Attention and the motion aftereffect

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**Abstract**

We measured the effects of attentional distraction on the time course and asymptote of motion adaptation strength, using visual search performance (percent correct and reaction time). In the first two experiments, participants adapted to a spatial array of moving Gabor patches, either all vertically oriented (Experiment 1) or randomly oriented (Experiment 2). On each trial the adapting array was followed by a test array in which all of the test patches except one were identical in orientation and movement direction to their retinotopically corresponding adaptors, but the target moved in the opposite direction to its adaptor. Participants were required to identify the location of the changed target with a mouse click. The ability to do so increased with the number of adapting trials. Neither search speed nor accuracy was affected by an attentionally demanding conjunction task at the fixation point during adaptation, suggesting low-level (pre-attentive) sites in the visual pathway for the adaptation. In Experiment 3 the same participants were required to identify the one element in the test array that was slowly moving. Reaction times in this case were elevated following adaptation, but once again there was no significant effect of the distracting task upon performance. In Experiment 4 participants were required to make eye movements, so that retinotopically corresponding adaptors could be distinguished from spatiotopically corresponding adaptors. Performance in Experiments 1 and 2 correlated positively with reaction times in Experiment 3, suggesting a general trait for adaptation strength.
Introduction

Our experiments were designed to develop a performance-based (i.e. “Type 1,” Sperling, Dosher, & Landy, 1990) measure of motion adaptation. Performance-based measures have many applications, but we specifically wanted to learn whether the motion aftereffect (MAE) is reduced when observers’ attention is distracted away from the adapting stimulus, as reported by Chaudhuri (1990), Rees, Frith, and Lavie (1997), and Taya, Adams, Graf, and Lavie (2009). This possibility is theoretically interesting because there is good evidence that the locus of adaptation underlying the MAE is visual area V1 (Kohn & Movshon, 2003). An effect of attentional distraction on the MAE would thus imply a top-down effect of attention on visual processing in V1 or earlier.

To date, almost all prior investigations of this question used phenomenological (“Type 2”) measures of the MAE. Prolonged inspection of a moving image such as a waterfall causes subsequently viewed, stationary stimuli to appear as if they are moving in the opposite direction (Addams, 1834; Wohlgemuth, 1911; Mather, Verstraten, & Anstis, 1998). The measurement of this effect by its duration is potentially subject to criterion and expectation effects (Sinha, 1952). It is difficult to decide when a stimulus has stopped moving, particularly if it is known not to be moving in the first place.

Wohlgemuth (1911; see Wade, Thompson, & Morgan, 2014) measured the MAE by its apparent duration. He employed a task involving random, serial, visual presentations (RSVP) that was designed to distract observers from the adaptor. This task did not affect MAE duration in Wohlgemuth’s study. Chaudhuri (1990) and Rees et al. (1997), on the other hand, reported positive results with similar methods. A positive result was also reported by Taya et al. (2009), who measured the MAE by the speed of test motion required to compensate for (or “null”) it, which has the same problems as the measurement of duration. Nishida & Ashida (2000) found no effect of distraction on MAE duration, but did they did find an effect of distraction on the contrast assigned to a moving test pattern that was required to null the interocular MAE only (i.e. there was no effect on the
Morgan (2011, 2012, 2013) has repeatedly found no effect of distraction on the MAE. The 2012 study used naïve students and MAE duration. It also used more experienced observers and the nulling paradigm. The 2013 study measured the MAE by its effect on perceived speed (Thompson, 1981), interleaving various pedestals to defeat any simple decision strategy (e.g. “when in doubt respond that the adapted stimulus is slower”). However, even the 2013 experiment is in essence a Type 2 measure. The 2011 study is the only one to date to use a Type 1 measure, namely the direction-specific loss of contrast sensitivity following adaptation. However, the measurement of contrast sensitivity is lengthy and not well suited to measuring the growth of adaptation over time. Consequently, it may obliterate attentional effects during the build-up of adaptation. Bartlett, Adams, and Graf (2016) have suggested that attentional distraction might affect the rate of growth of adaptation to asymptote, without affecting the asymptote itself. The purpose of the experiments we report here was to develop a rapid, simple, Type-1 measure of adaptation that allowed us to track the growth of adaptation over trials.

Our new method builds upon previous research demonstrating that adaptation can facilitate visual search (Wissig, Patterson, & Kohn, 2013). Our observers adapted to an array of Gabor patches, moving in different directions (Fig. 1). We used a ‘top up’ procedure, in which brief periods of adaptation (2, 3, or 5 s in different experiments) alternated with the presentation of a brief test stimulus, with a 1-s temporal gap between adaptor and test to prevent transient-based detection. The test array was identical to the adapt array except that one of the patches (the "target") reversed its direction from the adapting direction (the "Target-change" condition). All the other patches (the "distractors") moved in the same direction as their spatially corresponding adaptors. Morgan & Hauperich (2016) reported that, in these circumstances, the target can pop out from the distractors, and its position can be detected. In the present series of experiments, we measure the growth of performance over trials and the effects of distracting attention from the adapting stimulus with a difficult central RSVP
task. Growth was expected because the adaptation trials were brief and the adapting stimulus remained the same over all trials within a session. Between sessions, the adapting stimulus was changed, with random sampling of the motion direction and/or orientation of the Gabors.

Our task differed from that of Wissig et al. (2013), whose target had a different orientation from its distractors, and could thus be detected without adaptation. In our task, the adaptation is logically necessary to define the target.

Given that attentional distraction was expected to reduce adaptation, and thus to impair performance in the visual search task, we also wished to develop a complementary task, in which the reverse would be expected. This was achieved (Experiment 3) by requiring participants to find the single moving target, in a test array of otherwise stationary distractors. The logic here was that adaptation should produce the MAE, causing apparent motion in the distractors as well as the target, and thus impeding search. In these circumstances, attentional distraction during adaptation would be expected to reduce the MAE, and thus facilitate search. In other words, we expected a double dissociation, such that distraction should impair performance in "target-change" conditions (Experiments 1 and 2) but improve performance in "moving target" conditions (Experiment 3). Similar logic has been used to design tasks where the performances of dichromats are both better and worse than those of trichromats (Morgan, Adam, & Mollon, 1992) and tasks where synaesthetes are both better and worse than non-synaesthetes (Gheri, Chopping & Morgan, 2008). Our design controls for any general effects of distraction on performance, such as reductions or increases in arousal level, motivation, and pupil size. In Experiment 4 we explicitly test for any individual differences in fixation.

**General Method**

**Apparatus and Subjects**
Stimuli were presented on a 60-Hz frame-rate Sony Trinitron monitor in a darkened room, viewed from 0.75 m, so that one pixel subtended 1.275 arcmin at the observer’s
eye. Viewing was binocular through natural pupils, with observers wearing their normal correcting lens for the viewing distance if necessary. A total of 12 observers participated in the experiments, comprising the two authors and a number of postgraduates/undergraduate students from City, University of London and the Max-Planck Institute for Metabolism Research at Cologne, all of whom were naïve to the purpose of the experiment. Two of the participants were paid volunteers.

Stimuli

The stimuli (e.g. Fig. 1) consisted of rectangular arrays of Gabor patches, each of which comprised a sinusoidal grating multiplied by a circular Gaussian envelope. Spatial and temporal frequencies of the grating were 3.75 cyc/deg and 7.5 Hz. The Gaussian envelope had a spread (σ) of 0.21 deg. The mean luminance and contrasts of the Gabors were 70 cd/m² and 0.6 (60%) respectively. The envelope did not move. In most of the experiments the envelope was truncated at ±2σ, so that it had a just-noticeable edge. In Experiment 2 truncation was at ±3σ. Unless otherwise stated, the array comprised 4 × 4 equally spaced Gabor patches, with a centre-to-centre spacing of 1.87 deg (8.75 σ).
Fig. 1. The figure shows a representation of two successive trials from Experiment 1. The arrows symbolize the direction of motion of each patch and were not visible during the experiment. Observers adapted to the array shown in the left panels. During adaptation, observers were required to report rare combinations of the shape (upright vs inverted) and colour (red, green, blue, or yellow) of crosses that appeared (at fixation) at a rate of 1.5 Hz. Each 2-s adapt period was followed by a 1-s test in which all the patches moved in the same direction as their respective adaptors except the target, which moved in the opposite direction. The test was followed by presentation of circular placeholders. These placeholders remained visible until observers indicated (with a mouse click) which of them occupied the target's position. In the experiment illustrated here the adapt and test arrays contained the same number of elements and the Gabor patches were all horizontal.

Procedure
Adaptation was produced by presenting one of these Gabor arrays for an initial 2, 3, or 5 s (in different experiments), during which the observer was instructed to fixate a stationary point in the centre of the display, and to carry out a task based on additional stimuli presented there. In Experiments 1 and 3, all Gabors were horizontal. Half moved upwards and the other half downwards. The direction of motion for each Gabor was randomly selected at the start of each session but held constant within each session (see Fig. 1). In Experiments 2 and 4, Gabors could have any orientation (and thus move in any direction; see Fig. 4). The first adaptation period was followed, after 1 s (1.5 s in Experiment 4), by a 1-s test. Change was introduced by reversing the direction of drift of one of the carrier gratings. After the test, the stimuli were replaced by a set of circular placeholders, and the observer used a mouse to click on the position of the target. To give feedback, the target’s placeholder was switched off to show the target’s position after the mouse click. After the mouse click, the screen went blank while the next set of Gabors was calculated (approx. 1 s) and then the next adapting stimulus was presented.

All observers were given several sessions of practice with the central crosses absent before the main experiment in order to become accustomed to the task. Our intent was to establish detection above chance levels before collecting any data. However, this proved to impossible with observer EL, who failed to show convincing evidence of detection. Two other subjects (DP, TP) also found the task difficult. EL, DP, and TP were included in the main experiments anyway, to see if they would eventually learn.
The RSVP Task for Distracting Attention

To take attention away from the adapting stimulus during adaptation, observers in some conditions carried out a demanding RSVP task based on stimuli appearing at fixation. In the centre of the adapting array, superimposed on the white fixation point, a series of asymmetrical, coloured crosses were presented at a frequency of 1.5 Hz (2 crosses per trial in Experiment 1; 6 per trial in Experiments 2 and 4, and 3 per trial in Experiment 3). When the last cross was presented there was a cross-free interval, to give time to respond if an exception had been seen, before the placeholders appeared. This gap was 0.667 s, in Experiment 1 and 1 s in Experiments 2–4. In the high-load (i.e. attentionally demanding) version of the task (see Morgan, 2011; Schwartz, Vuilleumier, et al., 2005), the observer’s task was to press a button when there was a rare conjunction of colour and orientation. On all but 9.75% of the trials in Experiments 1 & 3 and 4.94% of the trials in Experiments 2 and 4, upright crosses were either red or green, and inverted crosses were yellow or blue. The four combinations were equally probable. On the remaining trials the first and following crosses were exceptions to this rule, for example the cross was red and inverted. Observers were instructed to press a key as soon as they saw an exception. As soon as they did so, the rule was reinstated. The observer was told that the exceptions were rare and that they should not produce false-positives. In practice FP rates were very low (0.0148 over all conditions), therefore, no measures were taken to eliminate trials on which they occurred. In the low-load versions of the task, the crosses were absent and/or the observer was instructed merely to maintain fixation on them.

Experiment 1

Methods

The stimulus configuration is shown in Fig. 1. The adapting duration, blank interval between adaptation and test, and the test interval were 3 s, 1 s, and 1 s, respectively. Each session began with 5 trials in which the adapting and test stimuli were absent. During these trials, observers performed the RSVP task and selected a placeholder at random. These initial trials were followed by 32 trials, with a total of 2 targets in each of the 16 positions, randomly interleaved without replacement. There were three attentional load conditions during adaption: crosses absent, high load, and low load (Conditions 1-3 respectively). In the low-load condition the crosses were present, but
the observer had no task to perform. The colours were red, green, yellow, and blue. All observers carried out at least 2 sessions of 32 trials in each of the 3 load conditions (6 sessions; 192 trials in total). Some observers did more. The number of sessions performed by each of the observers (in order of their appearance in Fig. 2) was as follows: \{25, 9, 13, 7, 6, 11, 18, 9, 6, 5, 10\}. All 12 observers took part, but one of them (LP) did only the low-load condition and her results are not presented in this section, although they are included in Fig. 9.

Results

Fig. 2 shows that there was no systematic effect of attentional load during adaption on the overall success rate combined over trials and sessions, such as might arise from differences either in growth rate or asymptote of performance. To see specifically if load affected the build-up of adaptation during a session (as suggested by Bartlett et al., 2016), growth curves over 8 successive 4-trial blocks (combined over sessions) were fit with the two-parameter function

\[ P(x) = \frac{1}{16}[(16a - 1)\text{erf}(bx) + 1], \]  

(1)

where \( P(x) \) is the probability correct on trial \( x \), and parameters \( a \) and \( b \) describe the asymptote of performance and the growth rate, respectively \((1/16 \leq a \leq 1, 0 \leq b)\). The fits of the growth curves are shown in Fig. 3. The model was fit to the data using the MATLAB \texttt{fminsearch} function.

Data from each observer were fit with Equation (1). Maximumlikelihoods are provided in Table 1. The first question we ask is whether attentional load has any effect on either the asymptote of performance or the growth rate (“Experiment 1. Growth curve differences due to Load”). To begin with we fit a 6-parameter version of Equation (1) where \( a \) and \( b \) are different for each load (“6 parameter fit”). Then we fit a 4-parameter version where \( b \) was the same for all loads but \( a \) was allowed to vary (“4 parameter, equal growth”). Finally, we fit another 4-parameter version where \( a \) was the same for all loads but \( b \) was allowed to vary (“4 parameter, equal asymptote”). For 10 of 11 observers, neither constraint produced a \( \Delta \text{AIC} > 0 \). Thus, these data clearly do not contain compelling evidence for an effect of load on either aspect of the learning curve (growth or asymptote). Burnham and Anderson (2002, p. 70) would consider the data from every one of the 11 observers “substantial empirical
support" for the constrained models (NB: the largest value of ΔAIC, for subject DP with \( b \) constrained, was 1.2).

For completeness, we also tested the 6-parameter fit against a 2-parameter fit, where values of growth and asymptote were constrained to be independent of load. For 9 of 11 observers, the constraint failed to produce a ΔAIC > 0. The largest value of ΔAIC, for subject DP, was 1.7. Consequently, this too indicates that the data from every observer provide "substantial empirical support" for the constrained model.

Next we ask whether, independently of load, there is evidence for a progressive effect of adaptation. In other words, we ask whether performance was asymptotic right from the start. ("Experiment 1: 2-parameter Vs. 1-parameter fits by subject and by load")

To determine this, we fit each of the three load conditions separately; once with parameter \( b \) fixed at 10 (producing asymptotic performance for all trials, i.e. \( x \geq 1 \)), and once with parameter \( b \) free to vary. For example, AJ_1 is the one-parameter fit for subject AJ with \( b \) fixed, and AJ_2 is the two-parameter fit with \( b \) free to vary. In 20 of 33 cases (3 load conditions times 11 observers), a generalized likelihood-ratio test (Mood, Graybill, & Boes, 1974) allowed us to reject the (null) hypothesis of asymptotic performance on all trials [in each of these 20 cases \( \chi^2(1) > 3.84; p < 0.05 \)].

Similar conclusions can be obtained by fitting Equation 1 to all data simultaneously (and thus ignoring any differences between individual subjects: “Experiment 1: Group level tests for growth”). Specifically, we can reject the null hypothesis of asymptotic performance on all trials [\( \chi^2(1) > 3.84; p < 0.05 \) for all three load conditions], and we have substantial empirical support for no effect of load on either growth rate (\( \Delta \text{AIC} = -3.0 \)) or asymptotic performance (\( \Delta \text{AIC} = -3.8 \)).

An even simpler test is to subtract the mean success rate on trials 2–32 from the first-trial success rate. At the group level this difference score was negative (indicating improvement) in all conditions (–0.30, –0.28, and –0.20 for Conditions 1–3, respectively). It was also negative for all observers in Condition 1, 10 of 11 observers in Condition 2, and 9 of 11 observers in Condition 3. This is strong evidence that improvement was taking place, but it provides no clear evidence for a difference due to attentional load. Of course, the improvement
could be general rather than due to adaptation, although all observers had been given several sessions of practice before the main experiment in order to become accustomed to the task. To check this point, we analysed performance in only the second session of 32 trials. This did not alter the situation: difference scores remained negative at the group level (−0.23, −0.31, and −0.37, for Conditions 1–3, respectively), and the numbers of observers with negative scores were 11, 10, and 10. We conclude that performance did improve during individual sessions of 32 trials, and we conjecture that this was due to the build-up of adaptation.

Fig. 2. Performances of all 11 observers who completed Experiment 1 under three conditions of attentional load during adaptation, indicated by the numeral on the horizontal axis (1: crosses absent, 2: high load, 3: low load). Observer LP is excluded from this analysis because she completed only the low-load condition. Error bars for individual observers contain binomial 95% confidence intervals. The bottom right panel shows the mean performance ± 1 SE over observers.
Fig. 3. Growth curves in performance in Experiment 1 fit with the 2-parameter Equation (1) in the text. For legibility the data points have been binned into 4-trial blocks, but the fit is to the trial-by-trial data. Each panel shows results for a different observer. The bottom right shows the fits to the mean observer. The three curves are for the different conditions (magenta: crosses absent, blue: high load, black: low load).

**Experiment 2**

A possible criticism of Experiment 1 is that the adaptation periods were kept deliberately brief (2 s) in order to follow the build-up of adaptation over trials (32 per session). The periods may have been too brief to allow full deployment of selective attention to the crosses. Against this, we shall show later that detection rate for the exceptions (see General Methods) was high. However, as an additional precaution, in Experiment 2 the adaptation periods were lengthened to 5 s (6 crosses per trial). The high load condition was the same as in Experiment 1, and the low load was the same as Condition 3, i.e. crosses were present but required no response. The initial 5 trials of pre-adaptation in Experiment 1 were not used, as the observers were well used to the procedure. A further change from Experiment 1 is that the adapting array consisted of 6 x 6 elements of which only the central 4 x 4 were used for the test. This was in anticipation of Experiment 4, in which the observers moved their eyes between
adapt and test to demonstrate that the adaptation is retinotopic. The participants were the same as in Experiment 1, with the exception of LR and LP who did not take part.

Methods
The general arrangement of the display is shown in Fig. 4, taken from screen-shots of the stimuli. The orientations of the patches were randomised between sessions, but constant within each 32-trial session. In anticipation of Experiment 4, we made the (6 × 6) adapting array larger than the (4 × 4) test array. We also truncated each Gabor’s Gaussian envelope at ±3σ to give it a softer edge than those used in Experiment 1.

The initial and top-up adaptation periods were 5 s. These were followed by a 1-s blank, a 1-s test, and finally the 4 × 4 array of circular placeholders in the positions of the test patches. One of the moving patches changed direction through 180 deg between the adaptor and the test. The other patches continued in the same direction.

Ten observers participated in the experiment, including authors MM and JS. The others were a mixture of postgraduates, colleagues, and paid subjects, all of whom were naïve as to the purpose of the study. One observer (AJ) was available for only 4 sessions (2 of each Load Condition). The others, in order of their appearance in Fig. 5, performed {12, 11, 12, 11, 7, 10, 14, 17, 17} sessions.
Fig. 4. Stimuli used in Experiment 2. In the Adapting stimulus (left) each of the gratings moved either leftwards or rightwards with respect to their orientation. In the Test stimulus (right) one of the Gabor patches reversed its direction of motion while the others moved in the same direction as their corresponding adaptor. The central cross (shown here in red) changed colour and orientation 6 times during each adapting exposure.

Results

The results summarised in Fig. 5 show that most observers performed the task with an accuracy between 0.4 and 0.6. Growth curves (Fig. 6) from each observer were fit with Equation (1). Maximum likelihoods are provided in Table 1. As before, we fit each of the load conditions separately; once with parameter \( b \) fixed at 10 (producing asymptotic performance for all trials, i.e. \( x \geq 1 \)), and once with parameter \( b \) free to vary. In 9 of 20 cases (2 load conditions times 10 observers), a generalized likelihood-ratio test allowed us to reject the (null) hypothesis of asymptotic performance on all trials [in each of these 20 cases, indicated by asterisks in Fig. 6, \( \chi^2(1) > 3.84; p < 0.05 \)].

Next, we fit the two load conditions simultaneously; once with parameter \( a \) (representing asymptotic performance) constrained to be invariant with load and once with parameter \( b \) (representing growth rate) constrained to be invariant with load. For
9 of 10 observers, neither constraint produced a $\Delta AIC > 0$. Thus, these data clearly do not contain compelling evidence for an effect of load on performance. Burnham and Anderson (2002, p. 70) would consider the data from all 10 observers (NB: the largest value of $\Delta AIC$ was 0.2) as "substantial empirical support" for the constrained models, i.e. no effect of load on either growth rate or asymptotic performance.

For completeness, we also tested the 4-parameter fit against a 2-parameter fit, where values of growth and asymptote were constrained to be independent of load. For 9 of 10 observers, the constraint failed to produce a $\Delta AIC > 0$. The largest value of $\Delta AIC$, for subject KS was 2.4. Consequently, this indicates that the data from every observer but one provide "substantial empirical support" (Burnham and Anderson (2002, p. 70) for the constrained model, but the data from KS provide "considerably less support for the null hypothesis."

Largely similar conclusions can be obtained by fitting Equation 1 to all data simultaneously (and thus ignoring any differences between individual subjects). Our data provide substantial empirical support for no effect of load on either growth rate or asymptotic performance (in both cases, $\Delta AIC = -1.8$), and we can safely reject the null hypothesis of asymptotic performance on all trials in the high-load condition [$\chi^2(1) > 3.84; p < 0.05$].

However, we cannot safely reject the null hypothesis of asymptotic performance on the basis of the low-load data [$\chi^2(1) > 1.8; p = 0.18$]. This may be because each adaptation period lasted for 5 s rather than the 2 s in Experiment 1, so that most of the build-up may have occurred on the first trial. To test this we carried out the same test as in Expt 1, taking a difference score between the first trial in each session and the mean of the remaining 31 trials. Although the difference scores at the group level were negative in both load conditions (–0.19 and –0.14) and also negative for all observers in the high load condition, it was negative for just 6 of 10 observers in the low load condition. (NB: Just by chance, we would expect it to be negative in 5 of 10 observers.) A similar pattern was found when only the second session of trials was analysed (group-level difference scores: –0.26 and –0.07; number of observers with negative scores: 9 of 10 and 7 of 10).

Three of the observers (DP, TP, and EL) found the task very difficult and reported seeing no pop-out. Their scores barely reached the 0.25 level. DP and TP are siblings,
and had performed normally in other psychophysical experiments, including motion direction discrimination (cf. Morgan, Schreiber, & Solomon, 2016, where DP goes by the initials DW). Before concluding that these observers had reduced levels of adaptation, we wished to design an inverse task, where such a deficit would make the observer better, not worse. This was the purpose of Experiment 3.

Fig. 5. Performance of observers in Experiment 2 under two conditions of attentional load during adaptation (1: Crosses present, high load; 2: Crosses present low load). Error bars for individual observers contain binomial 95% confidence intervals. The bottom right panel shows the mean performance ± 1 SE over observers.
Figure 6. Growth curves in performance in Experiment 2 fit with the 2-parameter Equation (1) in the text. Each panel shows results for a different observer. The two curves are for the different attentional load conditions (blue: high load, black: low load). The coloured asterisks indicate conditions in which the growth curve was significantly $[\chi^2(1) > 5.64; p < 0.05]$ shallower than a step function (i.e. parameter $b < 10$); brackets indicate $[\chi^2(1) > 5.64; p < 0.01]$.

**Experiment 3**

In the Ishihara pseudo-isochromatic tests for colour deficiency, one of the plates contains numerals that should be invisible to normal trichromats but visible to dichromats. We wished to develop an analogous test of adaptation, where any effect of attentional load, instead of impairing performance as in Experiment 1 and 2, would have the reverse effect of making search performance better.

Our solution to this problem was suggested by the observation in Experiments 1 and 2 that the stationary, circular placeholders following the adaptation and test appeared to move, because of the well-known waterfall illusion (a. k. a. the motion aftereffect or MAE). We reasoned that this apparent movement of all the placeholders would camouflage real movement of one of them (analogous to Morgan, Adam, & Mollon,
1992 for textural camouflage). Therefore, individuals with genuinely weak or absent adaptation should perform better than “strong adapters” in detecting the moving target. Amongst observers whose adaptabilities genuinely differ, we predicted a negative correlation between performances in the current experiment and those in Experiments 1 & 2.

**Methods**

The adapting array and placeholder array were the same as in Experiment 2, but the test array was omitted. The adapting duration was 3 s, followed by a 1-s blank screen, and finally the placeholder array, which remained on until the observer clicked on the moving target. The measure of performance was the reaction time (RT) before the click; shorter RTs indicate better performances. During the display one of the circular placeholders moved vertically at a slow speed of 8.75 arcmin/s, either in the same direction as its spatially corresponding adaptor or in the opposite direction. The target-same and target-opposite conditions were randomly interleaved within a session, with an equal number of each. Because all the placeholders seemed to move initially, the observer had to wait for the MAE to die down before deciding which one was really moving. Typically, this took a few seconds. In a control condition, the patches in the adapting array were stationary. In this case, the distinction between target-same and target-opposite conditions was purely notional.

Attentional load was manipulated with central crosses, as in Experiment 2. In the high-load task there were 3 crosses in each adapting interval. In the low-load condition there were no crosses, as in Condition 1 of Experiment 1. The initial 5 trials of pre-adaptation in Experiment 1 were not used, as the observers were well used to the procedure. The observers were the same as in Experiment 1. The number of sessions performed by each of the observers (in order of their appearance in Fig. 7) was as follows: \{12, 10, 18, 6, 8, 12, 8, 12, 20, 32, 17, 2\}.

**Results**

A simple summary of the group level data in Fig. 7 is that the all the conditions are equivalent, except for the case where the adaptor is moving and the target is moving in the same direction as the adaptor. Detection was slower for targets moving in the same direction (Condition 1) as its corresponding adaptor than for targets moving in
the opposite direction (Condition 2). Of course, this difference was not found in the case where the adaptor was static (Stat.); only when it was moving (Mov.). The asymmetry is easily explained if adaptation to a moving Gabor patch causes a perceived movement of the spatially corresponding placeholder circle in the opposite direction. If the real movement is in the same direction as the adaptor, the aftereffect will slow it down and make the movement harder to detect. If it is in the opposite direction, the aftereffect and real motion will add and make it easier to detect.

To test for the significance of these effects at the group level, we calculated a statistic from the difference between the means of the moving and stationary adaptor conditions respectively. The null hypothesis is that this "movement effect" statistic should equal zero. A t-test ruled out this null hypothesis in the case of Condition 1 (same direction of movement; $p < 0.0035$), but not in Condition 2 (opposite direction of movement; $p = 0.2828$). These conclusions were not qualitatively altered by eliminating observer AJ, who showed the unusually high error rate. The asymmetry between same and opposite directions of movement can be explained easily, if adaptation to a moving Gabor patch were to cause a perceived movement of the spatially corresponding placeholder circle in the opposite direction.

Note, that in the individual data there seem to be genuine individual differences. Observers EL, DP, and TP do not show the predicted longer RTs in the target-same condition. These are the same three observers who found the task particularly difficult in Experiment 2, where pop-out was based on prior adaptation. We therefore conjecture that these observers are “weak adapters.”

The error rate in target selection was low (grand mean over all observers and conditions: 0.088) and not significantly different between conditions. Observer AJ was unusual in having a relatively high error rate (0.2891).

The effects of attentional load were not consistent over observers. However, if we set aside the results for the three weak adapters, we find that 7 out of the 8 remaining observers show longer reaction times in the low-load condition, consistent with the combined data (bottom right panel in Fig. 8). The exception is JS. However, it must
be acknowledged that the effect of load is also miniscule in observers MM and AJ. Overall, the effect of load is not very convincing.

To investigate possible effects of attentional load on the build-up of adaptation we first fitted negative exponential growth curves to the median RTs over observer (Fig. 8). Surprisingly, in view of the results of the first two experiments, there was little evidence for an increase in RT, as would be expected from build-up of adaptation, even in the crucial condition where the test and adapting stimulus moved in the same direction (Panel 1 in Fig. 8), except possibly from Trial 1 to Trial 2. In order to test for growth using the same likelihood tests used in Experiments 1 and 2, we need to estimate likelihoods because the data were RTs rather than probabilities. This can be done if the residual errors (i.e. the empirically measured reaction times minus the model's predicted reaction time) are independent of one another and identically distributed, with zero mean. In this case, we used a negative exponential distribution to model reaction time \( R(x) \) on trial \( x \):

\[
R(x) = a(1 - e^{-bx}),
\]

where parameters \( a \) and \( b \) describe the asymptotic reaction time and the growth rate, respectively \((a \leq 1, 0 \leq b)\); and the maximum log likelihood is \(-n \left[ \ln(\text{RSS}/n) + c \right]/2\), where RSS is the sum of the squared residuals, the constant \( c \) is model-independent (and thus irrelevant) and \( n \) is the number of data points (Burnham & Anderson, 2002, p. 63), which -- for each of the tests we report here -- is 64, i.e. twice the number of trials per session.

Initially, we compared the fits of two models to each of 6 subsets from each individual observer's data. Residual sums of squares are provided in Table 1. The unconstrained model is given by Equation 2, with both parameters free to vary. The constrained model is also given by Equation 2, but with parameter \( b \) fixed at 15 (producing asymptotic performance for all trials, i.e. \( x \geq 1 \)). The subsets (A–F) were: A) all trials (i.e. regardless of load) in which targets moved in the direction opposite to their adaptor, B) all trials in which they moved in the same direction, C) all low-load trials in subset B, D) all high-low trials in subset B, E) half of the trials (those in the notional 'target-same' condition), in which the adaptor was static, and F) the other half of the trials in which the adaptor was static. Just 5 of 66 (i.e. 6 subsets times 11 observers) generalized likelihood-ratio tests suggested there might be significant evidence [i.e. \( \chi^2(1) > 3.84; p < 0.05 \), without any correction for multiple comparisons] for growth (i.e. \( b \neq 15 \)): subset C from observer BD; and subsets B, C, D, and E from
observer DP. On the other hand, all of the remaining 61 comparisons yielded substantial support (with $\Delta \text{AIC} < 2$) for the constrained model. Consequently, we consider the bulk of our data—from all observers except DP—to support the null hypothesis of asymptotic performance in all trials (i.e. $b = 15$).

Next, we pooled the data from all observers, before dividing them into the aforementioned six subsets. Two of these subsets are illustrated in each panel of Fig. 8. For example, the top left panel shows subsets A and B. Each panel illustrates the fit of an unconstrained, in which the two subsets were allowed both different growth rates and different asymptotic reaction times. Not shown are the best fits of two constrained models: one that allowed only growth rate to vary between the two subsets and another that allowed only asymptote to vary between subsets. Each constrained model fit was compared with the fit the unconstrained model.

Two of these eight comparisons suggest essentially no support of the constrained model [in both cases, $\Delta \text{AIC} > 40$ and $\chi^2(1) > 40; p < 10^{-9}$], thus we feel safe rejecting two null hypotheses: asymptotic reaction times for trials in which the target moved in the same direction as its adaptor were equal neither to those from trials in which the target moved in the opposite direction nor to those from trials in which the adaptor was static.

Two of the other six comparisons [in both cases, $\Delta \text{AIC} < 0.3$] indicate substantial support for the constrained models, in which asymptotic reaction times were not affected by attentional load, nor were those attained for targets moving in the direction opposite to their adaptors different from those attained with static adaptors. The remaining four comparisons (in all cases $\Delta \text{AIC} < -1$) all support the constrained model in which there is no effect on the growth rate.

To investigate further the differences between observers, we assigned each observer a score in Experiment 1 (the detection probability, or hit rate) and plotted this against the difference score between median reaction times in the target-same and control (i.e. static adaptors, in the notional target-same condition) conditions in the present experiment (data from both high and low-load conditions were pooled). The difference score on trial $t$ was computed as $[R_1(x) - R_2(x)]/[R_1(x) + R_2(x)]$, where $x$ is the trial number and $R_1(x)$ and $R_2(x)$ are the individual's median reaction times on that trial in the two conditions respectively. The points Fig. 9 are the medians of
the set of difference scores and the vertical error bars contain 95% of the set over all trials. We expected low detection probabilities in Experiment 1 to correlate with low difference scores in Experiment 3, because both imply weak adaptation. The results shown in Fig. 9, comparing Experiment 3 with Experiments 1 and 2, confirm this conjecture. The three putatively weak adapters (EL, DP, and TP) form clusters in the bottom left of each panel.

Fig. 7. Results from Experiment 3, in which observers identified a slowly moving target circle amongst 15 stationary distractors, as quickly as possible, after adapting to a $4 \times 4$ array of Gabor patches (see Fig. 1). The key to the Static vs Moving conditions is given in Panel EL. The adapting patches were either static or moving (Stat. vs Mov.). In the adaptor-moving conditions, the target moved either in the same direction as its preceding adapting patch (Condition 1) or in the opposite direction (Condition 2). In the adaptor-static conditions, the target was randomly assigned to the target-same or target-opposite condition. Shading indicates that the adaptation was carried out under a high attentional load condition. White bars are low load. Observer LP carried out the low load condition only; her data for this condition have been repeated. The vertical axes show the individual median times taken by the observer to click on the target. The error bars contain 50% of the data (i.e. the inter-quartile range). The small inset at the bottom right shows the Group Data (means over observers of median RTs).
Fig. 8. Each panel in the figure shows the median reaction times over observers (ordinate) plotted against trial number in the session (abscissa). The solid lines are fits to the data points of the same colour using the negative exponential growth curve described in the Text. Each panel shows a different set of conditions, as follows: 

**Top Left**: Contrasts targets moving in the same direction as their adaptor with targets moving in the opposite direction. Only trials with a moving adaptor are included. Load conditions are combined.

**Top Right**: Contrasts the two conditions of attentional load. Only moving adaptor + target-same conditions are included.

**Bottom Left**: Contrasts the moving-adaptor and static-adaptor conditions, when the target moves in the same direction as the adaptor. Load conditions are combined.

**Bottom Right**: Contrasts the moving-adaptor and static-adaptor conditions, when the target moves in the opposite direction from the adaptor. Load conditions are combined.
Fig 9. Median (±47.5 percentiles) RT-difference scores for 10 observers in Experiment 3 (ordinate) plotted against hit rate for the same subjects in Experiment 1 (left) and 2 (Right). Observer initials are shown to the right and above the horizontal line indicating the 95% binomial confidence limits for hit rate. Some observers’ initials have been nudged to prevent overlap with others. Observers DP, EL, and TP form a cluster in the bottom left of the space. The straight line shows the best-fitting linear relationship between hit rate and RT difference. Data have been combined across load conditions in both experiments.

The RSVP Task for Distracting Attention in Experiments 1–3

To test whether observers were actually paying attention to the crosses in the RSVP task, we analysed their success rate and reaction times in spotting the rare exceptions in high-load conditions. Due to a keyboard connection error occurring in some sessions, which was only discovered after the data had been collected, some data were lost, but the remaining data (from 61% of all sessions in high-load conditions) were sufficient to show that detection was indeed occurring. False-positive rates, over all sessions where data are available, were 0.0092, 0.0213, and 0.0138 in Experiments 1, 2, and 3, respectively. The mean hit rates over observers and the mean RT are shown in Table 2, with the standard deviations in parentheses. The longer RTs and higher hit rates in Experiment 2 are most likely due to the fact that observers had longer to
respond (5 s) than in Experiment 1 (2 s) or in Experiment 3 (3 s). To see if there was any relationship between perceptual load and hit rate, we calculated a summary statistic for the effects of load. In Experiments 1 and 2 this was the difference in target detection probability between high and low load conditions. In Experiment 3 it was the difference in RT between high and low loads in the condition where the target moved in the same direction as the adaptor. The Kendall correlation coefficients between these three measures and the overall hit rates were 0.11, −0.09, and 0.14 respectively, giving no evidence for an association (p > 0.1 in all cases).

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<tr>
<th>Experiment</th>
<th>P(hit)</th>
<th>RT (s)</th>
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<tbody>
<tr>
<td>1</td>
<td>0.61 (0.12)</td>
<td>1.39 (0.18)</td>
</tr>
<tr>
<td>2</td>
<td>0.78 (0.22)</td>
<td>2.70 (0.86)</td>
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<tr>
<td>3</td>
<td>0.72 (0.15)</td>
<td>1.79 (0.42)</td>
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**Table 2**

**Experiment 4**
The purpose of Experiment 4 was to determine whether the adaptation found in Experiments 1 and 2 was retinotopic or spatiotopic (Turi & Burr, 2012; Morgan, 2014). It is important to show that it is retinotopic, if we are make a link with other studies of attention and the MAE, since this is known to be the case with the traditional MAE (e.g. Wenderoth & Wiese, 2008; Turi & Burr, 2012; review by Mather et al, 1998).

**Methods**
This experiment was similar to Experiment 2, with a large $6 \times 6$ adapting array and a smaller $4 \times 4$ test array, except that a 1.5-s blank (rather than a 1-s blank) was introduced between adaptor and test in order to leave time for an eye movement to a new fixation position. On half of the trials the fixation point (FP) remained in the same position on the screen (this is the “retino-spatiotopic” condition). On the remaining trials the fixation point jumped during the blank interval to a new position, one inter-patch distance away from the centre of the large array, in either the N, S, E, or W direction. The observer was instructed to make an eye movement to follow the
FP. On one-half of these trials (those in the “retinotopic” condition) the test stimulus consisted of the $4 \times 4$ patches that had originally been centred on the FP during adaptation, except that one of them had changed motion direction. On the remaining trials (those in the “spatiotopic” condition) the test consisted of the $4 \times 4$ elements that had been in that screen position during adaptation, except that one of them had changed direction. A subset of 8 observers from previous experiments participated, including the three who had been identified as weak adapters (DP, TP, and EL). All observers carried out the high-load RSVP task with central crosses during adaptation.

Results

The results in Fig. 10 show that performance in the spatiotopic condition (Condition 3) was not significantly above chance [$t(7) = 1.00, p = 0.35$] and was significantly inferior to performance in the retino-spatiotopic condition [$t(7) = 4.36; p = 0.003$] and in the retinotopic alone condition [$t(7) = 5.54, p = 0.0008$]. The latter two conditions did not differ significantly [$t(7) = 0.39, p = 0.70$]. The difference between retinotopic and spatiotopic conditions was smallest in the putatively weak adapters (EL, DP, and TP). If we take, for each subject, the mean direct hit rate in retino-spatiotopic and retinotopic conditions subtract from it the performance in the spatiotopic condition, we find that these three observers have the lowest difference scores (Mann-Whitney U test, $p = 0.0357$). It must be admitted, however, that DP has improved since the previous tests and is not significantly different from MM.

Eye-movement recordings were carried out to verify that observers shifted their fixation appropriately in the spatiotopic and retinotopic conditions, and also that they maintained fixation during the adaptation top-ups (Fig. 11). These recordings also showed that the three putatively weak adapters were just as accurate at fixating during adaptation as the other observers.
Fig. 10. Individual observers’ results in the three conditions of Experiment 4. Performance in the spatiotopic condition (Condition 3) is clearly inferior to performance in retino-spatiotopic (Condition 1) and retinotopic (Condition 2). Error bars are 95% confidence intervals. The bottom-right panel shows the mean across observers ± 1SE.

**Eye Movement Recording**

Eye-movement recordings were carried out in Experiment 4 with an EYELINK 1000 infrared reflection device to verify that observers maintained fixation during the adaptation top-ups, using the drift-corrected method described in full by Dillenburger & Morgan (2017). Points-of-regard sampled during individual trials for two observers are shown as individual symbols in the insets of Fig. 11. The outline circles show the position and size of the Gabor patches drawn to scale. The red symbols show data during the adaptation period; the blue symbols show position during the test, when the fixation point had either moved to a NSEW position, or stayed the same. Of the two subjects shown one (DP) is less variable in their fixation than the other (TP). To quantify differences between subjects in fixation variability, standard deviation of the point-of-regard relative to the fixation point was calculated over 64 adaptation periods. These scores were scaled by the separation between the Gabor patches to be meaningful. The scaled scores for individual subjects in Fig. 11
showed that the three putatively weak adapters (EL, DP, and TP) were no more variable at fixating during adaptation as the other observers, with the possible exception of TP.

Fig. 11. The data in the centre of the figure show the standard deviation in x (horizontal position) and y (vertical position) over all samples during adaptation in Experiment 4 for 8 observers. The inset boxes show individual fixations for two observers (TP and DP). Red circles indicate fixations during adaptation. Blue circles indicate fixations during the test in either the retino-spatiotopic condition (centre) or the retinotopic and spatiotopic conditions when fixation moved to the N S E or W neighbouring Gabor. DP is more typical than TP, who had relatively large fixation variability.

Discussion

As noted in the Introduction, there are conflicting claims regarding whether the MAE is decreased when observers’ attention is distracted away from the adapting stimulus. Bartlett et al. (2016) recently suggested that the discrepancy between these results might be because attention affects only the growth of adaptation to asymptote rather than the final level. Negative studies may have
missed the growth effect. Specifically for this reason, we looked at the growth of the adaptation effect in Experiments 1 & 2. Within-subjects analyses of our objective (or Type 1) measure of adaptation produced no convincing evidence for differences in growth rate or asymptote. A small effect of load was found in Experiment 3, but only at the population level, when weak adapters were excluded. Contrast in this experiment was between crosses-present (high load) and crosses-absent (low load) so we cannot exclude the possibility that any small effect was due to the crosses rather than to attentional distraction *per se*.

Our method of distracting attention with crosses was based on an fMRI study of Schwartz, Vuilleumier, *et al.* (2005), where it was shown to reduce the positive BOLD response to peripherally presented checkerboard stimuli in V1 and in successive visual areas up to V4. However, Schwartz, *et al.* did not report any psychophysical measure of its distracting effect. It is therefore possible that the task is not sufficiently distracting to interfere with adaptation. Schwartz, *et al.* noted that the effects of distraction were greatest in retinotopic regions nearest to the distractors. Thus, another possibility is that our Gabor stimuli escaped the effects of distraction because they were presented in retinal locations that were more peripheral than the RSVP.

Despite these caveats, it seems reasonable to conclude, taking into account the literature as a whole, and the negative effects reported in this paper, that the effect of attention on motion adaptation is at best small and inconsistent. Even if a recipe for producing the effect consistently were eventually found, it would be necessary to eliminate the possibility that it was due to peripheral effects of attention, such as microsaccade frequency, pupil size, and blinking, before we could conclude that it is a direct effect of attention on V1. Our view is that the effect, if it exists, is so small and variable over observers that it is not worth pursuing further in any detail.

Individual differences in putatively basic visual processes such as simultaneous contrast are attracting increasing interest (Bosten & Mollon, 2010; Mollon, Bosten, Peterzill & Webster, 2017). We found three observers who showed small
or non-existent effects of adaptation in a visual search task. Crucially, this was not because they were poor at search tasks in general; they were faster than most observers in searching for the moving placeholder in Experiment 3, a task that was impeded by adaptation. Nor was it because these observers were relatively poor at fixating the centre of the adapting stimulus (Fig. 11). We conclude that these observers most likely have a weaker MAE than the norm. Large individual differences in the duration of the MAE have previously been reported by Granit (1928) and Sinha (1952), including the remarkable and neglected case noted by Grindley (1930) of an observer who saw no movement aftereffect whatsoever. The exciting possibility of a basic polymorphism in adaptation between human observers deserves further investigation. The advantage of the method we have described in this paper is that, unlike the duration or P50 measures of the MAE (e.g. Morgan, Dillenburger, Raphael, & Solomon, 2012), it is performance-based and criterion free. It is a Type 1 task, for which there is a right answer (Sperling et al. 1990), and which therefore could be used to measure adaptation in non-human species.

Acknowledgements
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References


Dillenburger, B. & Morgan, M.J. (2017) Saccades to Explicit and Virtual Features in the Poggendorff Figure show Perceptual Biases, i-Perception, March-April, 1-21


**Experiment 1: Growth-curve differences due to load**

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**Experiment 1: Group-level tests for growth**

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**Experiment 2: Growth-curve differences due to load**

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**Experiment 2: Group-level tests for growth**

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**Sum of squares from Experiment 3**

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**Group-level analysis of Experiment 3**

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