The effects of attention and adaptation duration on the motion aftereffect

Laura Bartlett, Erich W. Graf, Wendy J. Adams*

Department of Psychology, University of Southampton, UK

Running head: Attention and the Motion Aftereffect

Word count: 6029

* Corresponding author:

Wendy J. Adams

Psychology, FSHMS

University of Southampton

Southampton, SO17 1BJ

ENGLAND

Tel: +011 (44) 0238059 3629

Email: w.adams@soton.ac.uk

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 report that MAEs are reduced if attention is diverted from the adaptation stimulus (e.g. Chaudhuri, 1990; Rees, Frith, & Lavie, 1997) but others argue that motion adaptation is independent of attention (Morgan, 2011, 2012, 2013). We explore several factors that might modulate the attention-adaptation relationship and therefore explain apparent inconsistencies, namely: (i) adaptation duration, (ii) motion type: translating vs. complex and (iii) response bias. Participants viewed translating (Experiments 1a and 2) or rotating (Experiment 1b) random dot patterns, whilst 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 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 apparent motion, but also low-level motion processing as evidenced by the MAE.

Keywords: motion aftereffect, attention, adaptation

Public significance statement: "Attention allows us 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 our 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 in order 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."

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, Adams, Graf, & Lavie, 2009), or to particular values within a dimension (e.g. upward, rather than downward motion; e.g. Lankheet & Verstraten, 1995). Finally, surface-, 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 are often 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 comprehensive review). However, the effects of attention on motion processing and motion adaptation remain contentious. The influence of attention is 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 apparent motion (Kohler, Haddad, Singer, & Muckli, 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 us 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, Cavanagh, & Intriligator, 1996). Given the key role of motion processing in guiding action and detecting threat, one might expect motion signals to be processed automatically (Vuilleumier, Armony, Driver, & Dolan, 2001). Consistent with this notion, motion is a strong cue for pop-out during visual search (Driver, McLeod, & Dienes, 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, Murray, & Boynton, 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 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, Krekelberg, & Dobkins, 2004) of the MAE. The attentional tracking paradigm has provided complementary findings: the MAE can be modulated by which one of two superimposed motion stimuli is attended during adaptation (e.g. Alais & Blake, 1999; Lankheet & Verstraten, 1995).

Neuroimaging studies have provided further evidence that attention modulates motion-related neural activity. For example, attending to moving dots 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 resulted in increased MT activation, relative to passive viewing (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 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, relative to high load conditions. Such an explanation seems at odds with reports of attentional modulation within groups of naïve subjects (e.g. Rezec et al., 2004). In addition, attentional modulation of the MAE has also been shown using 2AFC categorisation of test direction, which is arguably less susceptible to bias (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 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, vs. 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) are comprised 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, Wall, Williams, & Singh, 2006; Tanaka et al., 1986). Moreover, we now have evidence of enhanced activation in V1/MT due to surface-based attention (Kamitani & Tong, 2006; Wannig, Rodríguez, & Freiwald, 2007), potentially driven by feedback from MSTd. By directly comparing adaptation to translating and rotating motion, we can start to understand the relative importance of these different attentional mechanisms. Previous 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; 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 & Fox, 1974; Blake, Tadin, Sobel, Raissian, & Chong, 2006).

Experiments 1a and 1b directly compare adaptation to translational and complex motion, after multiple adaptation durations, under different attentional conditions. We hypothesised that, while 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 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.

Experiments 1a and 1b

Stimuli and Tasks

The experimental paradigm is shown in Figure 1. A single trial included 20 adaptation-test-response cycles. Each cycle began with a 10 sec 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˚. This region was enclosed by light and dark outer rings (see Figure 1) to enhance MAEs (Day & Strelow, 1971). In Experiment 1a, the dots drifted leftward or rightward at a rate of 4.8˚ / sec. 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˚ / sec; this rotation speed was chosen such that the median dot speed matched that of the translation experiment in terms of distance travelled per second.

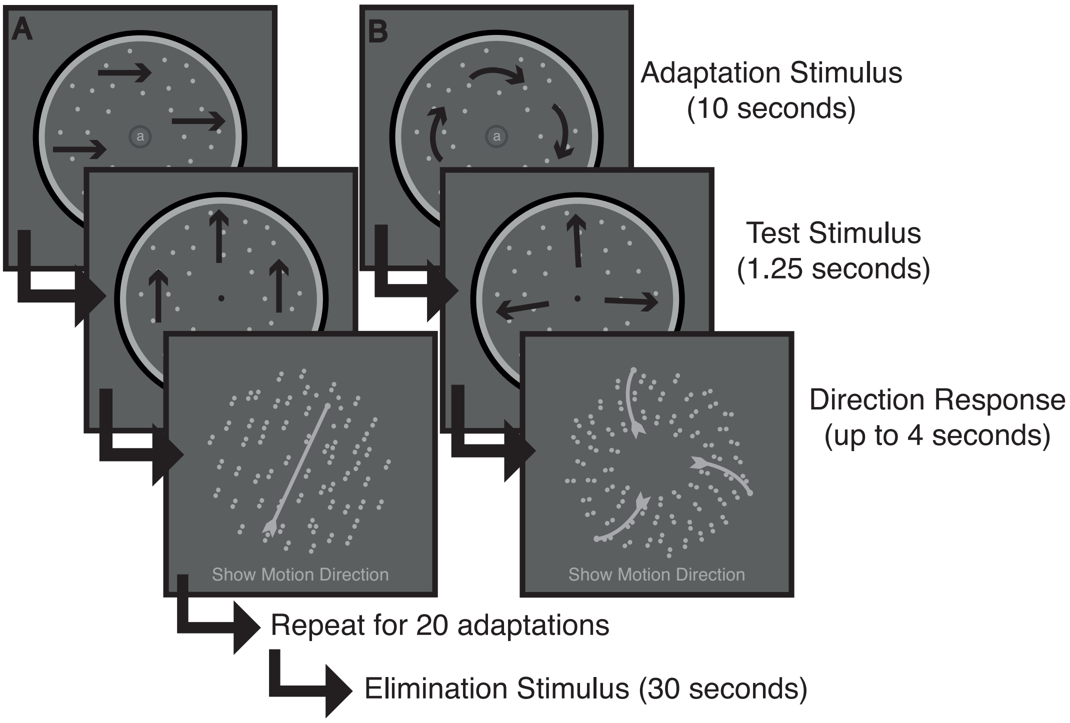

Figure 1. Schematic of a single trial. (a) Experiment 1a (translational motion) and (b) Experiment 1b (complex motion). Adaptation lasted 10 sec, whilst participants engaged in one of the two attentional tasks. The test stimulus was then presented for 1.25 sec, followed by a Glass pattern that was adjusted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

During each adaptation period the adaptation stimulus would, at unpredictable time points, briefly move with increased speed (for 3 frames / 50 msec). These motion changes were separated by random intervals within the range 1.5 sec – 6 sec. 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 second 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 sec and matched the adaptation stimuli in terms of spatial extent and number of dots (see Figure 1). In Experiment 1a, the test stimulus drifted either upwards or downwards (determined pseudo randomly) at 0.12˚ / sec. 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˚ / sec. 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 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 second window to complete this matching task, after which the next adaptation cycle began. The fixed time period for response ensured that the adaptation time course was matched across observers and conditions, and 4 seconds provided sufficient time to respond (average response times were 1.99 sec for Experiment 1a and 1.77 sec for Experiment 1b). 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 sec to prevent adaptation effects from carrying over to the subsequent trial. Participants pressed the space bar when ready to begin the next trial.

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 sec, 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 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˚/sec 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˚/sec (*SD* = 0.17), for Experiments 1a and 1b, respectively. Subjects 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” Apple iMac, with a nominal screen refresh rate of 60Hz and resolution of 2560 x 1440 pixels. A chinrest fixed the viewing distance at 54cm. The experiment was run using MATLAB (Mathworks) and the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007). The display was viewed binocularly, in a quiet dark room.

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, Fracasso, & Melcher, 2011; Taya et al., 2009). Power analyses for one-tailed within-sample *t*-tests were conducted in G*Power (Faul, Erdfelder, Lang, & Buchner, 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 subjects 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.

Results

Figure 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.

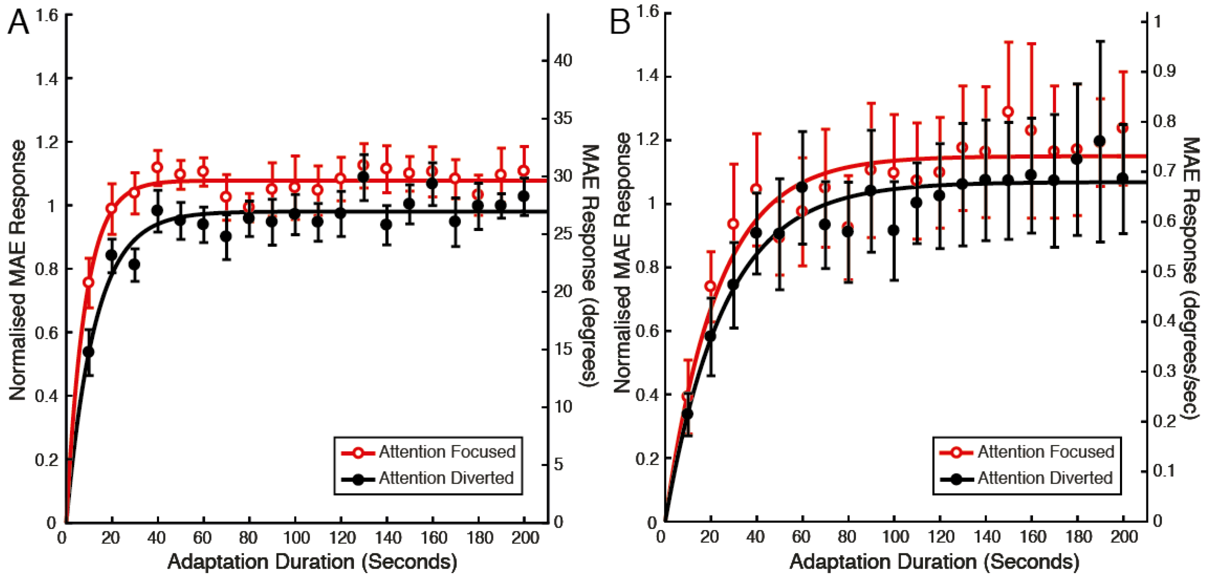

Figure 2. Measured MAEs for Experiment 1. (a) Translating adaptor (Expt 1a) and (b) Expanding / contracting adaptor (Expt 1b). Error bars represent standard error. Lines show exponential fits to the data.

Outliers (more than 2 standard deviations from the condition mean) and pre-emptive responses (those with a response time less than 0.5 seconds) 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, & Fairchild (2017), starting with the most complex model supported by the data, followed by stepwise elimination to remove extraneous factors. The initial model included attention, adaptation duration, motion type and subject naivety as fixed effects, in addition to their two-way interactions. Subject and by-subject variation in the effects of attention and motion type were included as random effects. 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 1.

Table 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
Subject naivety	0.56	0.07	8.09	7.67	< .001
Attention x Naivety	-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. Interestingly, and in contrast to our hypothesis, 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 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 subjects 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 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, 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 effect 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 vs. complex motion (F(1, 21) = 11.70, p = .003, d = 1.23): adaptation accumulates more quickly for translating than rotating motion.

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 timecourse of adaptation. In Experiment 2, we investigate the timecourse of adaptation with greater temporal resolution, by reducing each adaptation period from 10 seconds to 4 seconds. 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 3).

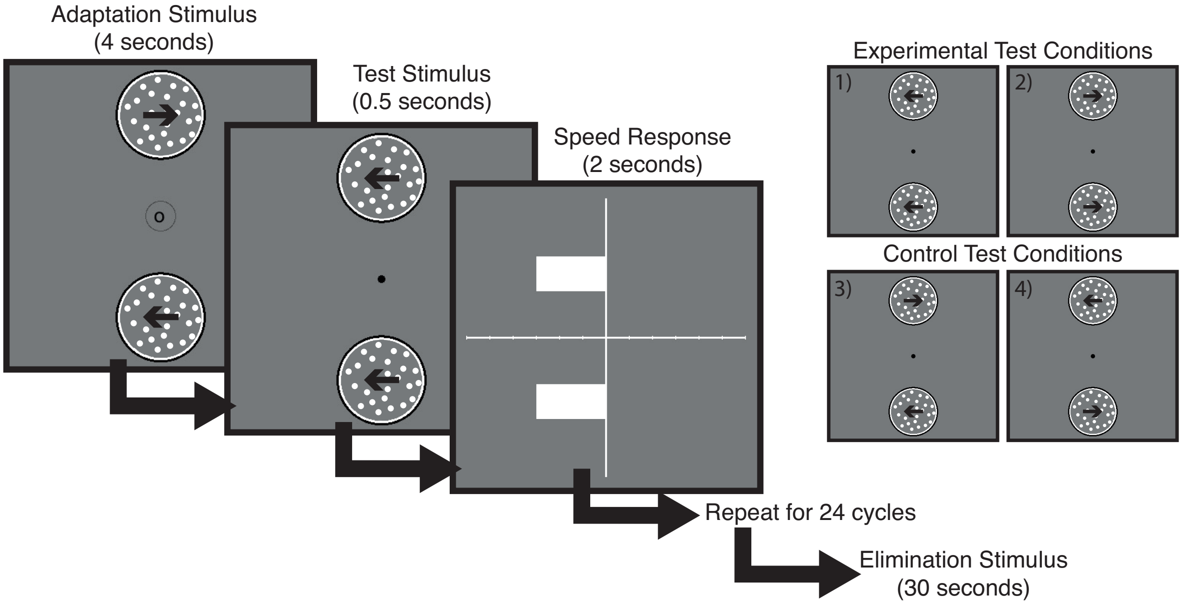

Figure 3. Schematic of trial in Experiment 2. The four possible test conditions are shown in the top right. Arrows illustrate the direction of motion, and were not present during the experiment.

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 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 faster. 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.

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 3). Light and dark rings enclosed each disk. Dots in the upper and lower patches drifted in opposite directions, either leftwards or rightwards, for 4secs, at 3.12° / sec. When reaching the disk edge, dots were reborn at the opposite side. Similarly to Experiment 1, dot speed could briefly increase during adaptation (for 50 msec), at random intervals in the range [1sec, 4sec]. 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 second of the change. Similarly, on attention-diverted trials, they had 1 second to detect light vowels within the letter stream. A tone provided feedback following false alarms or missed events.

The test stimuli (0.5 sec duration) matched the adaptation stimuli in spatial extent and number of dots. As shown in Figure 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 2.74°/sec and 3.19°/sec, or 2.89°/sec and 3.04°/sec, 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. (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. Subjects had 2 seconds 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 seconds, to prevent carryover effects across trials.

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 [2.30°, 3.63°] /sec, 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).

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.

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 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 seconds) were removed, corresponding to 8% of responses.

MAEs are shown in Figure 4 as a function of adaptation duration and attention condition. Similarly to 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 subject naivety, and two-way interactions were included as fixed effects. The random effects structure included subject, and per subject 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.

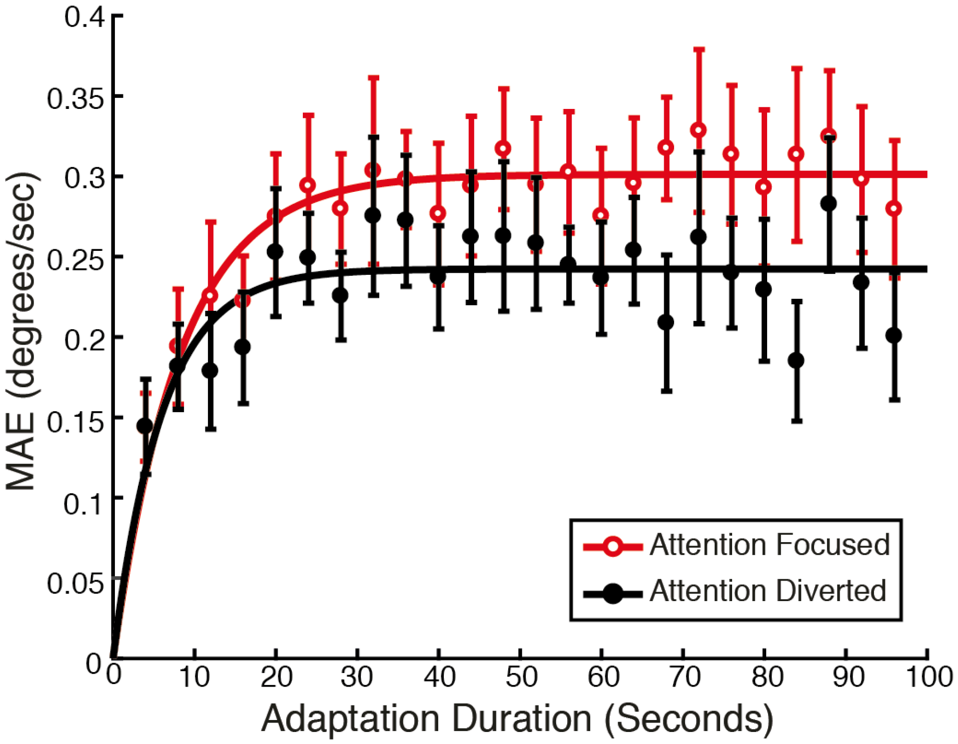

Figure 4. MAEs for Experiment 2. Error bars represent standard error. Lines show exponential fits to the data.

Table 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 / under-report 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 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). Similarly to Experiment 1, therefore, data from Experiment 2 suggest that attention predominantly effects the asymptotic MAE, rather than the rate at which it builds up.

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 complex motion (complex motion (Experiment 1b): *d* = 0.14, 8.79% increase vs. translational motion: *d* = 0.56, 10.23% increase (Experiment 1a), *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 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), i.e. 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, as subjects 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 & 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 & 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.

References

Addams, R. (1834). An account of a peculiar optical phenomenon seen after having looked at a moving body. *London and Edinburgh Philosophical Magazine and Journal of Science*, *5*(29), 373–374. https://doi.org/10.1080/14786443408648481

Alais, D., & Blake, R. (1999). Neural strength of visual attention gauged by motion adaptation. *Nature Neuroscience*, *2*(11), 1015–1018. https://doi.org/10.1038/14814

Anstis, S., Verstraten, F. A. J., & Mather, G. (1998). The motion aftereffect. *Trends in Cognitive Sciences*, *2*(3), 111–117. https://doi.org/10.1016/S1364-6613(98)01142-5

Bartlett, L., Hedger, N., Graf, E. W., & Adams, W. J. (2017). Attention modulates the motion aftereffect: A meta-analysis. *Journal of Vision*, *17*.

Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious mixed models. *arXiv*. Retrieved from http://arxiv.org/abs/1506.04967

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Blake, R., & Fox, R. (1974). Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature*, *249*, 488–490. https://doi.org/10.1038/249488a0

Blake, R., & Hiris, E. (1993). Another means for measuring the motion aftereffect. *Vision Research*, *33*(11), 1589–1592. https://doi.org/10.1016/0042-6989(93)90152-M

Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(12), 4783–4788. https://doi.org/10.1073/pnas.0509634103

Blaser, E., Papathomas, T., & Vidnyánszky, Z. (2005). Binding of motion and colour is early and automatic. *European Journal of Neuroscience*, *21*(7), 2040–2044.

https://doi.org/10.1111/j.1460-9568.2005.04032.x

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Büchel, C., Josephs, O., Rees, G., Turner, R., Frith, C. D., & Friston, K. J. (1998). The functional anatomy of attention to visual motion. A functional MRI study. *Brain*, *121*(7), 1281–1294. https://doi.org/10.1093/brain/121.7.1281

Burr, D. C., Baldassi, S., Morrone, M. C., & Verghese, P. (2009). Pooling and segmenting motion signals. *Vision Research*, *49*(10), 1065–1072. https://doi.org/10.1016/j.visres.2008.10.024

Burr, D., & Thompson, P. (2011). Motion psychophysics: 1985-2010. *Vision Research*, *51*(13), 1431–1456. https://doi.org/10.1016/j.visres.2011.02.008

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525. https://doi.org/10.1016/j.visres.2011.04.012

Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature*, *344*(6261), 60–62. https://doi.org/10.1038/344060a0

Day, R. H., & Strelow, E. (1971). Reduction or disappearance of visual after effect of movement in the absence of patterned surround. *Nature*, *230*(5288), 55–56. https://doi.org/10.1038/230055a0

Driver, J., McLeod, P., & Dienes, Z. (1992). Motion coherence and conjunction search: Implications for guided search theory. *Perception & Psychophysics*, *51*(1), 79–85. https://doi.org/10.3758/BF03205076

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/BF03193146

Frisby, J. P. (1979). *Seeing: Illusion, Brain and Mind*. Oxford University Press.

Georgiades, M. S., & Harris, J. P. (2000a). Attentional diversion during adaptation affects the velocity as well as the duration of motion after-effects. *Proceedings of the Royal Society of London B: Biological Sciences*, *267*(1461), 2559–2565. https://doi.org/10.1098/rspb.2000.1321

Georgiades, M. S., & Harris, J. P. (2000b). The spatial spread of attentional modulation of the motion aftereffect. *Perception*, *29*(10), 1185–1201. https://doi.org/10.1068/p3023

Glass, L. (1969). Moiré effect from random dots. *Nature*, *223*(5206), 578–580. https://doi.org/10.1038/223578a0

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, *383*(6598), 334–337. https://doi.org/10.1038/383334a0

Hershenson, M. (1993). Linear and rotation motion aftereffects as a function of inspection duration. *Vision Research*, *33*(14), 1913–1919. https://doi.org/10.1016/0042-6989(93)90018-R

Hopf, J. M., Heinze, H. J., Schoenfeld, M. A., & Hillyard, S. A. (2009). Spatiotemporal analysis of visual attention. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 235–250). Cambridge, MA: MIT Press.

Huk, A. C., & Heeger, D. J. (2000). Task-related modulation of visual cortex. *Journal of Neurophysiology*, *83*(6), 3525–3536.

Kamitani, Y., & Tong, F. (2006). Decoding seen and attended motion directions from activity in the human visual cortex. *Current Biology*, *16*(11), 1096–1102. https://doi.org/10.1016/j.cub.2006.04.003

Kaunitz, L., Fracasso, A., & Melcher, D. (2011). Unseen complex motion is modulated by attention and generates a visible aftereffect. *Journal of Vision*, *11*(13), 1–9. https://doi.org/10.1167/11.13.10

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception*.

Kohler, A., Haddad, L., Singer, W., & Muckli, L. (2008). Deciding what to see: The role of intention and attention in the perception of apparent motion. *Vision Research*, *48*(8), 1096–1106. https://doi.org/10.1016/j.visres.2007.11.020

Lankheet, M. J. M., & Verstraten, F. A. J. (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Research*, *35*(10), 1401–1412. https://doi.org/10.1016/0042-6989(95)98720-T

Lavie, N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(3), 451–468. https://doi.org/10.1037//0096-1523.21.3.451

Lavie, N. (2005). Distracted and confused?: Selective attention under load. *Trends in Cognitive Sciences*, *9*(2), 75–82. https://doi.org/10.1016/j.tics.2004.12.004

Lin, J. Y., Murray, S. O., & Boynton, G. M. (2009). Capture of attention to threatening stimuli without perceptual awareness. *Current Biology*, *19*(13), 1118–1122. https://doi.org/10.1016/j.cub.2009.05.021

Liu, T., Slotnick, S. D., Serences, J. T., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cerebral Cortex*, *13*(12), 1334–1343. https://doi.org/10.1093/cercor/bhg080

Lu, Z. L., & Sperling, G. (1995). Attention-generated apparent motion. *Nature*, *377*(6546), 237–239. https://doi.org/10.1038/377237a0

Martin-Key, N. A., Graf, E. W., Adams, W. J., & Fairchild, G. (2018). Facial emotion recognition and eye movement behaviour in conduct disorder. *Journal of Child Psychology and Psychiatry*, *59*(3), 247–257. https://doi.org/10.1111/jcpp.12795

Moors, A., & De Houwer, J. (2006). Automaticity: A theoretical and conceptual analysis. *Psychological Bulletin*, *132*(2), 297–326. https://doi.org/10.1037/0033-2909.132.2.297

Morgan, M. J. (2011). Wohlgemuth was right: Distracting attention from the adapting stimulus does not decrease the motion after-effect. *Vision Research*, *51*(20), 2169–2175. https://doi.org/10.1016/j.visres.2011.07.018

Morgan, M. J. (2012). Motion adaptation does not depend on attention to the adaptor. *Vision Research*, *55*, 47–51. https://doi.org/10.1016/j.visres.2011.12.009

Morgan, M. J. (2013). Sustained attention is not necessary for velocity adaptation. *Journal of Vision*, *13*(8), 1–11. https://doi.org/10.1167/13.8.26

Mukai, I., & Watanabe, T. (2001). Differential effect of attention to translation and expansion on motion aftereffects (MAE). *Vision Research*, *41*(9), 1107–1117. https://doi.org/10.1016/S0042-6989(00)00308-4

Nakayama, K., & Silverman, G. H. (1986). Serial and parallel processing of visual feature conjunctions. *Nature*, *320*(6059), 264–265. https://doi.org/10.1038/320264a0

Nishida, S., & Ashida, H. (2000). A hierarchical structure of motion system revealed by interocular transfer of flicker motion aftereffects. *Vision Research*, *40*(3), 265–278. https://doi.org/10.1016/S0042-6989(99)00176-5

O'Craven, K. M., Rosen, B. R., Kwong, K. K., Treisman, A., & Savoy., R. L. (1997). Voluntary attention modulates fMRI activity in human MT-MST. *Neuron*, *18*(4), 591–598. https://doi.org/10.1016/S0896-6273(00)80300-1

Pavan, A., & Greenlee, M. W. (2015). Effects of crowding and attention on high-levels of motion processing and motion adaptation. *PLoS ONE*, *10*(1), 1–27. https://doi.org/10.1371/journal.pone.0117233

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. https://doi.org/10.1080/00335558008248231

R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.r-project.org/

Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science*, *278*(5343), 1616–1619. https://doi.org/10.1126/science.278.5343.1616

Rezec, A., Krekelberg, B., & Dobkins, K. R. (2004). Attention enhances adaptability: Evidence from motion adaptation experiments. *Vision Research*, *44*(26), 3035–3044. https://doi.org/10.1016/j.visres.2004.07.020

Saproo, S., & Serences, J. T. (2014). Attention improves transfer of motion information between V1 and MT. *Journal of Neuroscience*, *34*(10), 3586–3596. https://doi.org/10.1523/JNEUROSCI.3484-13.2014

Scholl, B. J. (2001). Objects and attention: The state of the art. *Cognition*, *80*(1–2), 1–46. https://doi.org/10.1016/S0010-0277(00)00152-9

Sinha, D. (1952). An experimental study of a social factor in perception: The influence of an arbitrary group-standard. *Patna University Journal*, *6*(1), 7–16.

Smith, A. T., Wall, M. B., Williams, A. L., & Singh, K. D. (2006). Sensitivity to optic flow in human cortical areas MT and MST. *European Journal of Neuroscience*, *23*(2), 561–569. https://doi.org/10.1111/j.1460-9568.2005.04526.x

Takeuchi, T., & Kita, S. (1994). Attentional modulation in motion aftereffect. *Japanese Psychological Research*, *36*(2), 94–107.

Tanaka, K., Hikosaka, K., Saito, H., Yukie, M., Fukada, Y., & Iwai, E. (1986). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *Journal of Neuroscience*, *6*(1), 134–144.

Taya, S., Adams, W. J., Graf, E. W., & Lavie, N. (2009). The fate of task-irrelevant visual motion: Perceptual load versus feature-based attention. *Journal of Vision*, *9*(12), 1–10. https://doi.org/10.1167/9.12.12

Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology*, *19*(1), 11–14.

https://doi.org/10.1016/j.cub.2008.10.014

Treue, S., & Martínez-Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, *399*, 575–579. https://doi.org/10.1038/21176

Treue, S., & Maunsell, J. H. R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature*, *382*, 539–541. https://doi.org/10.1038/382539a0

Verstraten, F. A. J., Fredericksen, R. E., Grüsser, O. J., & Van De Grind, W. A. (1994). Recovery from motion adaptation is delayed by successively presented orthogonal motion. *Vision Research*, *34*(9), 1149–1155. https://doi.org/10.1016/0042-6989(94)90297-6

Verstraten, F. A. J., Fredericksen, R. E., Van Wezel, R. J. A., Lankheet, M. J. M., & Van De Grind, W. A. (1996). Recovery from adaptation for dynamic and static motion aftereffects: Evidence for two mechanisms. *Vision Research*, *36*(3), 421–424. https://doi.org/10.1016/0042-6989(95)00111-5

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: An event-related fMRI study. *Neuron*, *30*(3), 829–841. https://doi.org/https://doi.org/10.1016/S0896-6273(01)00328-2

Wannig, A., Rodríguez, V., & Freiwald, W. A. (2007). Attention to surfaces modulates motion processing in extrastriate area MT. *Neuron*, *54*(4), 639–651. https://doi.org/10.1016/j.neuron.2007.05.001

Watanabe, T., Harner, A. M., Miyauchi, S., Sasaki, Y., Nielsen, M., Palomo, D., & Mukai, I. (1998). Task-dependent influences of attention on the activation of human primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(19), 11489–11492. https://doi.org/10.1073/pnas.95.19.11489

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method.

Perception & Psychophysics, *33*(2), 113–120. https://doi.org/10.3758/BF03202828

Wertheimer, M. (1961). Experimental studies on the seeing of motion. In T.Shipley (Ed.), *Classics in Psychology* (pp. 1032–1089). New York: Philosophical Library.

Wohlgemuth, A. (1911). On the after-effect of seen motion. *British Journal of Psychology*, *1*, 1–117.