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

25

1. Background

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

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

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).
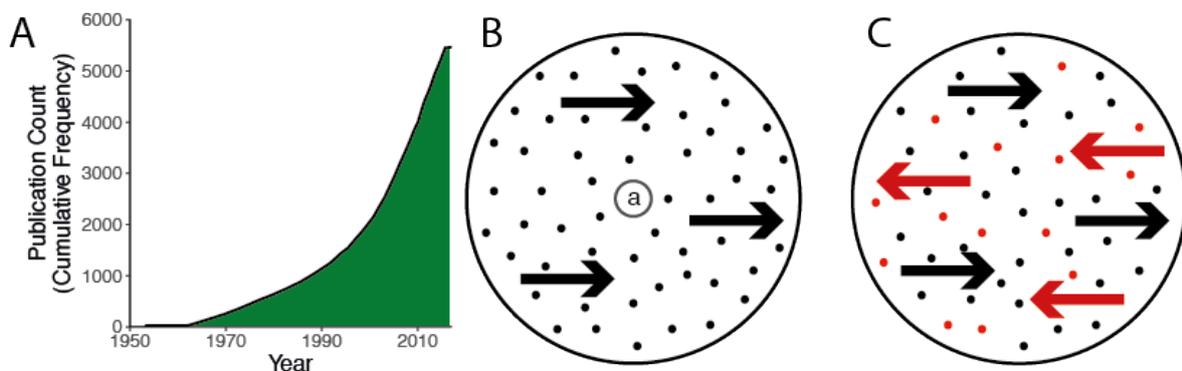
58

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, Wohlgemuth (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

1.2.2. Test stimulus characteristics

1.2.2.1. Static vs. dynamic test stimuli

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

1.2.3. Experimental paradigm

1.2.3.1. MAE measurement and response

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

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      $$d_{av} = \frac{M_{diff}}{\frac{SD_1 + SD_2}{2}}$$ *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      $$d_{RM} = \frac{t}{\sqrt{N}} \times \sqrt{2(1 - r)}$$ *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     $SE = \sqrt{\dfrac{\frac{1}{N+d^2}}{2N}}$ *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
Characteristics of adaptation stimulus					
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.	$k=76$ $N_1=46$ $N_2=30$	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.	$k=64$ $\mu=158.87°_2$ $\sigma=277.50°_2$ 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.	$k=55$ $\mu=1.03°$ $\sigma=1.08°$ 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.	$k=45$ $\mu=4.16°$/sec $\sigma=1.79°$/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.	$k=66$ $\mu=40.11$ sec $\sigma=21.40$ sec Range=1-90 sec	10
Test stimulus characteristics					
Static vs. dynamic test stimuli	Categorical	1=Static 2=Dynamic	The type of test stimulus used to measure the MAE.	$k=76$ $N_1=44$	0

(Section 1.2.2.1)				N_2=32	
Experimental paradigm					
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_1=51 N_2=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_1=64 N_2=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_1=70 N_2=6	0
Participant characteristics					
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_1=44 N_2=25	7

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

422

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_{RM}=1.12, 95% 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.
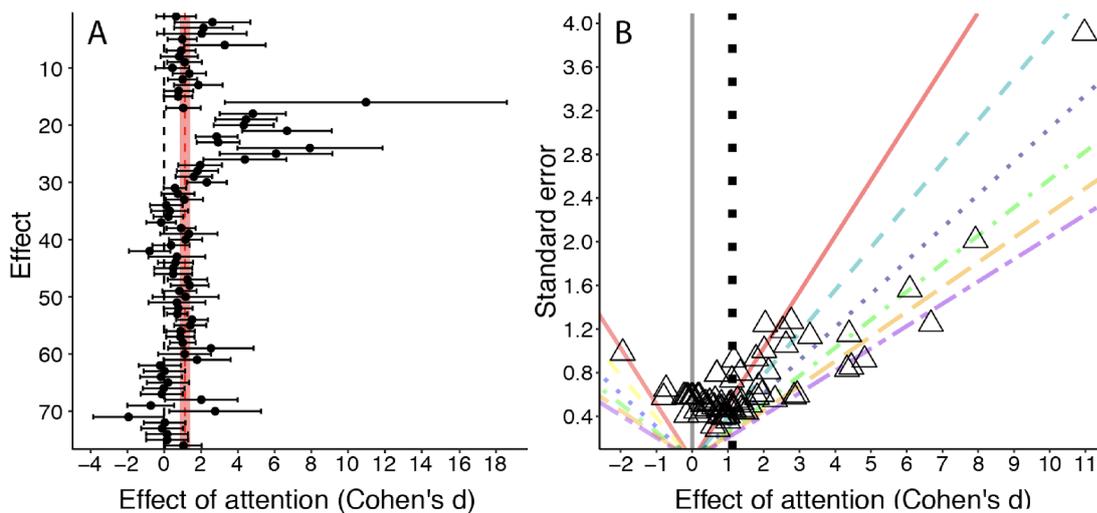
439 **Fig. 2.** Summary of the effect of attention on the MAE. a) Forest plot of all 76 effect sizes.

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 $x^2(1)$=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).
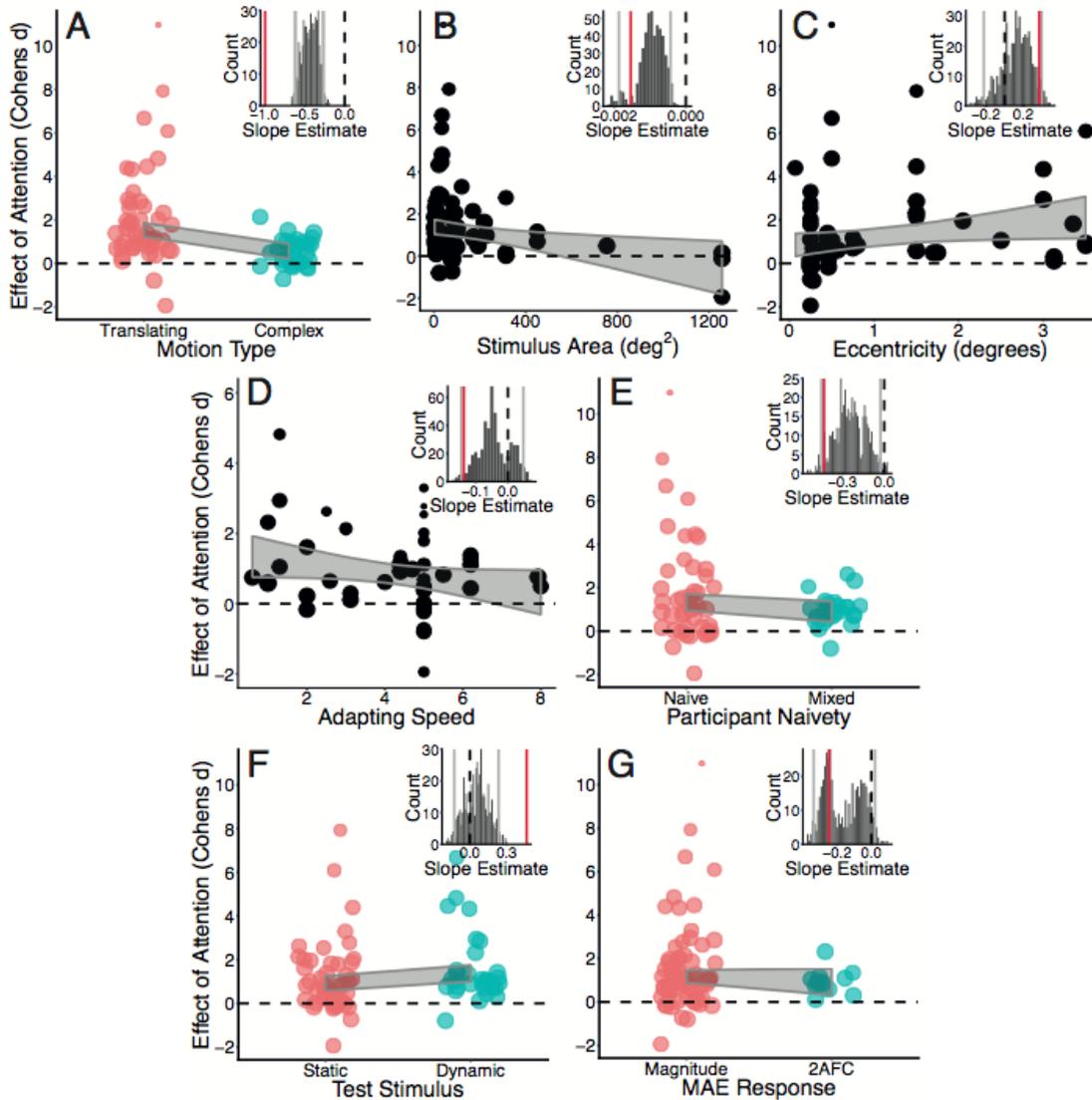
Fig. 3. Effect size summary for significant moderators (a-c) and factors that significantly contributed to the final model when considered alongside other moderators (d-g). The effect of attention (a) was larger for translational than complex motion, (b) decreased as stimulus size increased, (c) increased with greater eccentricity, (d) reduced with increasing adaptation speed, (e) was greater for naïve than mixed participant groups, (f) was greater for dynamic vs. static test stimuli, and (g) smaller when using a 2AFC response. Larger points indicate smaller standard error. The shaded ribbon indicates the 95% CI from the full dataset. Inset histograms detail the estimated slope parameter for 500 randomly selected datasets with dependency eliminated (see dependency information); red lines indicate estimated slope from

24

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.
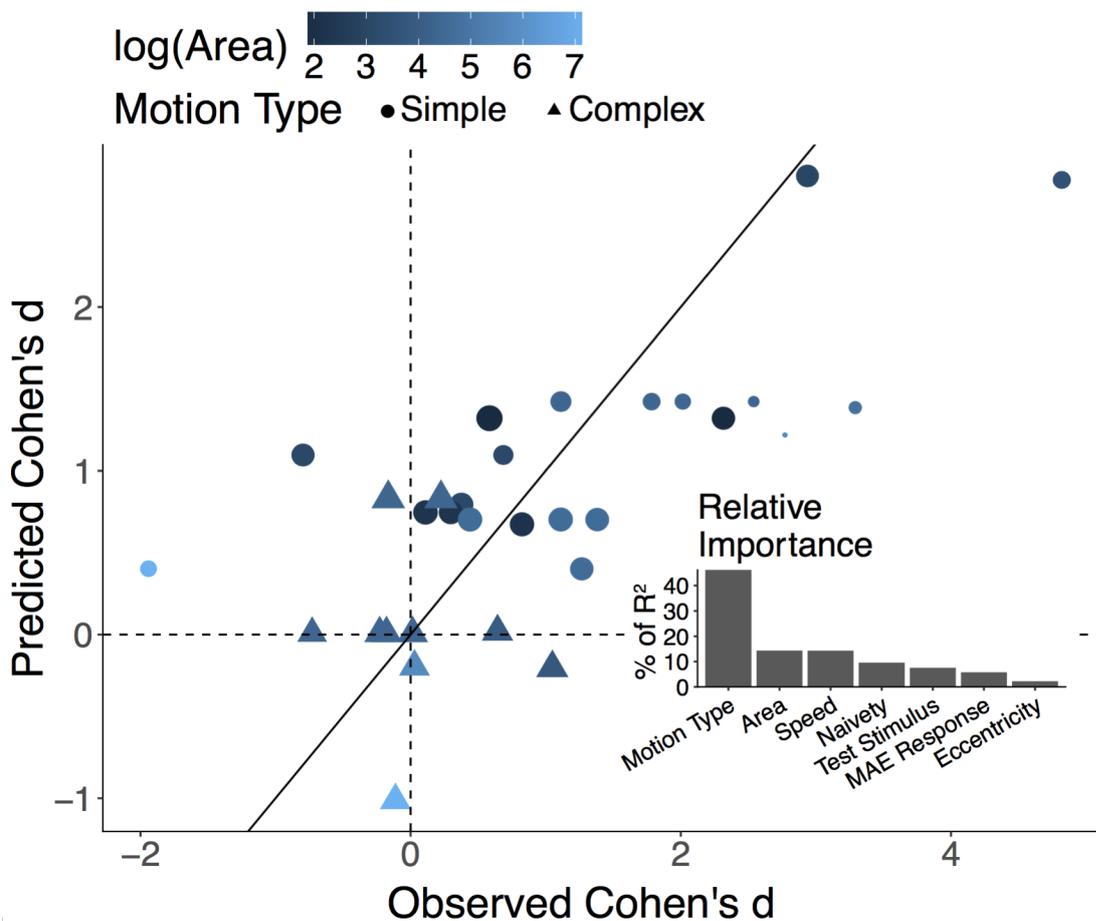

561
562   **Fig. 4.** Predicted Cohen's d_{av} values as a function of observed Cohen's d_{av} for each effect size

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

755

756

757

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759

760

761 **References**

762

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

764

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766   a moving body. London Edinburgh Philos. Mag. J. Sci. 5, 373–374.

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