distracting auditory task was completed during adaptation (Berman & Colby, 2002) and when attention was diverted by loading working memory (Houghton et al., 2003). Additionally, Murphy and Greene (2017) have provided practical evidence that attention may be a shared resource, finding that high auditory load during a driving simulation increased RTs to hazards, reduced awareness for visual objects, and resulted in more collisions than low auditory load.

Chapter 4 presents a novel method for assessing whether attention is a shared or separate resource between sensory modalities, contributing to a conflicted literature where an emphasis on vision and tactile processing is lacking (see Wahn & König, 2017, for a review of the cross-modal attention literature). Wahn and König (2017) site differences in attentional tasks as potentially driving inconsistent results, suggesting that attention can be both modality specific and supramodal depending on the task demands. It is possible that the tasks in *Chapter 4* did not effectively divert attention. For example, in the visual distraction condition, the average letter presentation duration was 0.13 s, compared to 0.3 s for translating motion (Experiment 1a) and 0.19 s for rotating motion (Experiment 1b) in *Chapter 2*. Further, the fastest possible letter duration in *Chapter 4* was 0.1 s, indicating that most participants were good at this task and may have been at floor levels. Future research should explore the influence of attentional task on the CAE-attention relationship. As the current findings did not establish an effect of within-modality attention, firm conclusions cannot be drawn without additional research to more fully understand the interplay between attention and adaptation across the senses.

5.2.5 Implications for future CAE research.

The findings reported in *Chapter 4* have a number of implications for our current understanding of the CAE. In particular, measurable CAEs were demonstrated using virtual curved surfaces, the magnitude of which paralleled those generated with real objects (as reported in van der Horst, Willebrands, et al., 2008). As cutaneous information is removed under these circumstances, this suggests that proprioception plays a key role in haptic curvature adaptation. Denisova et al. (2014) previously found stronger but more variable effects when a virtual surface was adapted with a stylus held like a pen. van Dam et al. (2016) suggested that hand posture and hand movement are adapted independently and simultaneously - these stronger CAEs may therefore reflect the fact that the stylus allowed a more consistent hand posture compared to a single finger moving over the stimulus. The stimuli used in *Chapter 4* directly matched those of van der Horst, Willebrands, et al. (2008), allowing the tentative conclusion that proprioception is the dominant driving force for the CAE. However, as a number of studies have shown that the CAE can be generated with static adaptation (rendering proprioception unnecessary), perhaps this is instead a substantively different form of the CAE. Indeed, transfer of the aftereffect between hands/fingers is complete for the dynamic CAE (van der Horst, Willebrands, et al., 2008) and only partial / absent for the static CAE (van der Horst, Duijndam, et al., 2008; Vogels et al., 1996), indicating that higher level bilateral processing is involved in the dynamic but not the static CAE. To investigate these differences further, future research should explore attentional modulation of the static CAE. The results from *Chapters 2 & 3* suggest larger attention effects in low level processing sites for the MAE, so it is possible that greater effects of attention would be evident for the low-level static CAE. However, direct comparisons should acknowledge and control for differences between static and dynamic adaptation stimuli (with larger, less curved stimuli for the dynamic CAE).

Previous research has looked into the characteristics of the CAE to understand the underlying processing of the aftereffect. The CAE has many commonalities with other documented visual aftereffects, for example increased adaptation magnitude with stronger adaptation stimulus properties (Vogels et al., 1996). Future research could manipulate these variables to determine whether they affect attentional modulation of the CAE. While we were unable to find evidence for a role of attention in haptic adaptation, the stimuli used may not have been conducive to finding an effect. This research would further our understanding of the CAE (and haptic perception in general), by revealing the conditions under which attention affects adaptation.

5.3 Conclusions

Attention and adaptation reflect fundamental processing mechanisms that are of great importance for sensory perception. *Chapter 3* details the first quantitative review of empirical research of attention and the MAE. Combined with a psychophysical investigation of the attention-MAE relationship (reported in *Chapter 2*) it has been revealed that: i) attention substantially affects the MAE, ii) feature-based attention exerts a stronger effect on the MAE, with increased attentional modulation for translating, than complex, motion adaptation, iii) the attention-MAE relationship increases with adaptation stimulus size and eccentricity from fixation, and iv) this relationship cannot be accounted for by response bias. *Chapter 4* represents the first experimental investigation into the effects of attention on haptic adaptation, finding that neither tactile or visual distraction affects the magnitude of the haptic CAE.

Taken together, these findings suggest pronounced differences between haptic and visual attention and adaptation, and that attention may not be a shared resource across modalities. The empirical findings of *Chapter 4* should guide necessary additional research, in order to fully understand the interplay between haptic adaptation and attention.

Appendix A Chapter 3. Summary of included effects.

Table A 1 Summary of included effects. *Method* refers to the statistical methods used to estimate effect size. *Source* refers to the page number within the reference where the data can be found.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
1) Aghdaee & Zandvakili, 2005		*Mdiff and SDav*	Investigated attentional modulation of local and global motion detectors using logarithmic spirals.	Excluded mirror-image spiral test stimulus; effect size for same-spiral stimuli only (see inclusion criteria).	p1103	Computed mean differences and standard deviations from figures on page 1103, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.
2) Alais & Blake, 1999		*Mdiff and SDav*	Investigated whether attention to superimposed brief coherent motion can bias MAE direction from coherent adapting motion.	Pooled effect across motion directions where the maximum aftereffect is expected (90° and 270°); an aftereffect is not expected at 0° or 180°.	p1016	Computed mean differences and standard deviations figure on page 1016, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error, averaged over maximum MAE directions.
3) Berman & Colby, 2002		*Mdiff and SDav*	Investigated the effect of visual and auditory attention on both MAE duration, and MT+ activity using fMRI.	Excluded auditory attention task and brain imaging data (see inclusion criteria).	p68	Computed mean differences and standard deviations from text on page 68, and then applied Equation 3.1. Standard deviations estimated from standard error.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
4) Blaser & Shepard, 2009	1	*Mdiff and SDav*	Explored how diverting attention towards a visual or auditory two-back memory task affects MAE duration.	Excluded experiment 2 as auditory attention task (see inclusion criteria).	p1177	Computed mean differences and standard deviations from text on page 1177, and then applied Equation 3.1. Exact standard deviations computed from subject means.
5) Buchel et al., 1998		*Mdiff and SDav*	Investigated the modulatory effect of attention on motion processing using fMRI, alongside a psychophysical control experiment.	Excluded brain imaging data (see inclusion criteria).	p1284	Computed mean differences and standard deviations from Table 2 on page 1284, and then applied Equation 3.1. Exact standard deviations computed from subject means. Effect represents difference between passive viewing and attention focused on the motion.
6) Chaudhuri, 1990	1	*Mdiff and SDav*	Investigated MAE duration when attention diverted (exp 1); strength of this effect with moving fixation (exp 2); the effect of attending colour of adapting motion (exp 3).	Experiment 2 excluded as looking at displaced fixation. Experiment 3 excluded as looking at a different feature (colour), rather than motion.	p61	Computed mean differences and standard deviations from figure on page 61, using GraphClick software, and then applied Equation 3.1. Exact standard deviation computed from subject means.
7) Culham et al., 2000 (i)	2	*t & N*	Looked at the effect of attentive tracking (exp1), attentively tracking a biased motion stimulus (exp2), and retinotopic specificity	Experiment 1 excluded as different motion stimulus for the attention conditions, and experiment 3 as adapt and test stimuli spatially	p609	Flicker MAE. Obtained t statistic from text on page 609, and then applied Equation 3.2. Same participants for both flicker and static MAEs.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
Culham et al., 2000 (ii)	2	*Mdiff and SDav*	(exp3) of MAEs for two superimposed sine wave gratings moving in opposite directions, for both static and dynamic tests.	separated (see inclusion criteria). Only including the biased motion condition to allow clearer comparison between passive and attended motion.	p610	Static MAE. Computed mean differences and standard deviations from figure on page 610, using GraphClick software, and then applied Equation 3.1. Exact standard deviations computed from subject means.
8) Dobkins et al., 2007 (i)	1a	*Mdiff and SDav*	Investigated the differential effects of attention (exp1), salience (exp2) and contrast on chromatic and achromatic motion, through measuring MAE duration.	Experiment 2 excluded as not manipulating attention. Excluded isoluminant chromatic stimuli (see inclusion criteria). Pooled effect over 8 stimulus contrasts.	p1899	Computed mean differences and standard deviations from figure on page 1899, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.
Dobkins et al., 2007 (ii)	1b	*Mdiff and SDav*		Excluded isoluminant chromatic and mixed stimuli (see inclusion criteria).	p1900	Computed mean differences and standard deviations from figure on page 1900, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.
9) Georgiades & Harris, 2002a (i)	1	*Mdiff and SDav*	Investigated how varying the spatial extent of surrounding stationary gratings and adapt/test stimuli alters attentional modulation of the MAE. Experiment 2 looked at size of adapting stimulus, and the	Pooled effect over two passive attention conditions. Only looking at the size of the adapting/test stimulus, not the surrounding stimulus, and so took data from figure 1a where separation is not taken into account.	p399	Experiment 1. Computed mean differences and standard deviations from figures on page 399, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error. First of two stimulus diameters (3.1°).

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
Georgiades & Harris, 2002a (ii)	1	*Mdiff and SDav*	separation of this stimulus from a reference grating.	Pooled effect over two passive attention conditions.	p399	Experiment 1. Second stimulus diameter (7.3°).
Georgiades & Harris, 2002a (iii)	2	*Mdiff and SDav*		Pooled effect over spatial separation and area of reference grating, as not concerned with these (see inclusion criteria).	p401	Experiment 2. Computed mean differences and standard deviations from figures on page 401, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.
Georgiades & Harris, 2002a (iv)	3	*Mdiff and SDav*		Effect size calculated from repeat-aloud digit (high load) and repeat-aloud zero (low load) conditions, to equate attentional tasks. This is the most conservative low load task.	p404	Experiment 3. Data for MAE duration. Same experimental session and participants as peak MAE velocity data. Computed mean differences and standard deviations from figures on page 404, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.
Georgiades & Harris, 2002a (v)	3	*Mdiff and SDav*			p405	Experiment 3. Data for MAE velocity.
10) Georgiades & Harris, 2002b (i)	1	*Mdiff and SDav*	Investigated the effect of attention on MAE duration and velocity for	The effect represents the pooled effect across all spatial and temporal frequencies.	p25	Computed mean differences and standard deviations from figure on page 25, using GraphClick software, and then applied

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
			a range of temporal and spatial frequencies.			Equation 3.1. Standard deviations estimated from standard error.
Georgiades & Harris, 2002b (ii)	1	*F & N*		The effect represents the pooled effect across all spatial and temporal frequencies.	p26	MAE velocity was measured in the same experimental session as above. Obtained F and N values from page 26, converted F to t statistic, and then applied Equation 3.2.
11) Georgiades & Harris, 2000a (i)		*Mdiff and SDav*	Looked at the effect of diverting attention on MAE duration and peak velocity, where irrelevant motion was presented at 3 eccentricities.		p2561	Effect size for MAE duration. Same experimental session and participants as peak MAE velocity data. Effect for the first of three stimulus eccentricities (1°). Computed mean differences and standard deviations from figures on page 2561, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error; maximum possible standard error was assumed when error bar was hidden, as this is the most conservative approach. This was the case for all effect sizes within this paper.
Georgiades & Harris, 2000a (ii)		*Mdiff and SDav*			p2561	MAE duration data for the second eccentricity (3°).

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
Georgiades & Harris, 2000a (iii)		*Mdiff and SDav*			p2561	MAE duration data for the third eccentricity (6°).
Georgiades & Harris, 2000a (iv)		*Mdiff and SDav*			p2561	Effect size for peak MAE velocity. Same experimental session and participants as MAE duration data. Effect for the first of three stimulus eccentricities (1°). Computed mean differences and standard deviations from figures on page 2561, using GraphClick software, and then applied Equation 3.1.
Georgiades & Harris, 2000a (v)		*Mdiff and SDav*			p2561	MAE velocity data for the second eccentricity (3°).
Georgiades & Harris, 2000a (vi)		*Mdiff and SDav*			p2561	MAE velocity data for the third eccentricity (6°).
12) Georgiades & Harris, 2000b (i)	2	*Mdiff and SDav*	Explored how MAE duration is affected by attentional load and the spatial spread of stimuli. Experiment 1 looked at adapting stimulus eccentricity, experiment 2 displaced fixation, experiment 3 altered stimulus size, and	Experiment 1 and 3 excluded due to between-subject design (see Inclusion and Coding Decisions). Excluded the displaced fixation condition of experiment 2 (see inclusion criteria).	p1193	Experiment 2. For one of two stimulus eccentricities (3°). Computed mean differences and standard deviations from figures on page 1193, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error; maximum possible

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
			experiment 4 again looked at eccentricity but held spatial extent constant.			standard error was assumed when error bar was hidden, as this is the most conservative approach. This was the case for all effect sizes within this paper.
Georgiades & Harris, 2000b (ii)	2	*Mdiff and SDav*			p1193	Experiment 2. The second stimulus eccentricity (7°).
Georgiades & Harris, 2000b (iii)	4	*Mdiff and SDav*			p1197	Experiment 4. Computed mean differences and standard deviations from figures on page 1197, using GraphClick software, and then applied Equation 3.1. Effect for first of three stimulus eccentricities (1.2°).
Georgiades & Harris, 2000b (iv)	4	*Mdiff and SDav*			p1197	Experiment 4. The second eccentricity stimulus (2.7°).
Georgiades & Harris, 2000b (v)	4	*Mdiff and SDav*			p1197	Experiment 4. The third eccentricity stimulus (3.8°).
13) Houghton et al., 2003	1	*Mdiff and SDav*	Investigated the effect of visual, auditory, and cognitive attentional load on MAE duration.	Excluded auditory string data, as only looking at visual attentional modulation. High load data is the pooled effect across number of targets, as it is unclear whether	p734	Computed mean differences and standard deviations from figures on page 734, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
				fewer targets could be construed as lower load (as observers are expecting a target, if there are none this might increase attentional vigilance throughout the trial). Excluded experiments 2 and 3 as they were investigating cognitive, rather than perceptual, load (see inclusion criteria).		
14) Jung & Chong, 2014 (i)	1	*Mdiff and SDav*	Investigated the effect of attention on aftereffects for both visible motion adaptation and perceptually invisible tilt adaptation. Attention focused on one of two motion patches (detect contrast decrements or a dot), test in attended or unattended location.	Excluded suppressed adaptor data (see inclusion criteria), and tilt aftereffect data. Experiment 3 excluded as not looking at the MAE.	p558	Computed mean differences and standard deviations from figures on page 558, using GraphClick software, and then applied Equation 3.1. As error bars were not labelled, we assumed they signified standard error, as is common in psychology. Standard deviations estimated from standard error. This is also the case for experiment 2. Eye movements assumed to be controlled as fixation cross presented, however they were not controlled.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
Jung & Chong, 2014 (ii)	2	*Mdiff and SDav*		Excluded suppressed adaptor data (see inclusion criteria), and tilt aftereffect data.	p562	Computed mean differences and standard deviations from figures on page 562, using GraphClick software, and then applied Equation 3.1.
15) Kaunitz et al., 2011 (i)	4	*Mdiff and SDav*	Investigated the effect of awareness and attention on MAE strength. Experiments 1 and 3 looked at awareness in the monocular MAE, experiment 2 looked at interocular transfer of the MAE, while experiments 4 and 5 looked at attention and awareness of the monocular MAE.	Experiments 1, 2 and 3 were excluded, as they were not assessing attention. Only seen adaptor data included (see inclusion criteria). Pooled effect across low- and no-load attention conditions.	p6	Simple motion effect size. Computed mean differences and standard deviations from figures on page 6, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error. All details the same for both effect sizes.
Kaunitz et al., 2011 (ii)	5	*Mdiff and SDav*		Only seen adaptor data included (see inclusion criteria). Pooled effect across low- and no-load attention conditions.	p6	Complex motion effect size.
16) Morgan, 2013 (i)	1	*Mdiff and SDav*	Looked at the effect of attention on the MAE using a bias-free MAE measure, using high and low contrast adaptors.	Pooled effect of ‘experimental’ test conditions, excluded ‘control’ conditions as no motion aftereffect is expected in these trials.	p7	Computed mean differences and standard deviations from figures on page 7 (figure 5, experimental data represented as blue and red), using GraphClick software, and then applied Equation 3.1. Exact standard deviation computed from subject means

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
						averaged over the two experimental test configurations.
Morgan, 2013 (ii)	2	*Mdiff and SDav*		Pooled effect of 'experimental' test conditions, excluded 'control' conditions as no motion aftereffect is expected in these trials.	p9	Computed mean differences and standard deviations from figures on page 9 (figure 6, experimental data represented as blue and red), using GraphClick software, and then applied Equation 3.1. Exact standard deviation computed from subject means averaged over the two experimental test configurations.
17) Morgan, 2012 (i)	1	*Mdiff and SDav*	Looked at the attentional modulation of MAE duration with naïve subjects (experiments 1 & 2) and using a nulling procedure to measure the MAE (experiments 3 & 4).	Excluded experiment 3 and 4 because could not calculate effect sizes; statistics were not reported, and could not be computed from the data presented.	p48	Computed mean differences and standard deviations from figure on page 48, using GraphClick software, and then applied Equation 3.1. Exact standard deviations computed from subject means.
Morgan, 2012 (ii)	2	*Mdiff and SDav*			p48	Details as above.
18) Mukai & Watanabe, 2001 (i)	1	*F & N*	Investigated the effect of attending superimposed simple (experiment 1) or complex (experiment 3) motion within the same stimulus on the MAE, and the interocular transfer of the MAE. Experiment 2		p1110	Experiment 1. Calculated t from F statistic reported in text on page 1110, and then applied Equation 3.2. Due to the available statistics, effect represents the pooled effect across same/different adapt-test conditions. Effect represents the

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
			assessed the attention effect, interocular transfer and stimulus luminance.			difference between passive viewing and attention focused on the motion (for all effects from this paper).
Mukai & Watanabe, 2001 (ii)	2	*Mdiff and SDav*		Averaged over two luminance conditions. Excluded 68.5 cd/m2 condition as data from experiment 1. Excluded different adapt-test eye data (see inclusion criteria).	p1112	Computed mean differences and standard deviations from Table 2 on page 1112, and then applied Equation 3.1. Exact standard deviations computed from subject means.
Mukai & Watanabe, 2001 (iii)	3	*F & N*			p1113	Experiment 3. Calculated t from F statistic reported in text on page 1113, and then applied Equation 3.2. Due to the available statistics, effect represents the pooled effect across same/different adapt-test conditions.
19) Nishida & Ashida, 2000 (i)	3	*Mdiff and SDav*	Looked at the influence of eccentricity, method of measuring MAE (static/dynamic test) and attention on interocular transfer (IOT) of the flicker MAE.	Excluded experiment 1 and 2, as they did not manipulate attention. Only included monocular data (see inclusion criteria)	p272	Effect is for the static MAE (measured in the same experimental session as the flicker MAE, Nishida & Ashida, 2000 (ii)). Computed mean differences and standard deviations from figures on page 272, using GraphClick software, and then applied Equation 3.1. Exact standard deviation computed from subject means.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
						All statistical details are the same for Nishida & Ashida, 2000 (ii).
Nishida & Ashida, 2000 (ii)	3	*Mdiff and SDav*		Only included monocular data (see inclusion criteria)	p272	Flicker MAE.
Nishida & Ashida, 2000 (iii)	4	*Mdiff and SDav*		Only included monocular data. Effect represents the pooled effect across conditions where the same type (first- or second-order) of motion was shown for adapt and test, excluding crossover effects, as this was not pertinent to the research question (see inclusion criteria).	p274	Computed mean differences and standard deviations from figures on page 274, using GraphClick software, and then applied Equation 3.1. Exact standard deviation computed from subject means averaged over the two types of motion stimulus.
20) Patterson et al., 2005		*Mdiff and SDav*	Investigated attentional modulation of the cyclopean MAE (displacement of disparity information) and luminance MAE durations.	Excluded cyclopean MAE (see inclusion criteria). Pooled effect across low- and no-load attention conditions.	p2605	Computed mean differences and standard deviations from figures on page 2605, using GraphClick software, and then applied Equation 3.1. Exact standard deviation computed from subject means averaged over no- and low-load conditions.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
21) Rees et al., 2001	3	*Mdiff and SDav*	Investigated the effect of auditory attentional load on processing irrelevant motion using PET (exp 1), MAE duration (exp 2) and the effect of visual load on MAE duration (exp 3).	Only experiment 3, as others used an auditory attention task, and exp 1 was not behavioural.	p945	Computed mean differences and standard deviations from figure on page 945, using GraphClick software, and then applied Equation 3.1. Exact standard deviation computed from subject means.
22) Rees et al., 1997		*Mdiff and SDav*	Investigated the effect of load on the processing of irrelevant motion in V5 using fMRI, and through measuring MAE durations.	Only included the behavioural data (see inclusion criteria)	p1619	Reference 23 describes the descriptive statistics. Means were provided and standard deviations were calculated, and then Equation 3.1 was applied. Exact standard deviation computed from subject means.
23) Rezec et al., 2004 (i)	1	*Mdiff and SDav*	Looked at the effect of spatial attention on MAE duration across a range of stimulus contrasts, for static and dynamic tests.	The effect represents the pooled effect across all stimulus contrasts (=11).	p3039	Computed mean differences and standard deviations from figure on page 3039, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.
Rezec et al., 2004 (ii)	1	*Mdiff and SDav*		The effect represents the pooled effect across all stimulus contrasts (=8).	p3040	Computed mean differences and standard deviations from figure on page 3040, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
24) Rose et al., 2003		*Mdiff and SDav*	Looked at attentional modulation of the depth aftereffect and the MAE.	Excluded the depth aftereffect data as not investigating motion adaptation. Pooled effect across low- and no-load conditions.	p637	Computed mean differences and standard deviations from figures on page 637, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.
25) Shiori & Matsuiya, 2009 (i)	4	*Mdiff and SDav*	Investigated spatiotemporal and orientation tuning of MAEs with static and dynamic test stimuli, and whether attention can account for these effects. Using two oppositely moving superimposed gratings of different spatial and temporal frequencies.	Excluded experiments 1, 2, 3 & 5 as attention not manipulated. Pooled effect across temporal frequencies, as these were different for each superimposed motion adaptation stimuli.	p9	Static MAE. Computed mean differences and standard deviations from figure on page 9, using GraphClick software, and then applied Equation 3.1. Exact standard deviations computed from subject means. All details the same for both effect sizes.
Shiori & Matsuiya, 2009 (ii)	4	*Mdiff and SDav*			p9	Flicker MAE. Details as above.
26) Shulman, 1993 (i)	1	*Mdiff and SDav*	Looked at the effect of diverting attention from adapting motion (experiment 1), attending one of two motion stimuli (experiments 2, 3, 5), and the impact of eye movements (experiment 4).	Excluded experiment 4 as no attention manipulation. Averaged over two rotation directions (for all effect sizes except experiment 1 in this paper).	p951	Obtained mean differences and computed standard deviations from text on page 951, using GraphClick software, and then applied Equation 3.1. Standard deviations estimated from standard error.
Shulman, 1993 (ii)	2	*t & N*			p954	Obtained t statistics from text on page 954, and then applied Equation 3.2.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
						Effect sizes were then averaged across motion direction.
Shulman, 1993 (iii)	3	*t & N*			p955	Obtained t statistics from text on page 955, and then applied Equation 3.2. Effect sizes were then averaged across motion direction.
Shulman, 1993 (iv)	5	*t & N*			p958	Obtained t statistics from text on page 958, and then applied Equation 3.2. Effect sizes were then averaged across motion direction.
27) Shulman, 1991 (i)	1a	*t & N*	Investigated the effect of attentional modulation of the 3-dimensional motion aftereffect. Participants attended one of two squares, each made up of 4 dots, rotating in depth.	Excluded experiment 2 as attention not manipulated. Averaged over two rotation directions (for all effect sizes in this paper).	p728	Obtained t statistics from text on page 728, and then applied Equation 3.2. Effect sizes were then averaged across motion direction.
Shulman, 1991 (ii)	1b	*t & N*			p729	Obtained t statistics from text on page 729, and then applied Equation 3.2. Effect sizes were then averaged across motion direction.
Shulman, 1991 (iii)	3	*t & N*		Only included polar projection ‘opponent’ data, as require attention comparisons to be from	p734	Obtained t statistics from text on page 734, and then applied Equation 3.2.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
				the same adapting stimulus (see inclusion criteria).		Effect sizes were then averaged across motion direction.
28) Takeuchi & Kita, 1994 (i)	1	*Mdiff and SDav*	Looked at how attentional modulation of the MAE is affected by type of motion, adaptation duration, and stimulus spatial extent.		p97	Simple motion, first of three adaptation durations (20 s). Computed mean differences and standard deviations from figures on page 97, using GraphClick software, and then applied Equation 3.1. For all effect sizes, exact standard deviations computed from subject means.
Takeuchi & Kita, 1994 (ii)	1	*Mdiff and SDav*			p97	Simple motion, second adaptation duration (40 s). Details as above.
Takeuchi & Kita, 1994 (iii)	1	*Mdiff and SDav*			p97	Simple motion, third adaptation duration (80 s). Details as above.
Takeuchi & Kita, 1994 (iv)	1	*Mdiff and SDav*			p98	Expansion/contracting motion, first of three adaptation durations (20 s). Computed mean differences and standard deviations from figures on page 98, using GraphClick software, and then applied Equation 3.1.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
Takeuchi & Kita, 1994 (v)	1	*Mdiff and SDav*			p98	Expansion/contracting motion, second adaptation duration (40 s). Details as above.
Takeuchi & Kita, 1994 (vi)	1	*Mdiff and SDav*			p98	Expansion/contracting motion, third adaptation duration (80 s). Details as above.
Takeuchi & Kita, 1994 (vii)	1	*Mdiff and SDav*			p98	Rotation motion, one of three adaptation durations (20 s). Details as above.
Takeuchi & Kita, 1994 (viii)	1	*Mdiff and SDav*			p98	Rotation motion, second adaptation duration (40 s). Details as above.
Takeuchi & Kita, 1994 (ix)	1	*Mdiff and SDav*			p98	Rotation motion, third adaptation duration (80 s). Details as above.
Takeuchi & Kita, 1994 (x)	2	*Mdiff and SDav*			p100	Simple motion. Computed mean differences and standard deviations from figures on page 100, using GraphClick software, and then applied Equation 3.1.
Takeuchi & Kita, 1994 (xi)	2	*Mdiff and SDav*			p100	Motion in depth. Details as above.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
Takeuchi & Kita, 1994 (xii)	3	*Mdiff and SDav*		First stimulus size (5°) excluded from experiment 3 effect sizes, as data is from experiment 1.	p103	Simple motion, second of three stimulus sizes (10°). Computed mean differences and standard deviations from figures on page 103, using GraphClick software, and then applied Equation 3.1.
Takeuchi & Kita, 1994 (xiii)	3	*Mdiff and SDav*			p103	Simple motion, third stimulus size (20°). Details as above.
Takeuchi & Kita, 1994 (xiv)	3	*Mdiff and SDav*			p103	Expansion/contracting motion, second of three stimulus sizes (10°). Details as above.
Takeuchi & Kita, 1994 (xv)	3	*Mdiff and SDav*			p103	Expansion/contracting motion, third stimulus size (20°). Details as above.
Takeuchi & Kita, 1994 (xvi)	3	*Mdiff and SDav*			p104	Rotational motion, second of three stimulus sizes (10°). Computed mean differences and standard deviations from figures on page 104, using GraphClick software, and then applied Equation 3.1.
Takeuchi & Kita, 1994 (xvii)	3	*Mdiff and SDav*			p104	Rotational motion, third stimulus size (20°). Details as above.

Study/Effect	Exp no.	Method	Study details	Excluded conditions	Source	Notes
29) Taya et al., 2009	3	*Mdiff and SDav*	Looked at load effects on the MAE when attending a feature (colour) in the same (experiments 1 and 2), or different (experiment 3) spatial locations.	Only experiment 3 was included as exp 1 and 2 were looking at the effects of a different feature (colour) on processing. Averaged over low- and no-load conditions.	p7	Computed mean differences and standard deviations from figure on page 7, using GraphClick software, and then applied Equation 3.1. As error bars were not labelled, we assumed they signified standard error, as is common in psychology. Standard deviations estimated from standard error.

Appendix B Chapter 3. Search terms and omissions.

PUBMED search terms:

(attention[Title/Abstract] AND motion[Title/Abstract]) AND aftereffect[Title/Abstract] AND "humans"[MeSH Terms]

Filtered for only ‘humans’, and only looking at ‘journal article’

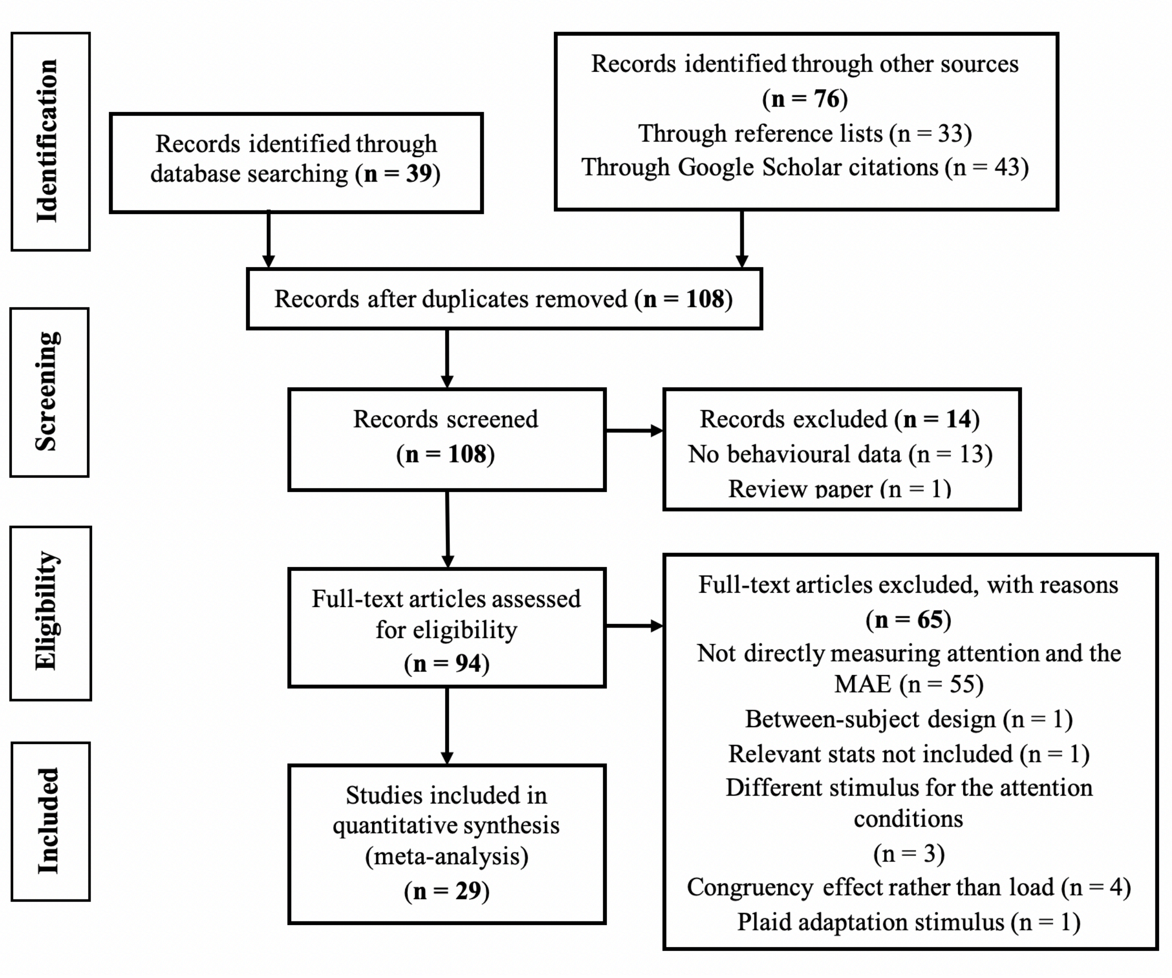

Figure A 1 PRISMA flow diagram.

Appendix C Chapter 3. Standard deviation when averaging across conditions.

In some cases, means and variances were reported separately for different levels of an irrelevant factor. To include data after pooling across these levels requires an estimate of the variance of the averaged data (σ^2_{av}). To do this, we assumed that the correlation across conditions (x and y) was 0.5:

$$\sigma^2_{av} = \frac{1}{4}(\sigma^2_x + \sigma^2_y + \sigma_x \sigma_y)$$

As repeated measures designs have high precision, the correlation across conditions tends to be quite high – however, incorrectly assuming a high correlation would result in a smaller estimated standard deviation than would be accurate, which in turn would give an inflated effect size estimate. Assuming a correlation of 0.5 is conservative as the generated standard deviation will likely be larger than it truly is, consequently reducing effect size.

Appendix D Chapter 3. Effect size calculations and considerations.

As outlined by Lakens (2013), in paired designs, effect sizes are standardised by a value $\sqrt{2(1-r)}$ larger than independent observation standard deviations. As such, estimates using dz were adjusted to dRM, which transforms the effect size into the raw-score (Morris & DeShon, 2002).

$$d_z = \frac{t}{\sqrt{N}}$$

As paired correlations were not reported for any study reports, they were computed with the equations given in Morris & DeShon (2002), using the available data. The variance of difference scores were first computed from available test statistics using the equation,

$$SD_D^2 = \frac{n\left(M_{post} - M_{pre}\right)^2}{t_{RM}^2}$$

This value was then used to compute the correlation between conditions:

$$r = 1 - \frac{SD_D^2}{2SD_P^2}$$

where SD_P is the pooled standard deviation.

Appendix E Chapter 3. Pseudo R^2.

The pseudo R^2 statistic (López-López et al., 2014) estimates heterogeneity reduction when moderators are included, and is computed with the formula:

$$R^2 = \frac{\tau_{RE}^2 - \tau_{ME}^2}{\tau_{RE}^2}$$

Where τ^2_{RE} is the estimated heterogeneity of the random effects model without moderators, and τ^2_{ME} is the estimated residual heterogeneity from the mixed effects model including the moderators. Note that the formula essentially estimates the proportional reduction in effect size heterogeneity (τ^2) after including moderators, but it does not incorporate sampling variability. Hence, it is possible to observe large R^2 values, even when there are discrepancies between the regression line and the observed effect sizes (when those discrepancies do not exceed what one would expect based on sampling variability alone). In fact, when $\tau^2_{\mathrm{ME}} = 0$, then $R^2 = 1$. However, unlike the interpretation of a conventional R^2 statistic, this does not imply that all data fall perfectly on the regression line, but only that the residuals do not exceed what is expected due to sampling variability. As such, this statistic should be interpreted with caution for analyses that have small k (number of effects).

Appendix F Chapter 3. Summary of coding for each effect.

Table A 2 Summary of coding for each effect. See Table 3.2 for more specific details regarding each factor. Categorical variables were coded; for Type of Motion, 1 refers to translational motion, 2 to complex motion; for Test Stimulus, 1 is static, 2 is dynamic; for naivety, 1 is naïve participants, 2 is experienced or mixed naïve and experienced participant pools; for MAE Measure, 1 is MAE duration, 2 is a strength measurement; for MAE Response, 1 refers to MAE magnitude estimation, 2 is 2-alternative-forced-choice paradigms; for Attentional Manipulation, 1 is the distractor paradigm, 2 is the attentional tracking paradigm.

Study/Effect	Exp	N	Sample	Effect Number	Type of Motion	Test Stimulus	Eccentricity (°)	Stimulus Area ($°^2$)	Naivety	MAE Measure	MAE Response	Adaptation Duration (sec)	Attentional Manipulation	Adapting Speed (°/sec)
1) Aghdaee & Zandvakili, 2005 (i)	1	4	1	1	2	1	0.42	50.27	2	1	1	60	1	35.1
2) Alais & Blake, 1999 (i)	1	4	2	2	1	1		8.81	2	2	1	32	2	2.5
3) Berman & Colby, 2002 (i)	1	5	3	3	2	1	1.5	169.65		1	1	36	1	3
4) Blaser & Shepard, 2009 (i)	1	2	4	4	1	1		95.03	2	1	1	60	1	3
5) Buchel et al., 1998 (i)	1	9	5	5	2	1		226.98		1	1		1	4.7
6) Chaudhuri, 1990 (i)	1	5	6	6	1	1	0.25	120.75	1	1	1	60	1	5
7) Culham et al., 2000 (i)	2	5	7	7	2	2	3.5	172.76	2	2	1		2	
Culham et al., 2000 (ii)	2	5	7	8	2	1	3.5	172.76	2	2	1		2	
8) Dobkins et al., 2007 (i)	1	7	8	9	1	2	0.45	99.19	2	1	1	30	1	6.2
Dobkins et al., 2007 (ii)	2	5	8	10	1	2	0.45	99.19	2	1	1	30	1	6.2
9) Georgiades & Harris, 2002a (i)	1	9	9	11	1	1		1.89	1	1	1	24	1	

Study/Effect	Exp	N	Sample	Effect Number	Type of Motion	Test Stimulus	Eccentricity (°)	Stimulus Area ($^{\circ 2}$)	Naivety	MAE Measure	MAE Response	Adaptation Duration (sec)	Attentional Manipulation	Adapting Speed (°/sec)
Georgiades & Harris, 2002a (ii)	1	9	9	12	1	1		10.46	1	1	1	24	1	
Georgiades & Harris, 2002a (iii)	2	6	10	13	1	1		1.89		1	1	24	1	
Georgiades & Harris, 2002a (iv)	3	8	11	14	1	1		190.72		1	1	17	1	
Georgiades & Harris, 2002a (v)	3	8	11	15	1	1		190.72		2	1	17	1	
10) Georgiades & Harris, 2002b (i)	1	4	12	16	1	2	0.5	41	1	1	1	40	1	
Georgiades & Harris, 2002b (ii)	2	4	12	17	1	2	0.5	41	1	2	1	40	1	
11) Georgiades & Harris, 2000a (i)	1	15	13	18	1	2	0.5	34.71	1	1	1	40	1	1.3
Georgiades & Harris, 2000a (ii)	1	15	13	19	1	2	1.5	31.57	1	1	1	40	1	
Georgiades & Harris, 2000a (iii)	1	15	13	20	1	2	3	20.96	1	1	1	40	1	
Georgiades & Harris, 2000a (iv)	1	15	13	21	1	2	0.5	34.71	1	2	1	40	1	
Georgiades & Harris, 2000a (v)	1	15	13	22	1	2	1.5	31.57	1	2	1	40	1	
Georgiades & Harris, 2000a (vi)	1	15	13	23	1	2	3	20.96	1	2	1	40	1	1.3
12) Georgiades & Harris, 2000b (i)	2	8	14	24	1	1	1.5	64.82	1	1	1	24	1	
Georgiades & Harris, 2000b (ii)	2	8	14	25	1	1	3.5	33.41	1	1	1	24	1	
Georgiades & Harris, 2000b (iii)	4	8	15	26	1	1	0.07		1	1	1	24	1	
Georgiades & Harris, 2000b (iv)	4	8	15	27	1	1	2.05	22.05	1	1	1	24	1	
Georgiades & Harris, 2000b (v)	4	8	15	28	1	1	3.35	21.49	1	1	1	24	1	
13) Houghton et al., 2003 (i)	1	9	16	29	1	1		219.03	1	1	1	90	1	2

Study/Effect	Exp	N	Sample	Effect Number	Type of Motion	Test Stimulus	Eccentricity (°)	Stimulus Area (°^{2})	Naivety	MAE Measure	MAE Response	Adaptation Duration (sec)	Attentional Manipulation	Adapting Speed (°/sec)
14) Jung & Chong, 2014 (i)	1	12	17	30	1	2	1.5	6.28	2	2	2	90	1	1
Jung & Chong, 2014 (ii)	2	12	17	31	1	2	1.5	6.28	2	2	2	10	1	1
15) Kaunitz et al., 2011 (i)	4	6	18	32	1	2		4.91	2	2	2	68	1	0.6
Kaunitz et al., 2011 (ii)	5	6	18	33	2	2		4.91	2	2	2	68	1	0.6
16) Morgan, 2013 (i)	1	5	19	34	1	2	3.125	9.82	2	2	2	4	1	3.1167
Morgan, 2013 (ii)	2	4	19	35	1	2	3.125	9.82	2	2	2	4	1	3.1167
17) Morgan, 2012 (i)	1	6	20	36	2	1	0.46	77.91	1	1	1	60	1	2
Morgan, 2012 (ii)	2	6	21	37	2	1	0.46	77.91	1	1	1	60	1	2
18) Mukai & Watanabe, 2001 (i)	1	5	22	38	1	2			2	2	2	45	2	4.4
Mukai & Watanabe, 2001 (ii)	2	3	22	39	1	2			2	2	2	45	2	4.4
Mukai & Watanabe, 2001 (iii)	3	5	22	40	2	2			2	2	2	45	2	4.4
19) Nishida & Ashida, 2000 (i)	3	4	23	41	1	1	0.28	23.69	2	1	1	30	1	5
Nishida & Ashida, 2000 (ii)	3	4	23	42	1	2	0.28	23.69	2	1	1	30	1	5
Nishida & Ashida, 2000 (iii)	4	2	23	43	1	2	0.28	23.69	3	1	1	30	1	5
20) Patterson et al., 2005 (i)	1	5	24	44	1	1	0.57		1	1	1	64	1	4
21) Rees et al., 2001 (i)	3	4	25	45	2	1	1.75	753.98		1	1	60	1	8
22) Rees et al., 1997 (i)	2	4	26	46	2	1	1.7	192.20		1	1		1	5
23) Rezec et al., 2004 (i)	1	6	27	47	1	1	0.45	99.80	2	1	1	30	1	6.2

Study/Effect	Exp	N	Sample	Effect Number	Type of Motion	Test Stimulus	Eccentricity (°)	Stimulus Area (°^{2})	Naivety	MAE Measure	MAE Response	Adaptation Duration (sec)	Attentional Manipulation	Adapting Speed (°/sec)
Rezec et al., 2004 (ii)	2	7	27	48	1	2	0.45	99.80	2	1	1	30	1	6.2
24) Rose et al., 2003 (i)	1	6	28	49	1	1	0.8	8.82	2	1	1	30	1	5.5
25) Shiori & Matsuiya, 2009 (i)	4	2	29	50	1	1	0.75	450	2	1	1	30	1	
Shiori & Matsuiya, 2009 (ii)	4	2	29	51	1	2	0.75	450	2	1	1	30	1	
26) Shulman, 1993 (i)	1	8	30	52	2	2			1	2	1	20	1	18.18
Shulman, 1993 (ii)	2	8	30	53	2	2			1	2	1	20	1	
Shulman, 1993 (iii)	3	8	31	54	2	2			1	2	1	60	1	
Shulman, 1993 (iv)	5	7	32	55	2	2			1	2	1	60	1	
27) Shulman, 1991 (i)	1a	5	33	56	2	2			1	2	2	33	1	
Shulman, 1991 (ii)	1b	5	34	57	2	2			1	2	2	33	1	
Shulman, 1991 (iii)	3	7	35	58	2	2			1	2	1	33	1	
28) Takeuchi & Kita, 1994 (i)	1	3	36	59	1	1	0.25	78.29	1	1	1	20	1	5
Takeuchi & Kita, 1994 (ii)	1	3	36	60	1	1	0.25	78.29	1	1	1	40	1	5
Takeuchi & Kita, 1994 (iii)	1	3	36	61	1	1	0.25	78.29	1	1	1	80	1	5
Takeuchi & Kita, 1994 (iv)	1	3	36	62	2	1	0.25	78.29	1	1	1	20	1	5
Takeuchi & Kita, 1994 (v)	1	3	36	63	2	1	0.25	78.29	1	1	1	40	1	5
Takeuchi & Kita, 1994 (vi)	1	3	36	64	2	1	0.25	78.29	1	1	1	80	1	5
Takeuchi & Kita, 1994 (vii)	1	3	36	65	2	1	0.25	78.29	1	1	1	20	1	5

Study/Effect	Exp	N	Sample	Effect Number	Type of Motion	Test Stimulus	Eccentricity (°)	Stimulus Area (°^{2})	Naivety	MAE Measure	MAE Response	Adaptation Duration (sec)	Attentional Manipulation	Adapting Speed (°/sec)
Takeuchi & Kita, 1994 (viii)	1	3	36	66	2	1	0.25	78.29	1	1	1	40	1	5
Takeuchi & Kita, 1994 (ix)	1	3	36	67	2	1	0.25	78.29	1	1	1	80	1	5
Takeuchi & Kita, 1994 (x)	2	3	36	68	1	1	0.25	78.29	1	1	1	80	1	5
Takeuchi & Kita, 1994 (xi)	2	3	36	69	2	1	0.25	78.29	1	1	1	80	1	5
Takeuchi & Kita, 1994 (xii)	3	3	36	70	1	1	0.25	313.91	1	1	1		1	5
Takeuchi & Kita, 1994 (xiii)	3	3	36	71	1	1	0.25	1256.39	1	1	1		1	5
Takeuchi & Kita, 1994 (xiv)	3	3	36	72	2	1	0.25	313.91	1	1	1		1	5
Takeuchi & Kita, 1994 (xv)	3	3	36	73	2	1	0.25	1256.39	1	1	1		1	5
Takeuchi & Kita, 1994 (xvi)	3	3	36	74	2	1	0.25	313.91	1	1	1		1	5
Takeuchi & Kita, 1994 (xvii)	3	3	36	75	2	1	0.25	1256.39	1	1	1		1	5
29) Taya et al., 2009 (i)	3	6	37	76	2	2	2.5	43.98	2	2	2	1	1	1.3

Appendix G Chapter 3. Publication bias analyses.

Rosenthal’s fail-safe N estimates the number of additional null studies needed to reduce the effect size to non-significance. Our analyses produced a huge fail-safe N of 7,767. However, the fail-safe N should be interpreted with caution: the method considers only unpublished null effects, ignoring possible unpublished negative effects that would reduce the fail-safe N (Begg & Berlin, 1988). Furthermore, neither the heterogeneity of observed effects, nor the sample sizes of additional null studies are modelled directly (Becker, 2005).

Another limitation of the fail-safe N is its foundation in null hypothesis testing, in contrast to meta-analyses, which focus on effect size. An alternative, the Orwin method (1983), models the magnitude of the overall estimated effect size, as a function of the hypothesised number of additional, unpublished studies. The plot below (Figure A2a) shows the decreasing effect-size estimate, as an increasing number of (simulated) additional studies are added whose average effect size is 0. We note that a trim and fill analysis estimated the number of unpublished results to be only 7 (see Figure A2b).

(a) (b)

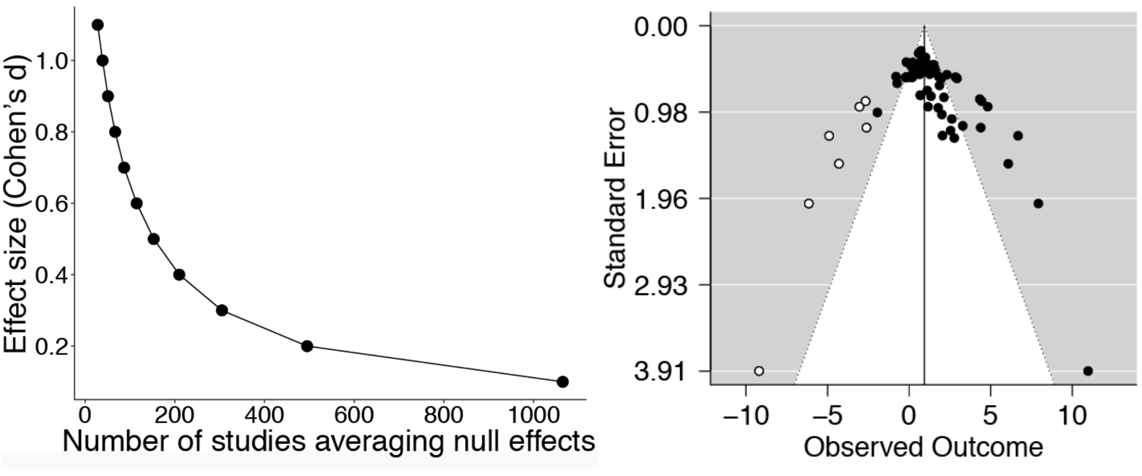

Figure A 2 Publication bias analyses. (a) Orwin plot. (b) Trimmed and filled funnel plot. Filled circles are observed effects and empty circles are additional effects needed to create a symmetrical funnel plot.

Sampling theory dictates that estimates of the underlying effect will become more accurate (more closely clustered around the true effect size) as sample size increases. Effect size estimates from small samples are expected to be more variable. This is reflected in the broad base of the funnel plot, corresponding to estimates from small samples. The ‘file drawer’ effect suggests that non-significant findings are less likely to be published. In addition, studies with small samples (and low power) will only be statistically significant if a large effect is found. For this reason, the suppression of non-significant studies is expected to produce a negative correlation between effect size and sample size. To explore this effect, funnel plot asymmetry (see Figure A2) was analysed in two ways. The rank correlation test suggested by Begg and Mazumdar (1994) was significant: Kendall's Tau = 0.26, p = .0007. Similarly, a regression analysis, detailed by Egger, Smith, Schneider and Minder (1997) was significant, z = 6.96, p < .001. These findings are consistent with the presence of some publication bias, which may have inflated the overall effect size estimate. As noted in the main manuscript, the estimated effect size after including the (simulated) supressed studies is slightly smaller, but still substantial: d_{RM} = 0.94, 95% CI [0.61, 1.28].

Appendix H Chapter 3. Moderators for attentional modulation of the MAE - Main effects.

Table A 3 Moderators for attentional modulation of the MAE - Main effects.

Moderator	*k*	*df*	Q^O	*p*	R^2
Type of motion	76	1	17.43	<.001	24.92%
Adaptation duration	66	1	0.01	.917	0%
MAE measurement	76	1	0.49	.485	0%
MAE response	76	1	0.52	.470	0%
Test stimulus	76	1	3.29	.070	7.12%
Stimulus area	64	1	7.40	.007	11.38%
Eccentricity	55	1	4.05	.044	8.59%
Speed	45	1	3.36	.067	2.74%
Naivety	69	1	1.98	.159	0%
Attention manipulation	76	1	0.01	.904	0%

Appendix I Chapter 3. Information regarding the effect of sample size (N).

We explored the idea that increased effect size for naïve participants compared to mixed/experienced subject groups could be explained by increased N in studies using naïve participants. While it is the case that studies with more participants show a stronger MAE attention effect, we found the number of participants in studies with naïve participants did not significantly differ from those with experienced participants, *t*(66.19) = 1.69, *p* = .096.

Appendix J Chapter 3. Moderators for attentional modulation of the MAE – Two-way interactions.

We explored interactions between subject naivety and MAE measurement (2AFC vs. magnitude response; MAE duration vs. MAE strength). While measuring the MAE with a 2AFC design minimises the impact of bias, measuring MAE duration is the method most susceptible to bias. The use of non-naïve subjects, who have a clearer understanding of the study aims, may exacerbate the issue of bias in MAE duration designs, leading to stronger attentional modulation. This was not the case, however.

Table A 4 Moderators for attentional modulation of the MAE - Two-way interactions.

Moderators	*k*	Model matrix full?	*df*	Q^1	*p*	R^2
Naivety x measure	69	N	1	0.05	.828	0%
Naivety x response	69	N	1	0.33	.568	0%
Motion type x stimulus area	64	N	1	4.29	.038	36.48%

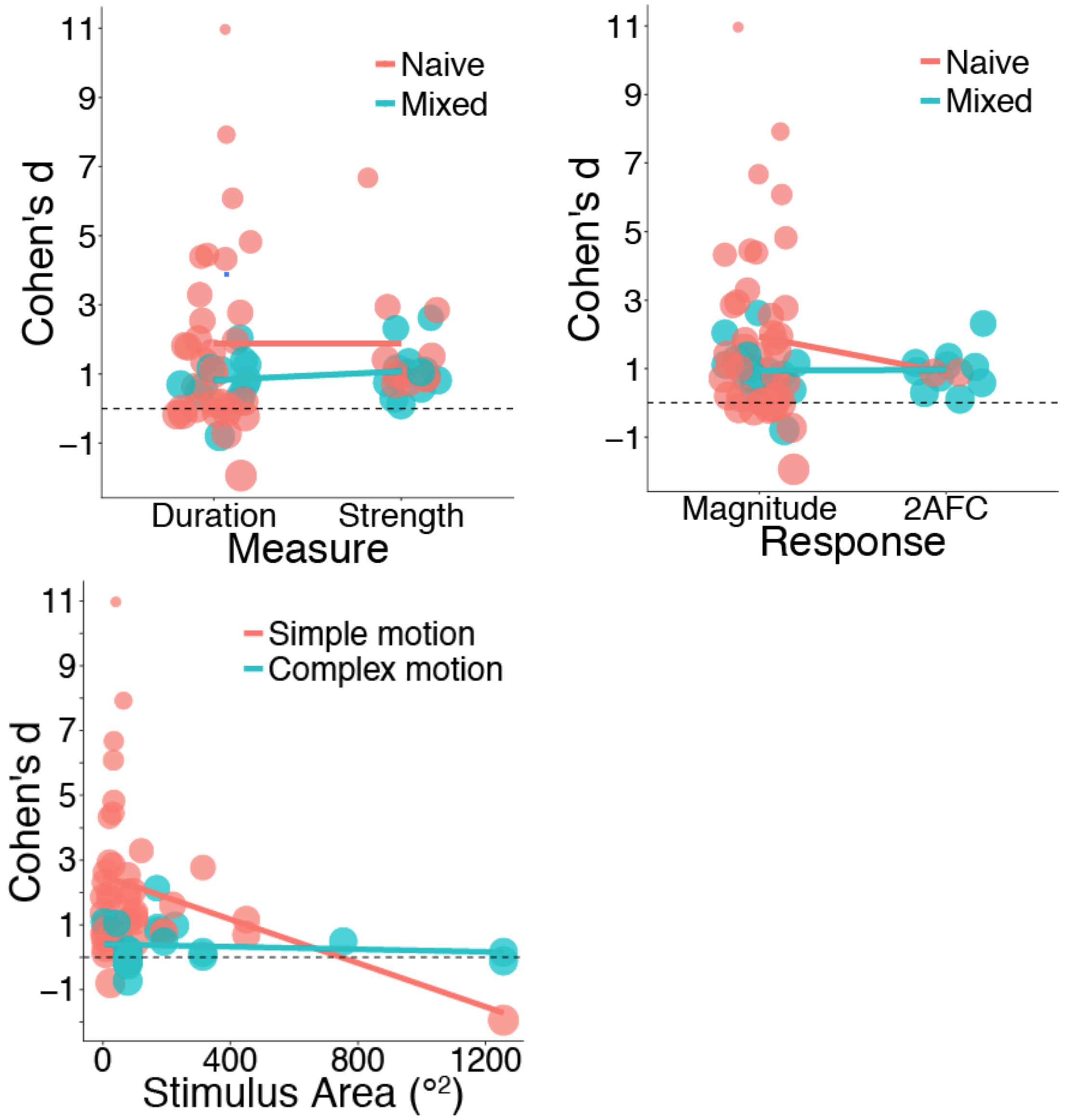

Figure A 3 Moderators for attentional modulation of the MAE - Two-way interactions.

Appendix K Chapter 3. Effects for moderators included in final regression model.

Table A 5 Effects for moderators included in final regression model.

Moderator	*b*	*se*	*p*	*CI*
Type of motion	-1.41	0.41	.001	-2.21, -0.62
MAE response	-0.89	0.72	.218	-2.31, 0.53
Test stimulus	0.30	0.48	.528	-0.63, 1.24
Naivety	-0.68	0.46	.145	-1.58, 0.23
Stimulus area	-0.001	0.001	.161	-0.002, 0.0003
Eccentricity	0.01	0.28	.986	-0.54, 0.55
Speed	-0.27	0.13	.031	-0.52, 0.02

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