



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

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Motion adaptation and attention: A critical review and meta-analysis.

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3
4 The motion aftereffect (MAE) provides a behavioural probe into the mechanisms underlying
5 motion perception, and has been used to study the effects of attention on motion processing.
6 Visual attention can enhance detection and discrimination of selected visual signals.
7 However, the relationship between attention and motion processing remains contentious: not
8 all studies find that attention increases MAEs. Our meta-analysis reveals several factors that
9 explain superficially discrepant findings.

10
11 Across studies (37 independent samples, 76 effects) motion adaptation was significantly and
12 substantially enhanced by attention (Cohen's $d=1.12$, $p<.0001$). The effect more than doubled
13 when adapting to translating (vs. expanding or rotating) motion. Other factors affecting the
14 attention-MAE relationship included stimulus size, eccentricity and speed. By considering
15 these behavioural analyses alongside neurophysiological work, we conclude that feature-
16 based (rather than spatial, or object-based) attention is the biggest driver of sensory
17 adaptation.

18
19 Comparisons between naïve and non-naïve observers, different response paradigms, and
20 assessment of 'file-drawer effects' indicate that neither response bias nor publication bias are
21 likely to have significantly inflated the estimated effect of attention.

22
23 Keywords:
24 *Attention, motion adaptation, motion aftereffect, systematic review, meta-analysis*

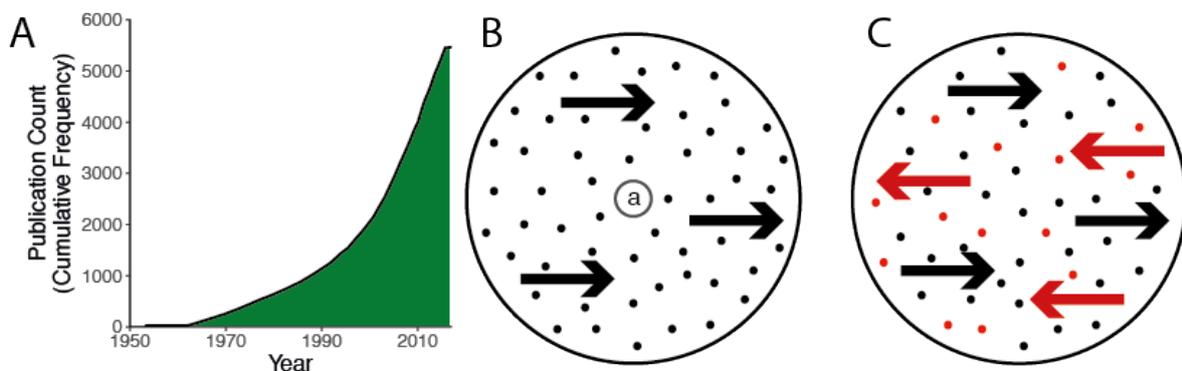
25

26 **1. Background**

27 Attention refers to our ability to selectively process certain aspects of a visual scene, such
28 that particular regions or features are enhanced, and irrelevant stimuli are inhibited (Carrasco,
29 2011). The effects of attention on perceptual processes are usually measured via
30 manipulations of covert attention in which attention is directed independently of eye
31 movements. This contrasts with overt attention, in which a redirection of attention is
32 accompanied by an eye movement to fixate the attended region. Covert spatial attention
33 enhances signals from the attended location, reducing noise, and changing decision criteria
34 (see Carrasco, 2011 for an overview), and has been shown to operate at all levels of the visual
35 hierarchy, even early visual areas previously believed to be pre-attentive and entirely sensory,
36 i.e. the primary visual cortex (V1) (e.g. Silver et al., 2007; Somers et al., 1999). Whether such
37 attentional effects generalize to motion processing, however, remains contentious. Here we
38 consider evidence for the influence of covert attention on motion processing, as evidenced by
39 effects of attention on motion adaptation.

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

51 The effect of attention on luminance-defined motion processing has been probed
52 behaviourally via the motion after-effect (MAE): following prolonged inspection of a moving
53 stimulus, illusory motion is perceived in the opposite direction. Descriptions of the MAE date
54 back to Aristotle, and it was popularised by Addams (1834) as the ‘the waterfall effect’.
55 After-effects have earned the label of the “psychologist’s microelectrode” (Frisby, 1979) and
56 the MAE is viewed as a powerful research tool for probing motion-sensitive mechanisms (see
57 Fig. 1a).



58
59 **Fig. 1.** (a) Cumulative frequency of publications related to the motion aftereffect. A PubMed
60 search (keywords: motion aftereffect OR motion adaptation) revealed 5470 publications since
61 1950. (b & c) A schematic of typical paradigms used to measure the effect of covert attention
62 on motion adaptation. (b) A moving stimulus is presented within an annulus. To manipulate
63 attention, a centrally presented stimulus such as a stream of letters is fixated, while observers
64 perform either a difficult / high-load task, or an easy / low-load task, or passively view the
65 stimulus. (c) The motion tracking paradigm: two populations of dots (indicated here by
66 different colours) each follow a different motion trajectory. Observers attend to one of the
67 two superimposed motion patterns.

68
69 If basic motion mechanisms are affected by spatial attention, we expect to find larger
70 MAEs when attention is directed towards, rather than away from a moving adaptation
71 stimulus. However, in an influential paper exploring the MAE, Wohlgenuth (1911) reported

72 that diverting attention to a central rapid serial visual presentation (RSVP) task had no effect
73 on adaptation to a spiral motion stimulus, leading to a long-held view that the mechanisms
74 responsible for motion adaptation are pre-attentive. Indeed, some recent papers continue to
75 endorse this view (Morgan, 2013, 2012, 2011). This suggestion – that motion adaptation is
76 independent of attention - is aligned with previous reports that adaptation to other simple
77 visual features (spatial frequency, orientation) is unaffected by attention or awareness (Blake
78 & Fox, 1974; He, Cavanagh, & Intriligator, 1996).

79 A landmark study by Chaudhuri (1990) challenged this pervasive view. Observers viewed
80 a large moving stimulus for 60 seconds. During this adaptation period, numbers and letters
81 appeared within a small central aperture and observers either engaged in a demanding
82 alphanumeric task, or passively viewed the stimulus (see Fig. 1b). Observers subsequently
83 viewed a static stimulus and reported the MAE duration. Attending to the central task caused
84 a substantial reduction in the duration of the subsequent motion after-effect. Subsequently,
85 multiple studies have similarly found that diverting attention away from a moving adaptor
86 reduces the duration (e.g. Chaudhuri, 1990; Rezec, Krekelberg, & Dobkins, 2004) or velocity
87 of the subsequent MAE (e.g. Georgiades & Harris, 2000a; Taya, Adams, Graf, & Lavie,
88 2009).

89 In broad agreement with this behavioural data, neuroimaging evidence suggests that,
90 under similar attentional manipulations, motion-related activity in medial temporal (MT) /
91 medial superior temporal (MST) areas is modulated by attention (Beauchamp et al., 1997;
92 Rees et al., 1997). Load theory of selective attention suggests that during a demanding task,
93 limited resources are available to process task-irrelevant information (such as a peripheral
94 motion stimulus). Conversely, a low-load task requiring fewer resources leads to greater
95 processing of task irrelevant stimuli (Lavie, 2005). Rees, Frith, & Lavie (1997) presented
96 irrelevant expanding motion in the periphery and words at fixation. In line with attentional

97 load theory, a low load task (detect uppercase words) resulted in increased activation across
98 several areas (MT, V1/V2 and the superior colliculus) and longer MAE durations, relative to
99 a high-load task (detect bisyllabic words).

100 A clear consensus on whether (or under what conditions) attention increases motion
101 adaptation is yet to emerge, however, due to null (Morgan, 2013, 2012, 2011; Pavan and
102 Greenlee, 2015), or inconsistent findings (e.g. Georgiades & Harris, 2002b; Takeuchi & Kita,
103 1994). One might argue that, given the importance of motion for fundamental tasks such as
104 segmentation (including breaking camouflage), depth perception and guiding self-motion
105 (e.g. Gibson, 1958; Nakayama, 1985), it would be evolutionarily advantageous if motion
106 were processed independently of attention. Certainly, motion is a powerful cue for pop-out in
107 visual search (Driver et al., 1992; Nakayama and Silverman, 1986). If motion adaptation
108 mechanisms are pre-attentive, why have many studies reported an effect of attention on
109 MAEs? One suggestion is that affirmative findings reflect response bias: observers expect
110 weaker MAEs to follow diverted-attention conditions and bias their responses accordingly.
111 Measures of MAE duration (as used by Chaudhuri, 1990 and others) may be particularly
112 susceptible to bias / criterion effects because observers struggle to determine the point at
113 which the MAE has completely disappeared (Morgan, 2012; Blake & Hiris, 1993).

114 Other factors, such as the choice of stimuli and experimental paradigm almost
115 certainly contribute to variability across the findings from different studies. Paradigms differ
116 in the extent to which the attentional manipulations direct spatial, featural and surface /
117 object-based attention. As reviewed below (see section 1.2.1.1), a coherently translating
118 stimulus may recruit feature-based attention more effectively than complex (rotating and /or
119 expanding) stimuli. Others have demonstrated that the eccentricity of the adaptor (Georgiades
120 and Harris, 2000a, 2000b) and the type of test stimulus (static vs. dynamic; Culham,
121 Verstraten, Ashida, & Cavanagh, 2000) may modulate the effect of attention. Attentional

122 tracking paradigms, in which observers attend one of two superimposed motion stimuli (e.g.
123 Lankheet & Verstraten, 1995; Mukai & Watanabe, 2001; see Fig. 1c) may reveal larger
124 attentional effects than those that direct attention towards or away from the location of a
125 single motion stimulus (Morgan, 2011). A meta-analysis allows us to evaluate all of these
126 factors and others (as detailed in Section 1.2) such that we can better understand whether, and
127 under what conditions, motion processing (and motion adaptation) is modulated by attention.

128

129 *1.1. The current review: justification and objectives*

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

137

138 *1.2. Factors that may affect the relationship between attention and motion processing*

139 *1.2.1. Characteristics of the adaptation stimulus*

140 *1.2.1.1. Type of motion*

141 The effect of attention on neural responses to motion stimuli may depend on the type
142 of motion being presented. Spatial attention has been shown to increase the overall response
143 gain of MT neurons corresponding to the attended region (Treue and Martínez-Trujillo,
144 1999). In contrast, feature-based attention has a substantial direction-specific effect, such that
145 neurons in V1, MT and MST tuned to the attended motion direction show a response gain,
146 while neurons tuned to the opposite direction are suppressed (Saproo and Serences, 2014;

147 Treue and Martínez-Trujillo, 1999; Treue and Maunsell, 1996). Importantly, this effect of
148 feature-based attention spreads across the visual field, such that attending to leftward motion
149 in one location will enhance processing of leftward motion across all retinal locations. One
150 would expect this direction-specific modulation of neural activation to have a large role in the
151 enhancement of MAEs. When observers attend to a large, coherently translating stimulus
152 (vs. central letters, for example), spatial and feature-based attention will combine (Treue and
153 Martínez-Trujillo, 1999) to enhance the neural representation of the moving stimulus across
154 multiple motion-sensitive cortical regions.

155 In contrast to translating stimuli, rotating or expanding motion patterns are composed
156 of local motion signals whose directions vary as a function of position (Carrasco, 2011).
157 Attending to these complex motion stimuli will not, therefore, enhance V1/MT activity via
158 simple feature-based attention mechanisms. However, there is now evidence from
159 neurophysiology (Wannig et al., 2007) and fMRI (Kamitani and Tong, 2006) that surface, or
160 object-based attention can enhance V1 and MT activation as a function of both direction and
161 position, when more complex motion patterns are attended. These effects could be driven by
162 feedback from the dorsal section of MST (MSTd), an area known to have larger and more
163 complex receptive fields that have been implicated in optic flow processing (Graziano et al.,
164 1994; Saito et al., 1986; Tanaka and Saito, 1989).

165 Behavioural studies of attention and motion processing often assume, implicitly, that
166 increased motion-related activation (due to attention) can be inferred from changes in
167 adaptation. However, adaptation effects may vary across regions. Following prolonged
168 activation, V1 neurons show substantial reductions in responsiveness and sensitivity to
169 motion directions close to the adapted direction. However, reductions in responsivity in MT
170 are much smaller (Kohn and Movshon, 2004, 2003). Thus, differences in adaptation across
171 the cortex, in addition to variations in the effects of spatial, featural and surface-based

172 attention on neural responses to translating vs. complex motion patterns, strongly suggest that
173 the effect of attention on adaptation will depend on the type of motion stimulus.

174

175 *1.2.1.2. Size of adaptation stimuli*

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

183

184 *1.2.1.3. Eccentricity of adaptation stimuli*

185 Most paradigms used to explore the attention-motion relationship use an attentional
186 task related to a central stimulus to draw attention away from a peripheral motion stimulus.
187 One might expect that when the adaptation stimulus is close to the distracting stimulus,
188 attentional resources may ‘spill over’ to the motion stimulus more easily. A key component
189 of the load theory of attention is that the target and distractor must be spatially separated
190 (Lavie, 2005). A demanding task at fixation may reduce the extent to which peripheral
191 distractors are processed, by narrowing the window of spatial attention around the central,
192 task relevant stimuli. Thus, more eccentric adaptation stimuli may reveal larger effects of
193 attentional modulation. Conversely, there is some empirical evidence that attentional
194 modulation is stronger for adaptation stimuli closer to fixation (Georgiades and Harris,
195 2000a, 2000b).

196

197 *1.2.1.4. Speed of adaptation stimuli*

198 Many studies have considered how motion adaptation varies as a function of adaptor
199 speed, classically reported to follow an inverted U-shape (see Thompson, 1998 for an
200 overview). In terms of attention, Georgiades & Harris (2002b) found that attention modulated
201 motion adaptation for faster adaptation stimuli. However, for slower adaptation stimuli, the
202 effect of attention increased with spatial frequency. The relationship between speed,
203 attention, and motion processing has rarely been examined within studies. However, the wide
204 range of adaptation speeds used across different studies allows us to explore this in the
205 current analysis.

206

207 *1.2.1.5. Adaptation duration*

208 As adaptation duration increases, MAEs increase (Hershenson, 1993). In previous
209 work, we explored how the effects of attention vary across the adaptation period by
210 measuring the MAE at regular intervals during an extended adaptation period (Bartlett et al.,
211 2018). Attention affected the asymptotic MAE magnitude, but not the rate at which it
212 accumulated (i.e. the time constant). This finding is broadly consistent with Takeuchi & Kita
213 (1994), who found that diverted attention led to reduced MAEs across adaptation durations of
214 20, 40 and 80 seconds.

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

222

223 *1.2.2. Test stimulus characteristics*

224 *1.2.2.1. Static vs. dynamic test stimuli*

225 Motion adaptation can be quantified using static test stimuli (e.g. Chaudhuri, 1990) or
226 dynamic tests, such as random dot motion patterns (e.g. Mukai and Watanabe, 2001; Taya et
227 al., 2009) or counterphase flicker (e.g. Nishida and Ashida, 2000; Rezec et al., 2004). Nishida
228 & Sato (1995) suggested that static test stimuli reflect adaptation to first order motion,
229 whereas dynamic (flicker) tests reveal second order MAEs. Static and dynamic tests may
230 also differ in terms of sensitivity to monocular vs. binocular motion mechanisms (e.g.
231 Nishida & Ashida, 2000), and to storage effects (e.g. Verstraten, Fredericksen, Van Wezel,
232 Lankheet, & Van De Grind, 1996). Using an attentional tracking paradigm (see Fig. 1c),
233 Culham, Verstraten, Ashida, & Cavanagh (2000) reported that attention modulated the MAE
234 only when measured via a dynamic test. In summary, MAEs obtained from static and
235 dynamic test stimuli may reflect different motion mechanisms that are differentially
236 modulated by attention.

237

238 *1.2.3. Experimental paradigm*

239 *1.2.3.1. MAE measurement and response*

240 Many studies have quantified the effects of attention on motion adaptation by asking
241 observers to report the cessation of the (illusory) motion of a static test stimulus, i.e. the MAE
242 duration (Chaudhuri, 1990; Morgan, 2012; Rezec et al., 2004). As noted above, this reporting
243 method has been criticised as susceptible to response bias. Alternatively, MAE magnitude
244 has been quantified via velocity matching (Georgiades and Harris, 2000a). 2AFC designs
245 have also been implemented, in which participants select one of two response options, such
246 as the test stimulus' motion direction (e.g. Kaunitz, Fracasso, & Melcher, 2011; Taya et al.,

247 2009) or which of two test stimuli was moving faster (Morgan, 2013). Some 2AFC
248 paradigms use nulling techniques in which the percentage of test stimulus dots moving
249 oppositely to the aftereffect (Blake & Hiris, 1993; e.g. Mukai & Watanabe, 2001) or the
250 phase shift of the test (e.g. Culham et al., 2000) is adjusted to counteract the aftereffect.
251 2AFC / two interval forced choice (2IFC) designs have been considered preferable to
252 duration or matching tasks in terms of minimising response bias (Morgan, 2013).

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

256

257 *1.2.3.2. Attentional manipulation*

258 Two distinct methods of manipulating attention have been used in the context of
259 motion adaptation. ‘Distractor’ paradigms involve diverting attention away from a moving
260 adaptation stimulus – usually towards a centrally presented, difficult task (see Fig. 1b). This
261 condition is compared with one in which more attention is deployed to the adaptation
262 stimulus, for example during passive viewing. This paradigm involves spatial attention (the
263 moving adaptor and central task are spatially separated). Depending on the type of motion, it
264 may also involve feature and / or surface based attention, as discussed above. Some would
265 also consider it to involve ‘dimension’ based attention, i.e., attention to motion rather than
266 another visual dimension such as colour or shape, because the central task does not usually
267 rely on motion. Reductions in motion-related activation in V1 and MT/MST have been found
268 when attention is directed to the colour or luminance of a moving stimulus, rather than its
269 motion (Beauchamp et al., 1997; Saproo and Serences, 2014), with corresponding changes in
270 the resultant MAE also reported (Taya et al., 2009).

271 In contrast, ‘attentional tracking’ paradigms ask subjects to attend to one of two
272 superimposed motion patterns (see Fig. 1c). This relies on feature-based attention: i.e.
273 attention is directed to one motion direction, at the expense of another motion direction.
274 Studies that have used attentional tracking have fairly consistently demonstrated attentional
275 modulation of motion adaptation (e.g. Alais and Blake, 1999; Culham et al., 2000; Lankheet
276 and Verstraten, 1995). Accordingly, it has been suggested that the two paradigms probe
277 distinct attentional mechanisms that vary in their effects on motion processing (Morgan,
278 2012, 2011).

279

280 *1.2.4. Participant characteristics*

281 *1.2.4.1. Participant naivety*

282 It is often noted that the risk of response bias increases with certain paradigms (as
283 discussed in Section 1.2.3.1), and also with non-naïve observers who may know the research
284 hypotheses. As noted above, there have been claims that some reports of attentional
285 modulation of motion adaptation are not just inflated by, but due to response bias (Morgan,
286 2013, 2012). Indeed, Morgan (2012) failed to find attentional modulation of motion
287 adaptation with naïve observers. The overall picture, however, is less clear, with other studies
288 finding significant effects within groups of naïve observers (e.g. Chaudhuri, 1990; Patterson
289 et al., 2005).

290

291 **2. Method**

292 *2.1. Inclusion and coding decisions*

293 *2.1.1. Inclusion criteria*

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

- 295 1. The study manipulated attention during motion adaptation and reported the
296 subsequent behavioural motion aftereffect.
- 297 2. The stimuli did not differ across attentional manipulations.
- 298 3. The study was published in an English language journal on or before August 2016.
- 299 4. Participants were healthy human adults – studies using patient populations were
300 excluded.
- 301 5. The study was not a re-analysis of existing data
- 302 6. Sufficient information was provided in order to estimate an effect size (see section
303 2.3).
- 304 7. Only within subject designs were included, due to well-known issues equating within
305 subject and between subject effect size measurements (Lakens, 2013). This removed
306 7.32% of effects.

307

308 *2.1.2. Other coding and inclusion decisions*

- 309 1. If the study assessed both a low load and a no load (passive) condition, these data
310 were pooled into a single ‘low load’ condition and compared against the high load
311 condition.
- 312 2. If the study included a manipulation that was not pertinent to the research questions
313 (e.g. different levels of contrast in the adapting stimulus; Rezec et al., 2004), data
314 were pooled across this manipulation (see Supplementary Material S1 for a full list).
- 315 3. In order to reduce un-modelled variability, data from conditions / experiments with
316 atypical presentation conditions were excluded. For example, in studies investigating
317 interocular transfer, only data from conditions in which adaptation and test stimuli
318 were presented to the same eye(s) were included (e.g. Nishida and Ashida, 2000). See

319 Supplementary Material S1 for a full list of included effects and details regarding
320 excluded conditions.

321 4. If the study was investigating awareness, we only included the data from conditions
322 where observers were aware of the adapter (e.g. Kaunitz et al., 2011).

323 5. Only visual manipulations of attention were included; auditory attention conditions
324 were excluded (e.g. Houghton, Macken, & Jones, 2003).

325

326 *2.2. General search and coding strategies*

327 One of the authors (LB) conducted the search for relevant studies and coded the data,
328 in consultation with all authors. A PubMed database search was first conducted.

329 Subsequently, the reference sections of all relevant studies were examined to identify
330 additional relevant papers. Next, articles citing any of the relevant studies were identified via
331 Google Scholar, and the reference lists of all of these articles were then examined. A
332 summary of the excluded articles and the database search terms are presented in the
333 Supplementary Material S2, according to the ‘Preferred Reporting Items for Systematic
334 reviews and Meta Analysis’ guidelines (PRISMA: Moher, Liberati, Tetzlaff, Altman, & The
335 PRISMA Group, 2009).

336

337 *2.3. Methods*

338 *2.3.1. Effect size metric*

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

343

344 2.3.2. Standardisers for d

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

$$348 \quad d_{av} = \frac{M_{diff}}{\frac{SD_1 + SD_2}{2}} \quad \text{Equation 1.}$$

349 This formula is recommended for repeated measures designs where there is no pre-post
350 distinction (e.g. before or after treatment). Because both SD measures are equally good
351 estimators of population variability, averaging the two gives the best estimate (Cumming,
352 2012). In cases where standard deviations were only reported for multiple levels of an
353 irrelevant experimental variable, these values were pooled to reflect the standard deviation
354 collapsed across these levels (see Supplementary Material S3).

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

$$358 \quad d_{RM} = \frac{t}{\sqrt{N}} \times \sqrt{2(1 - r)} \quad \text{Equation 2.}$$

359 In practice, few effect sizes were calculated using d_{RM} (13.16% of overall). As
360 Equation 2 indicates, this estimate corrects for the paired correlation (r) between conditions.
361 These correlations were calculated using equations reported by Morris & DeShon (2002),
362 after first computing the variance of difference scores using reported N , M_{diff} and t values (see
363 Supplementary Material S4). Paired correlations were estimated for the five effects for which
364 the required data were available, however one was removed as it fell outside the possible
365 range, leaving 4 correlations in total ($M = 0.81$, $SD = 0.31$). The mean of these correlations
366 was then assumed for the remaining calculations of d_{RM} .

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

368 $SE = \sqrt{\frac{1}{\frac{N+d^2}{2N}}}$ Equation 3.

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

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

376

377 2.4. Model and analysis decisions

378 Effect size data were analysed in a random effects model. This model assumes that
379 studies are estimating independent, randomly sampled values of the population parameters,
380 and it is tolerant to heterogeneity across effect sizes (Cumming, 2012). Total effect size
381 heterogeneity was estimated using the standardised measure Cochran’s *Q*, while *I*² was used
382 to estimate additional heterogeneity beyond that expected in a fixed effects model (Cumming,
383 2012). Parameter estimates were derived via restricted maximum likelihood estimation to
384 minimise bias (Viechtbauer, 2005).

385 To statistically assess model coefficients, Wald-type chi squared tests were computed.
386 The pseudo-*R*² statistic was used to quantify the heterogeneity across effect sizes that was
387 explained by moderators (see Supplementary Material S5). The unstandardized regression
388 coefficient (*b*) indicated the direction and magnitude of effects. Likelihood ratio tests were
389 used to compare models (whose parameters were derived via maximum likelihood
390 estimation), in order to identify moderators that made a significant contribution to explained

391 heterogeneity. All analyses were carried out in *R*, using the ‘metafor’ package (Viechtbauer,
392 2010).

393

394 *2.5. Dependency among effect sizes*

395 The number of included conditions (nested within samples) and the number of
396 independent samples (nested within studies) were coded. In some cases, samples were
397 exposed to many conditions, resulting in multiple effect sizes from a single group of
398 participants. Collapsing the data across these effects would ignore important information.
399 However, the contribution of multiple effect sizes by a sample introduces dependency in the
400 data; the results of the meta-analysis can become biased towards the (correlated) effect size
401 estimates due to a single unrepresentative sample. The influence of dependency was
402 examined by creating multi-level models (Cheung, 2014) where conditions (level 2) were
403 nested within their samples (level 3). This allowed us to determine whether there was a
404 significant effect size dependency (i.e. whether a 3-level model provides a better fit than a 2-
405 level model). In addition, we investigated the influence of dependency by creating resampled
406 data sets that included one effect size from each independent sample. This allows an
407 examination of the data under conditions where dependency is eliminated (Greenhouse and
408 Iyengar, 1994).

409

410 **3. Results**

411 *3.1. Summary of included data*

412 In total, 29 studies were analysed, involving 229 participants across 37 independent
413 samples, yielding 76 effect size estimates. Detailed information about each effect is available
414 in the Supplementary Material S1. Two effect sizes were more than ± 3 SDs from the mean.
415 However, removing these outliers reduced the overall effect size by only 0.04 and all

416 significant moderators remained significant. They were therefore included in the main
417 analysis. The coding for each moderator variable can be found in Table 1, and a summary of
418 moderator coding for each effect can be found in Supplementary Material S6.
419

420 Table 1

421 *Moderator coding*

Moderator	Type	Values	Description of variable	Descriptive Statistics*	Missing Cases
<u>Characteristics of adaptation stimulus</u>					
Type of motion (Section 1.2.1.1)	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 _i =46 N _j =30	0
Adaptation stimulus area (Section 1.2.1.2)	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 1.2.1.3)	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°-5°	21
Speed of adaptation stimuli (Section 1.2.1.4)	Continuous	0.6°/sec-8°/sec	The speed of the adaptation stimulus. Calculated tangential speed at average eccentricity for rotational motion.	k=45 μ=4.16°/sec σ=1.79°/sec Range=0.6°/sec-8°/sec	31
Duration of adaptation (Section 1.2.1.5)	Continuous	1 sec-90 sec	The duration of a single adaptation period within each trial.	k=66 μ= 40.11 sec σ=21.40 sec Range=1-90 sec	10
<u>Test stimulus characteristics</u>					
Static vs. dynamic test stimuli	Categorical	1=Static 2=Dynamic	The type of test stimulus used to measure the MAE.	k=76 N _i =44	0

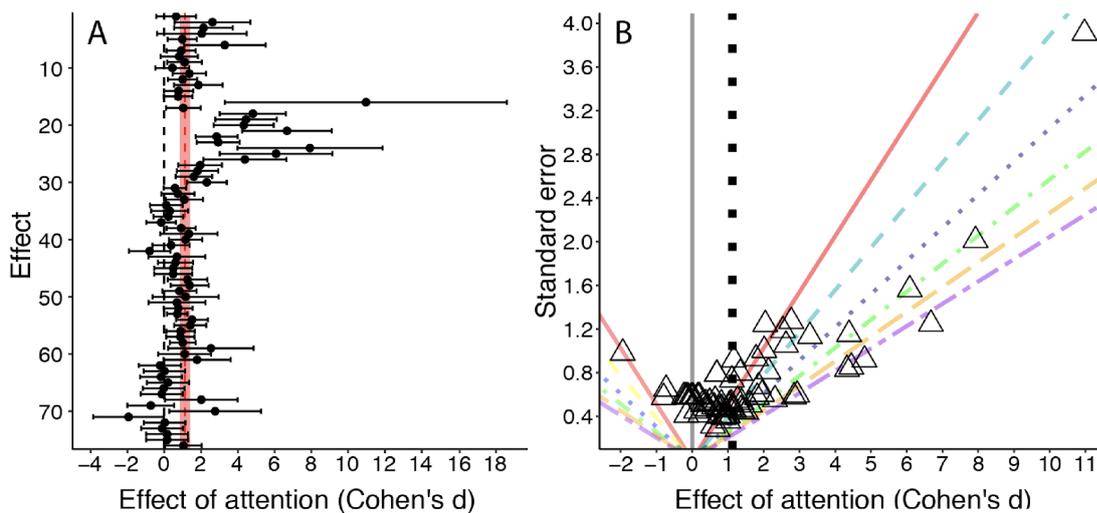
(Section 1.2.2.1)					$N_i=32$	
<u>Experimental paradigm</u>						
MAE measurement (Section 1.2.3.1)	Categorical	1=Duration 2=Strength	The method of measuring the MAE. ‘Duration’ paradigms record the time until MAE cessation. The ‘strength’ category includes all other methods of MAE measurement (e.g. nulling, 2AFC).	$k=92$ $N_i=51$ $N_i=25$		0
MAE response (Section 1.2.3.1)	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.	$k=76$ $N_i=64$ $N_i=12$		0
Attentional manipulation (Section 1.2.3.2)	Categorical	1 = Distractor 2 = Tracking	The paradigm for manipulating attention. Distractor paradigms (see Fig. 1b) divert attention from adapting motion with a centrally presented task. Attentional tracking (see Fig. 1c) involves attending to one of two superimposed motion directions.	$k = 76$ $N_i=70$ $N_i=6$		0
<u>Participant characteristics</u>						
Participant naivety (Section 1.2.4.1)	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.	$k=69$ $N_i=44$ $N_i=25$		7

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

423 3.2. Overall effect size of attentional modulation of the MAE

424 Results of the meta-analyses are depicted in Fig. 2. A large effect of attention was
425 found ($k=76, N=229, d_{av}=1.12, 95\% \text{ CI } [0.87, 1.38], p<.001$). A number of analyses were
426 conducted to explore potential file-drawer effects (in which null effects are sometimes
427 unpublished). Rosenthal's (1991) fail-safe N indicated that 7,767 additional, null studies
428 would be required to reduce the pooled effect size to non-significance. The actual number of
429 unpublished (negative effect) studies was estimated to be 7, using the trim and fill method,
430 based on the symmetry of the data (Duval and Tweedie, 2000a, 2000b). Attentional
431 modulation of the MAE remained significant when these (simulated) effects were included,
432 reducing the effect by only 0.18. When any single contributing effect was removed, the
433 pooled effect remained significant (leave-one-out analysis, range $[1.07, 1.15], ps<.001$). See
434 Supplementary Material S7 for more details and figures.

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



438
439 **Fig. 2.** Summary of the effect of attention on the MAE. a) Forest plot of all 76 effect sizes.
440 Error bars are 95% confidence intervals. Red dashed line indicates the pooled summary

441 effect, surrounding shaded area depicts 95% CI. b) Funnel plot. Dashed line is the pooled
442 effect size, coloured lines represent p values (Purple/Two-dash=.000001, Orange/Long-
443 dash=.00001, Green/Dot-dash=.0001, Blue/Dotted=.001, Turquoise/Dashed=.01,
444 Red/Solid=.05, Black=1).

445

446

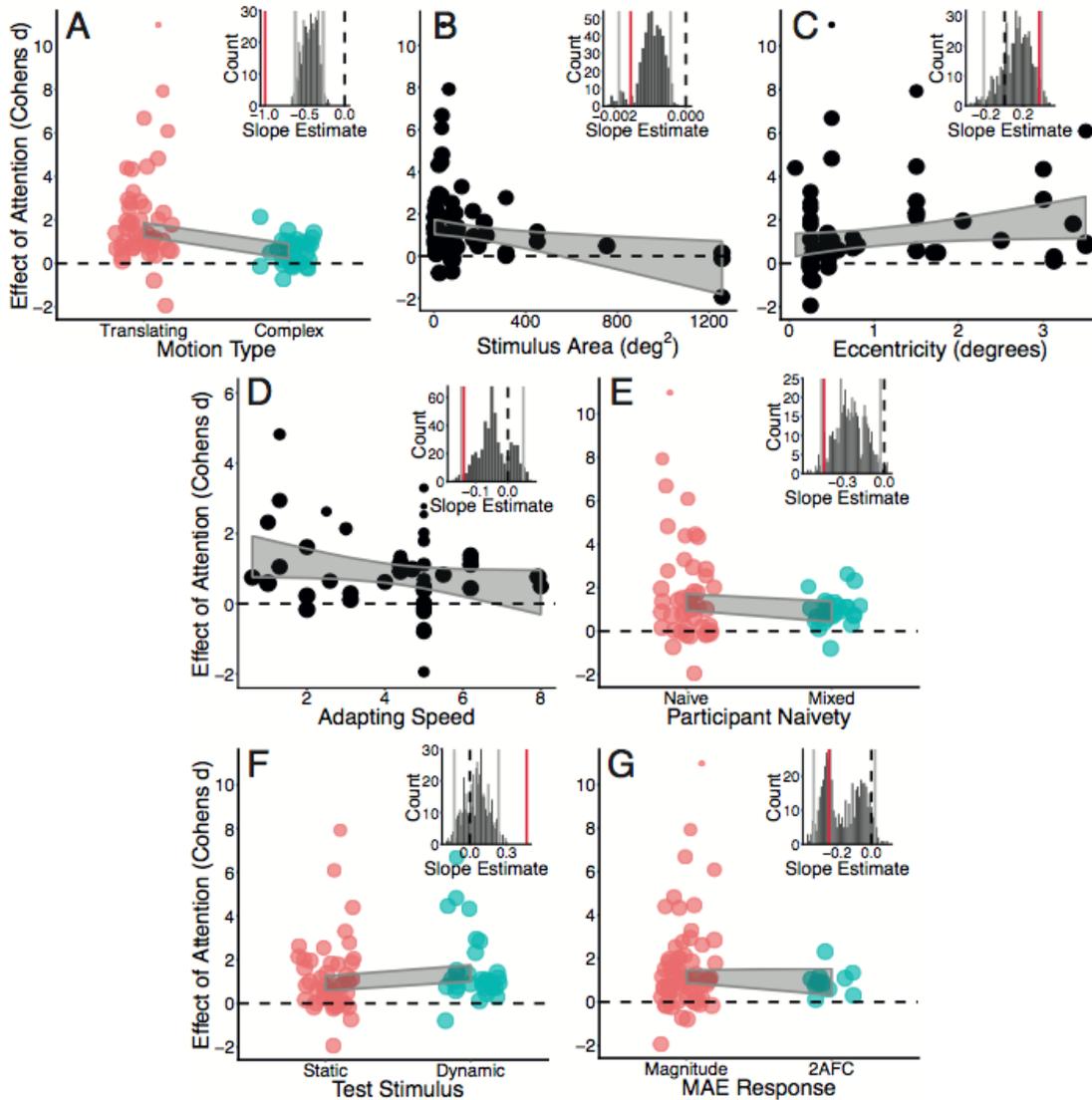
447 *3.3. Dependencies: overall analyses*

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

456

457 *3.4. Regression models with one moderator*

458 A table summarising all single moderator regression models can be found in
459 Supplementary Material S8. Important moderators (those that were individually significant or
460 contributed to the best multiple regression model) are shown in Fig. 3. Motion type
461 significantly affected the attentional modulation of the MAE ($Q(1)=17.43$, $b=-0.99$, $p<.001$),
462 accounting for 24.92% of the total heterogeneity: studies using translating motion stimuli
463 reported significantly larger effects than those using complex motion, (see Fig. 3a). However,
464 attention had a significant effect on motion adaptation within the subset of studies using
465 either translational motion, ($d=1.54$, $p<.001$) or complex motion ($d=0.56$, $p=.002$).



466

467 **Fig. 3.** Effect size summary for significant moderators (a-c) and factors that significantly
 468 contributed to the final model when considered alongside other moderators (d-g). The effect
 469 of attention (a) was larger for translational than complex motion, (b) decreased as stimulus
 470 size increased, (c) increased with greater eccentricity, (d) reduced with increasing adaptation
 471 speed, (e) was greater for naïve than mixed participant groups, (f) was greater for dynamic
 472 vs. static test stimuli, and (g) smaller when using a 2AFC response. Larger points indicate
 473 smaller standard error. The shaded ribbon indicates the 95% CI from the full dataset. Inset
 474 histograms detail the estimated slope parameter for 500 randomly selected datasets with
 475 dependency eliminated (see dependency information); red lines indicate estimated slope from

476 the full dataset; grey lines indicate the 95% CI determined by the resampled independent
477 sample estimates; dashed black lines indicate the zero point.

478

479 The size (area) of the adaptation stimulus significantly affected attentional modulation
480 of the MAE, $Q(1)=7.40$, $b=-0.002$, $p=.007$, accounting for 11.38% of the heterogeneity in the
481 effect (see Fig. 3b). As stimulus size increased, the magnitude of attentional modulation
482 decreased. In addition, there was a significant effect of the eccentricity of the adapting
483 stimulus, accounting for 8.59% of the total heterogeneity, $Q(1)=4.05$, $b=0.37$, $p=.044$ (see
484 Fig. 3c). The effect of attentional manipulations on the MAE was larger for stimuli that were
485 further from fixation.

486 When considered alone, the speed of the adaptation stimulus was not significant,
487 $Q(1)=3.36$, $b=-0.14$, $p=.067$, accounting for 2.74% of total heterogeneity. However, motion
488 speed did contribute to the final model (see below); slower stimuli resulted in stronger
489 attentional effects (see Fig. 1d).

490 Participant characteristics (i.e. naivety) did not significantly moderate the attention-
491 MAE effect in a single moderator model ($Q(1)=1.98$, $b=-0.43$, $p=.159$), but did contribute to
492 the overall model, with larger effects reported for studies using naïve participants. (This was
493 not driven by a relationship between sample size and sample type – see Supplementary
494 Material S9). Significant effects of attention on motion adaptation were found within the
495 subset of studies using naïve participants ($d=1.33$, $p<.001$) and within those using
496 experienced, or a mix of naïve and experienced, samples, ($d=0.90$, $p<.001$; see Fig. 3e).

497 The effect of test stimulus (static vs. dynamic) did not reach significance when
498 considered alone ($Q(1)=3.29$, $b=0.46$, $p=.070$) but did contribute to the best complete model
499 (see below). Using a static test stimulus to assess the MAE resulted in a weaker, though still

500 significant, effect of attention ($d=0.91, p<.001$) than using dynamic tests ($d=1.37, p<.001$).

501 This accounted for 7.12% of effect size heterogeneity (Fig. 3f).

502 The response paradigm made little difference to the measured effect of attention on
503 the MAE. The effect size was similar across studies that measured the MAE duration vs. its
504 strength ($Q(1)=0.49, b=0.19, p=.485$) with studies employing either method reporting
505 significant effects (MAE duration: $d=1.06, p<.001$; MAE strength: $d=1.24, p<.001$). Further,
506 effect size was not significantly modulated by whether a 2AFC design was used vs. a
507 magnitude estimation method ($Q(1)=0.52, b=-0.25, p=.470$), although the stronger attentional
508 modulation for magnitude designs compared to 2AFC designs contributed to the final model.
509 Both subsets of studies produced significant effects of attention on the MAE (2AFC: $d=.93,$
510 $p=.003$; magnitude estimation: $d=1.17, p<.001$, see Fig. 3g).

511 Neither the speed nor the duration of adaptation stimulus significantly affected the
512 attention-adaptation relationship (see table in Supplementary Material S8). Finally, a
513 significant effect of attention was reported within studies that used distractor paradigms (as
514 depicted in Fig. 1b: $d = 1.12, p<.001$) as well as those that used attentional tracking
515 paradigms (Fig. 1c; $d=1.18, p=.010$). The effect size was similar across both (no significant
516 effect of attention paradigm: $Q(1)=0.01, b=0.06, p=.904$).

517 As described above, the effect of dependencies was explored via resampling. The
518 distribution of regression coefficients across the 500 resampled sets of independent data can
519 be seen in inset histograms of Fig. 3. Analysing these reduced datasets (with dependencies
520 eliminated) reveals the same set of significant moderators. However, note that the regression
521 coefficient for motion type (translational vs. complex) is larger when estimated from the
522 complete data set than when estimated from reduced datasets. Some of the larger effect sizes
523 for translational motion were produced from samples contributing multiple effects. Thus, we
524 can be confident that studies with translating motion provide substantially larger effect sizes

525 than those using complex motion, but the estimated magnitude of this difference may be
526 inflated by dependencies across estimates from common subject groups.

527 Selected two-way interaction analyses were conducted, however none of these
528 reached significance (see Supplementary Material S10).

529

530 *3.5. Multiple regression models*

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

544

545 *3.5.1. Complete effects*

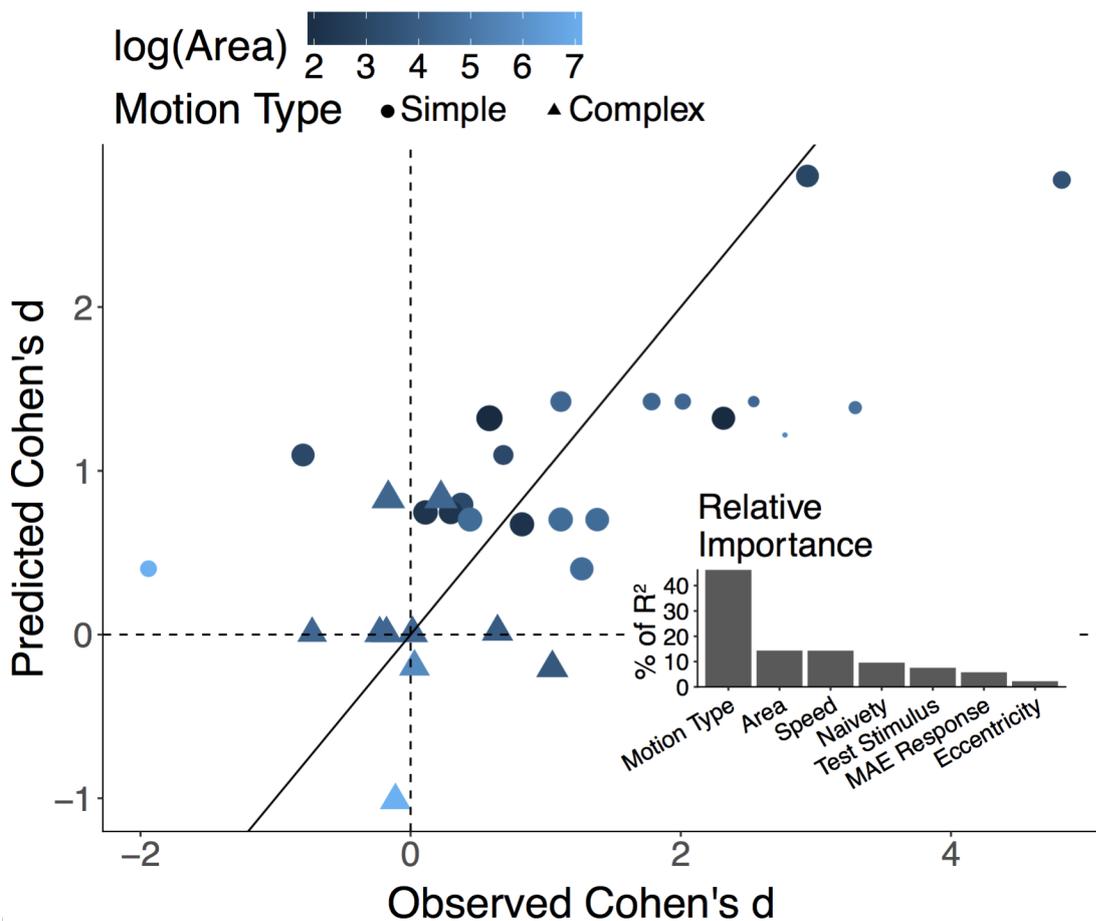
546 The initial model included all moderators for which values were available for all
547 effects: type of motion (translation vs. complex), MAE measurement (duration vs. strength),
548 MAE response (magnitude vs. 2AFC), test stimulus (static vs. dynamic) and attention
549 paradigm (distractor vs. tracking). Through backward elimination, the optimal complete

550 effects model included motion type, MAE response and test stimulus as predictors. This
 551 model accounted for 42.05% of the heterogeneity of the effect of attention on motion
 552 adaptation.

553

554 *3.5.2. Reduced effects*

555 The complete effects model was significantly improved by adding four reduced effect
 556 moderators. The addition of each one decreases the number of effect sizes (k) included in the
 557 model. These reduced effects were participant naivety ($k=69$), stimulus area ($k=57$),
 558 eccentricity ($k=50$) and adaptation speed ($k=31$). The final model accounted for 63.18% of
 559 the heterogeneity of the effect; it is shown in Fig. 4 and summarised in Supplementary
 560 Material S11.



561
 562

Fig. 4. Predicted Cohen's d_{AV} values as a function of observed Cohen's d_{AV} for each effect size

563 in final model. Size of the points indicates standard error; larger points have a smaller
564 standard error. Inset: The relative importance of each factor in the final model. This is
565 quantified by the pseudo R^2 statistic (see Supplementary Material S5), averaged across all
566 possible orderings of regressor input (Lindeman et al., 1980).

567

568 **4. Discussion**

569 *4.1. Summary of Findings*

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

579

580 *4.2. Discussion of adaptation and test stimulus characteristics*

581 *4.2.1. Type of motion*

582 The effect of attention on motion adaptation was around twice as large for translating
583 motion than for other motion patterns. This behavioural finding suggests that feature-based
584 attention plays a substantial role in increasing motion adaptation. Although translational
585 motion produced substantially stronger attentional effects, adaptation to complex motion was
586 also significantly enhanced by attention. When considered alongside neurophysiology and
587 fMRI evidence, the substantial difference between simple and complex motion suggests that

588 surface-based attention may drive some attentional modulation of activity within V1 / MT,
589 but that this effect is small compared to the effects of simple feature-based attention. In
590 addition, we know that neurons in MST can be tuned to large field translating, rotating or
591 expanding / contracting patterns (Smith et al., 2006; Wall et al., 2008). The relatively small
592 effect of attention on adaptation to complex motion therefore also suggests that attentional
593 effects on adaptation within MST are small compared to those in V1/MT.

594 Early fMRI studies reported a significant effect of attending to complex motion in
595 MT/MST but found no significant effects of attention in V1 (Büchel et al., 1998; O’Craven et
596 al., 1997; Watanabe et al., 1998). It is possible that the effects of surface-based attention in
597 V1 are relatively weak and hard to detect. Alternatively, V1 facilitation in a subset of neurons
598 may have been masked by suppressive effects within neurons tuned to unattended motion
599 directions. Facilitatory and suppressive effects of attention (in response to translating stimuli)
600 have recently been revealed in V1 using more sophisticated, voxel-based analyses (Saproo
601 and Serences, 2014), consistent with our findings.

602

603 *4.2.2. Stimulus size*

604 Our analyses revealed a relationship between stimulus size and the effect of attention,
605 with a smaller effect for larger adaptation stimuli, in line with Takeuchi and Kita (1994).
606 They suggested that small vs. large (or whole field) stimuli are processed by separate motion
607 mechanisms, with the former sensitive to object motion, and the latter sensitive to the optic
608 flow generated by self-motion. Our analyses revealed smaller attentional effects for larger
609 adaptation stimuli (which may be processed as optic flow), consistent with the idea that
610 selective attention affects the processing of object, rather than self-motion (Takeuchi & Kita,
611 1994).

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

618

619 *4.2.3. Eccentricity*

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

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

628

629 *4.2.4. Test stimuli*

630 Some researchers have suggested that dynamic and static MAEs correspond to
631 different motion mechanisms (e.g. Verstraten et al., 1996), which may differ in their
632 susceptibility to attention. Our analyses show that attention affects MAEs measured with both
633 dynamic and static test stimuli. Although larger effects were found with dynamic tests, this
634 was a modest difference, that did not reach significance when considered alone and may be
635 an artefact of dependencies within studies (see the resampling analyses in Fig. 3f).

636

637 *4.2.5. Adaptation speed*

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

642

643 *4.3. Factors related to response bias*

644 *4.3.1. Response type*

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

655

656 *4.3.2. Participant characteristics*

657 If response bias does inflate estimates of the effect of attention, one would expect this
658 to be an issue predominantly amongst non-naïve observers, who understand the attention
659 hypothesis: for response bias to modulate effect size, observers should not only bias their
660 responses in accordance with motion adaptation, but to systematically vary this bias as a
661 function of attention condition. On the contrary, participant naivety did not reach significance

662 as a single moderator, and experiments using naïve subjects reported *larger* effects, with this
663 effect contributing to the final model.

664

665 *4.4. Nonsignificant moderators*

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

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

680 Prior work has demonstrated that MAEs increase with adaptation duration (e.g.
681 Bartlett et al., 2018). As discussed above, this duration-related increase in MAEs is not
682 associated with increased attentional modulation. However, it is worth considering whether,
683 more broadly, larger MAEs are associated with increased attentional modulation. Could it be
684 that study designs that produce large MAEs (in terms of effect size) are more sensitive, and
685 therefore also report greater effects of attentional modulation? Moreover, could MAE
686 strength be a mediating variable that ‘explains’ the effects of some of our identified

687 moderators? To investigate this, we quantified baseline MAE strength (in the passive, or low-
688 load condition) using Cohen's D. (Equation 1 reduces to the mean difference between a null
689 result (i.e. no MAE) and the low-load / passive condition, divided by the low-load standard
690 deviation). A small number of effects (12) were excluded from this analysis because an
691 estimate of baseline MAE strength was not available. Within the remaining effects ($k=64$),
692 MAE strength was not substantially or significantly related to the effect of attention
693 ($Q(1)=0.20$, $b=-0.02$, $p=.655$). Further analyses confirmed that MAE strength did not
694 significantly contribute to the final model, $LRT=0.06$, $p=.800$ ($k=57$). Thus, significant
695 predictors of the modulatory effect of attention on motion adaptation (such as motion type, or
696 stimulus size) cannot be 'explained away' via effects on baseline MAE strength.

697

698 *4.5. Reconciling the literature*

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

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

710

711 *4.6. Relationship to neuroimaging*

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

725 Attentional modulation decreased for larger stimuli at smaller eccentricities,
726 conditions that may increase the extent to which spatial attention ‘spills over’ from a central
727 task, to a peripheral motion stimulus. This makes sense if spatial attention modulates
728 neuronal activity according to the extent of overlap between a neuron’s receptive field and
729 the spatial locus of attention (Maunsell and Treue, 2006). Large-field stimuli will be
730 particularly effective in driving activation in MSTd, where receptive fields are large and
731 more will overlap with a central attended region of visual space.

732 We compared the effect of attention on MAEs measured with dynamic and static test
733 stimuli. Previous authors have shown greater interocular transfer of the dynamic MAE
734 (Nishida et al., 1994) and suggested that static MAEs predominantly reflect adaptation in V1,
735 whereas dynamic MAEs also involve MT (Mather et al., 2008). Our findings are broadly

736 consistent with this suggestion – the larger effect of attention on the dynamic MAE may
737 reflect attentional modulation across V1 and MT/MST.

738

739 **5. Conclusions**

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

754

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761 **References**

762

763 References marked with an asterisk indicate studies included in the meta-analysis.

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