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Attention enhances adaptability: evidence from motion adaptation experiments

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Abstract

Several previous psychophysical and neurophysiological studies have investigated the separate effects of attention and adaptation on visual processing. Here, we investigated the combined effects of attention and adaptation on motion processing by measuring the effects of spatial attention on the duration of the motion after-effect (MAE) over a wide range of stimulus contrasts. MAE duration was compared between two conditions: *full-attention*, subjects were required to pay attention to the adapting motion stimulus, and *poor-attention*, subjects performed a difficult vowel detection task at the center of gaze and ignored the adapting motion stimulus. Attention was found to increase the MAE duration by a factor of 1.4, which was approximately constant over a wide range of stimulus contrasts (3.22–80.6%). Notably, this included contrasts for which the MAE duration had reached its asymptotic value. We show that a quantitative model based on known properties of directionally selective MT neurons can explain these results by assuming that attention enhances the effects of adaptation, a phenomenon we refer to as "*adaptation gain*". Specifically, attending to an adapting motion stimulus shifts the semi-saturation point (C_{50}) of the underlying contrast response function (CRF) of motion detectors roughly 1.4-fold more to the right than does ignoring that same stimulus. By enhancing the effects of adaptation in this fashion, attention is predicted to enhance the adaptability of the visual motion system.
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1. Introduction

Several psychophysical and neurophysiological studies have investigated the separate effects of adaptation and attention on visual motion processing. In the *adaptation* domain, perhaps the best, and most often studied, psychophysical example is the *motion after-effect (MAE)* phenomenon; after adapting to a stimulus moving in one direction, a stationary (or motion balanced) test stimulus will appear to move in the opposite direction. In addition to MAE experiments, the psychophys-

ical effects of adaptation have also been revealed in studies that measure contrast sensitivity after adapting to a stimulus moving in one direction. Here, sensitivity is reduced for test stimuli moving in the same, but not the opposite, direction as the adapting stimulus (Levinson & Sekuler, 1980). These findings are typically explained in terms of changes in the underlying "contrast response function" (CRF); neurons in the visual system exhibit an increase in firing rate with increasing stimulus contrast, which asymptotes at some contrast value. Specifically, it is proposed that adaptation lowers the gain of the CRF, selectively for motion detectors tuned to the direction of the adapting stimulus. In theory, this gain control could result from: (1) "contrast gain", i.e., adaptation shifts the CRF

rightward, resulting in a change in the semi-saturation constant (C_{50}), but no change in the maximum response (R_{max}), or (2) "response gain", i.e., adaptation shifts the CRF downward by a constant percentage, resulting in a change in R_{max}, but no change in C_{50}, or a combination of (1) and (2).

In psychophysical studies investigating the effects of adaptation on contrast discrimination, data favor the contrast gain control hypothesis (Greenlee & Heitger, 1988; Ross & Speed, 1991; Ross, Speed, & Morgan, 1993). A decrease in contrast gain due to adaptation is also supported by results from neurophysiological studies that have directly compared pre- and post-adaptation CRFs in cat area 17 (Ohzawa, Sclar, & Freeman, 1985) and in motion area MT of macaque monkeys (Kohn & Movshon, 2003). Specifically, Kohn and Movshon showed that adapting directionally selective MT neurons to stimuli moving in their preferred direction produces a rightward shift in the C_{50}, with little effect on the R_{max}, i.e., adaptation lowers the *contrast gain*. In comparison, adapting neurons to stimuli moving in the opposite (anti-preferred) direction has negligible effects (A. Kohn, personal communication; Kohn & Movshon, 2003; Van Wezel & Britten, 2002).

In the *attention* domain, the effects of spatial attention on the CRF have been investigated in both visual areas V4 (Reynolds, Pasternak, & Desimone, 2000) and MT (Martinez-Trujillo & Treue, 2002) of monkeys. In the Reynolds at al. experiment, two spatially segregated stimuli were presented; one that the monkey was instructed (via a pre-cue) to respond to (and thus, by definition, *attend* to) and one that the monkey ignored. Using this paradigm, the population CRF was determined for attended vs. ignored stimuli in receptive fields of V4 neurons. The results of this study revealed that attention produces mainly a leftward shift in the C_{50} of the CRF, with little effect on the R_{max}. Martinez-Trujillo and Treue (2002) employed a variation of this paradigm in MT neurons, with their results also suggesting a leftward shift of the CRF due to attention. These findings suggest that, like the effects of adaptation, attention alters the *contrast gain* of MT neurons, although in the opposite direction (i.e., attention *increases* the contrast gain). Moreover, the results are interpreted to mean that attention alters the "effective" contrast of a stimulus, i.e., that top-down influences of attention are, in essence, interchangeable with bottom-up changes in stimulus contrast.

The effects of spatial attention on motion processing have also been tested psychophysically, although only for a single or very narrow range of stimulus contrasts. For example, Chaudhuri (1990) showed that diverting attention away from a randomly patterned motion stimulus by requiring subjects to perform a difficult central task at the center of gaze diminishes the duration of the MAE resulting from that stimulus (see Alais &

Blake, 1999; Lankheet & Verstraten, 1995; Shulman, 1993 for similar psychophysical evidence; and see Rees, Frith, & Lavie, 1997 for a related fMRI study in human area MT+). However, no previous study has taken into account a peculiarity specific to studying the effects of attention on the MAE; by doing so, one is looking at the combined effects of attention and adaptation, which as described above, are thought to produce opposite effects on the contrast gain of the CRF.

In the present study, we set out to investigate the combined effects of attention and adaptation on motion processing by measuring the effects of spatial attention on the duration of the MAE over a wide range of stimulus contrasts. Note that MAE duration can be considered to reflect the strength of the MAE (see Pantle, 1998 for discussion). MAE duration was compared between two conditions: *full-attention*, subjects were required to pay attention to the adapting motion stimulus, and *poor-attention*, subjects were required to perform a difficult vowel detection task at the center of gaze and therefore ignore the adapting motion stimulus. The results of this study revealed a constant attention effect (full-attention MAE divided by poor-attention MAE) across stimulus contrast. We propose a model based on known properties of MT neurons that can account for this finding. A new hypothesis incorporated into the model is that attention enhances the effects of adaptation. We refer to this effect of attention as "adaptation gain", and show that it is distinctly different from contrast gain effects of attention.

2. Methods

2.1. Subjects

A total of 12 subjects participated as either volunteers or as paid research subjects (age range = 21–31 years). All had normal or corrected-to-normal vision, and with the exception of one (the first author) were naïve to the purpose of the experiment. Data were obtained from two different groups. Subject group 1 included six subjects. Subject group 2 included seven subjects, one of whom was also in subject group 1. Note that data from subject group 2 were obtained during the course of another experiment, in which we compared the effects of attention on motion processing for achromatic (yellow/black) vs. chromatic (red/green) gratings (Rezec, Krekelberg, & Dobkins, 2004).

2.2. Apparatus

Visual stimuli were generated using in-house OpenGL software driving an ATI Radeon 8500 graphics board (1280 ∗ 1024 pixel resolution) that resided in an AMD Athlon processor based PC. Stimuli were

displayed on an analog RGB monitor (NEC Multisync 1250+, 30.5 by 40.6 cm, 75 Hz, non-interlaced). For each subject, eye position was monitored using a closed couple device (CCD) infrared camera with variable focus (12.5–75 mm) lens (Model #Fc62, Image Sensor), which was focused on the left eye of the subject. The subjects' face was lit with an infrared illuminator and an enlarged image of the eye was viewed on a 12″ Monitor (Ultrak) outside the testing room. Before beginning each block of trials, subjects were instructed to fixate a black fixation square ($0.9° \times 0.9°$) in the center of the video display, and the outline of the pupil was drawn on transparency film that covered the monitor. Previous experiments in our laboratory have shown that this set-up allows for the easy detection of saccadic eye movements and eye drift within $\pm2°$ of fixation (Dobkins & Bosworth, 2001). Subjects were instructed to maintain fixation throughout the experiment and were informed that the experiment would be temporarily interrupted if eye movements or eye drift were detected. Thus, subjects were highly discouraged from breaking fixation, and the experiment never needed to be interrupted.

2.3. Stimuli

Stimuli consisted of horizontal achromatic sinusoidal gratings, with a spatial frequency of 0.4 cpd. The gratings subtended $10° \times 10°$, were centered on a black fixation square ($0.9° \times 0.9°$), and presented on a background of the same mean luminance (7.0 cd/m^2) and chromaticity (CIE: $x = 0.44$, $y = 0.40$). Each trial began with a "motion adaptation phase", in which gratings moved either upward or downward at 6.2 deg/s (TF = 2.5 Hz) for 30 s. During the adaptation phase, a rapid serial visual presentation (RSVP) of white letters (subtending $0.6° \times 0.6°$) was displayed within the fixation square. A total of 160 letters was presented with the duration of each letter lasting 0.08 s and 0.106 s blank in between each. All letters of the alphabet were presented. The frequency of a vowel appearing (A, E, I, O, U) was set to ~10% (~15 to 20 out of 160). The adaptation phase was followed by a "test phase", during which the duration of the motion after-effect (MAE) was measured (see below). The test stimulus consisted of a grating of the same contrast and spatial frequency as the moving adapting stimulus. The letters of the RSVP task were not shown during the test phase.

For subject group 1, the test grating was static. For subject group 2, the test stimulus was dynamic, consisting of a counterphase-reversing (in a temporal sinusoidal fashion) grating with the same temporal frequency as the moving adapting stimulus. This stimulus is mathematically equivalent to two gratings superimposed and moving in opposite directions, each at half the contrast of the counterphase grating. The use of both a static and dynamic test stimulus allowed us to address potential

differences between the two (see Nishida, Ashida, & Sato, 1997). For example, it has been suggested that the MAE generated with dynamic test stimuli may be more susceptible to higher-order attention effects (see Culham & Cavanagh, 1994 for review).

To investigate the effects of stimulus contrast, a broad range of luminance contrasts was employed. For subject group 1, eleven contrast values were employed, ranging in equal log steps (base 1.34) from 4.30% to 80.6%. For subject group 2, eight contrast values were employed, varying along the same log base and ranging from 3.22% to 25.0%. Note that the adaptation and test stimulus were always presented at the *same* contrast, which has been shown to maximize the strength of the MAE (Nishida et al., 1997).

2.4. Paradigm

Subjects were tested in a dark room and viewed the video display binocularly from a chin rest situated 57 cm away. In all conditions, they were instructed to maintain fixation on the central fixation square. Subjects began each trial with a key press, after which the moving adaptation stimulus appeared for 30 s, followed by the test stimulus. During this test phase, subjects perceived an MAE, i.e., the test stimulus appeared to move in the direction opposite to that of the adaptation stimulus. Subjects were required to signal (with a key press) when the MAE ended. [Entertaining the possibility that some stimuli/conditions may yield no MAE at all (specifically, the "poor-attention" condition, see below), subjects were also given the option of reporting "no MAE" with a separate key press. The frequency of this occurring and the way such trials were analyzed is discussed below under Data Analysis.] This was followed by a 20-second period in which subjects rested and were allowed to move their eyes. This period also allowed motion mechanisms to return to a pre-MAE baseline level of activity (e.g., van der Smagt & Stoner, 2002). The direction of the adapting stimulus (upward vs. downward) was randomized across trials. A timeline depicting the course of a single trial is presented in Fig. 1.

Data were obtained in two separate attention conditions, both of which contained the RSVP stimulus inside the fixation square during the adaptation phase. In one condition, which we refer to as "*full-attention*", subjects were instructed to simply attend to the moving stimulus in the 30-second adaptation phase, ignoring the (irrelevant) stream of letters at the center of gaze. In the other condition, which we refer to as "*poor-attention*", subjects performed an RSVP task during the adaptation phase. In this task subjects were required to press a key each time a vowel (A, E, I, O, U) appeared. Because the RSVP vowel-task was extremely demanding, subjects paid substantially less attention to the moving adapting stimulus in this condition. The two attention
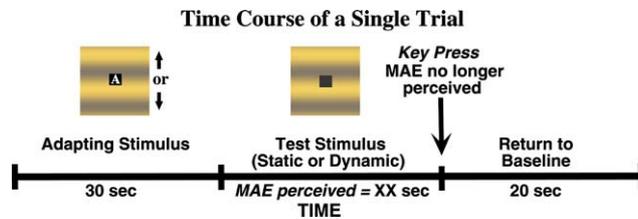
Time Course of a Single Trial

Fig. 1. *Time course of a single trial*. Subjects began each trial with a key press, after which the moving adaptation stimulus appeared for 30 s (moving upward or downward), with the RSVP stimulus presented on the central black square (only one letter shown here). This was followed by the presentation of the test stimulus, during which the motion after-effect (MAE) was perceived, i.e., motion in the direction opposite to that of the adaptation stimulus. Subjects were required to signal (with a key press) when the MAE ended (labeled XX sec). This was followed by a 20-second rest/recovery period (see Section 2 for further details).

conditions were interleaved in blocks of 11 trials. The purpose of interleaving was to avoid differential practice/criterion effects in reporting the duration of MAE between the two attention conditions. Stimulus contrast was varied randomly across trials within a block.

After each poor-attention block, subjects were provided with feedback regarding their RSVP performance on that block. Performance was computed as the percentage of correct detections minus the percentage of false alarms, with a correct detection considered a key press within 0.8 s after a vowel presentation and a false alarm considered any key press outside this time window. Before beginning this experiment, subjects received ample practice on the vowel-task alone. Note that the overall RSVP performance of both subject groups was at least as high during the main experiment (group 1: 74.6% ± 6.42% (sem), group 2: 78.8% ± 3.42%) as during the last practice session (group 1: 74.5% ± 6.23%, group 2: 62.4% ± 4.81%). This confirms that, in the main experiment, the presence of the motion stimulus did not lessen the amount of attention paid to the RSVP task, and thus we can be assured that subjects adequately ignored the motion stimulus in the poor-attention condition. In addition to computing overall performance on the RSVP task, we also computed performance separately for each stimulus contrast; a repeated measures ANOVA revealed no effect of stimulus contrast on RSVP task performance (subject group 1: $p = 0.65$; subject group 2: $p = 0.71$). This shows that any observed difference in MAE duration across the different contrast conditions in the *poor*-attention condition cannot be attributed to a variation in the amount of attention placed on the RSVP task.

2.5. Data analysis

For subject group 1, there were 22 total conditions (2 attention conditions × 11 contrasts), and 10 trials were

obtained for each (total trials = 220). For subject group 2, there were 16 total conditions (2 attention conditions × 8 contrasts), and 10 trials were obtained for each (total trials = 160). For trials in which a subject reported "no MAE", the MAE duration was pegged by using the lowest MAE observed for that subject. (We also analyzed the data using an MAE value of 0 s for trials where the subject reported "no MAE", and the results looked essentially identical.) In the *static* test condition, the need to peg any trial occurred in four of six subjects, and accounted for 9–22% of total trials, depending on the subject. In the *dynamic* test condition, the need to peg any trial occurred in two of seven subjects, and accounted for 1% and 4% of total trials in these two subjects. For each subject, a mean MAE duration was obtained by averaging across the 10 trials, separately for each condition.

An "attention effect" was obtained for each subject by dividing the MAE duration in the full-attention condition by that in the poor-attention condition, separately for the different stimulus contrast conditions. All statistical analyses were conducted using log MAE durations and log attention effects, and thus all data are plotted in log scale. The reason for using logs is twofold. First, population data conform more closely to normal distributions when logged. Second, using logs allows for easy visual comparison/interpretation of MAE data plotted for full- vs. poor-attention conditions, as the linear distance between the means of the two is equal to the attention effect ratio (full-attention divided by poor-attention).

3. Results

3.1. Example data

Example data obtained from two subjects tested with a static test stimulus (subject group 1) are presented in Fig. 2. Plotted is MAE duration as a function of stimulus contrast, for both the full-attention (*filled squares, solid curve*) and poor-attention (*open squares, dashed curve*) conditions. Note that contrast refers to the contrast of *both* the adapting and test stimulus, which were always set equal to one another (see Section 2). Both subjects exhibited a clear increase in MAE duration with contrast, which asymptoted around 20% contrast, in both the poor- and full-attention conditions. Both subjects also showed longer MAE durations in the full- vs. poor-attention condition, although the overall attention effect was larger for subject AR.

3.2. Group mean data: static MAE

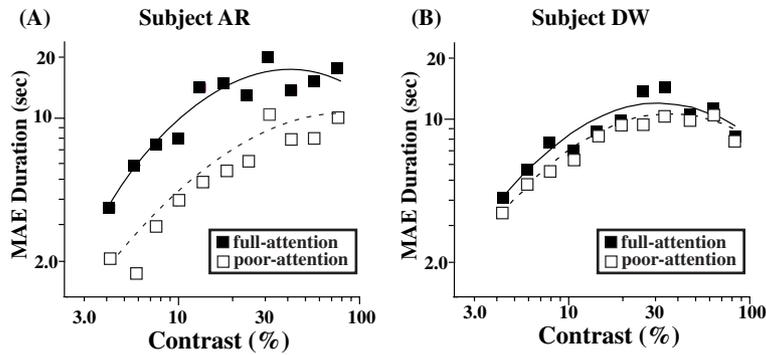Group mean MAE data for subjects tested with the static test stimulus (subject group 1, *n* = 6) are presented

Fig. 2. *Example static MAE data for two subjects: (A) and (B)*. MAE duration is plotted as a function of stimulus contrast, for both the full-attention (*filled squares, solid curve*) and poor-attention (*open squares, dashed curve*) conditions, with the data points fit by polynomial functions. Note that contrast refers to the contrast of *both* the adapting and test stimulus, which were always set equal to one another.

in Fig. 3A. As for individual data, in both the full-attention (*filled squares, solid curve*) and poor-attention (*open squares, dashed curve*) condition, group data revealed an increasing MAE duration with increasing contrast that asymptoted at roughly 20% (with a slight tendency for MAE duration to decrease at higher contrasts). Over the tested range, the increase in MAE duration with contrast was roughly 2.5-fold in both attention conditions. This effect of contrast was confirmed statistically in a two-factor ANOVA (stimulus contrast × attention condition), which revealed a significant main effect of contrast ($p < 0.0001$), and is in line with previous psychophysical reports (Nishida et al., 1997). The ANOVA also revealed a significant main effect of attention condition ($p < 0.025$), i.e., MAE duration was significantly longer when subjects attended to the moving adapting stimulus.

The group mean attention effect (i.e., full-attention divided by poor-attention MAE duration) is plotted as a function of stimulus contrast in Fig. 3B. These data demonstrate a roughly constant effect of attention across a broad range of stimulus contrasts (4.30–

80.6%), which includes contrasts where MAE duration had asymptoted. Averaged across contrasts, the effect of attention was 1.36-fold. This constant effect is supported statistically by the absence of a significant effect of contrast on the attention effect (one-factor ANOVA, $p = 0.23$).

3.3. Group mean data: dynamic MAE

Group mean MAE data for subjects tested with the dynamic test stimulus (subject group 2, $n = 7$) are presented in Fig. 4A. These subjects were tested over a more narrow contrast range (3.22–25.0%) than those in subject group 1. Like subject group 1, MAE duration for subject group 2 increased significantly with increasing contrast ($p < 0.001$) and MAE duration was significantly longer in the full- vs. poor-attention condition ($p < 0.005$). However, the asymptote for MAE duration occurred at somewhat lower contrasts ($\sim$6% to 8%) and the increase in MAE duration with contrast was smaller (roughly 1.6-fold) as compared to subject group 1. This difference might be explained by proposing that the
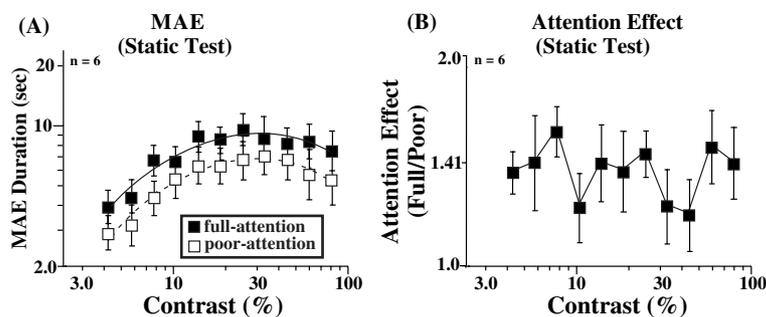

Fig. 3. *Static MAE: subject group 1*. (A) Group mean MAE duration data plotted as a function of contrast, for both the full-attention (*filled squares, solid curve*) and poor-attention (*open squares, dashed curve*) conditions, with the data points fit by polynomial functions. In both the poor- and full-attention condition, MAE duration asymptotes at roughly 20%, although there is a slight tendency for MAE duration to decrease at higher contrasts. (B) Group mean "attention effect" ratios (full-attention divided by poor-attention MAE duration) plotted as a function of stimulus contrast. The attention effect was found to be constant across the range of contrasts tested (see text for details). In both (A) and (B), error bars denote standard errors of the means.
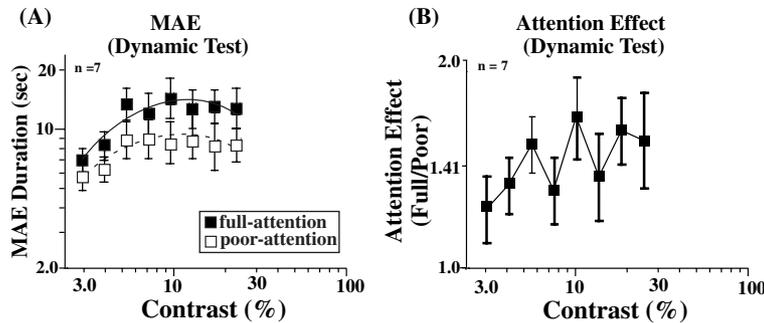
Fig. 4. *Dynamic MAE data: subject group 2.* (A) Group mean MAE duration data plotted as a function of contrast, for both the full-attention (*filled squares*, *solid curve*) and poor-attention (*open squares*, *dashed curve*) conditions, with the data points fit by polynomial functions. (Note that, in this experiment, subjects were tested over a more narrow contrast range than those in subject group 1.) In both the poor- and full-attention condition, MAE duration asymptotes at roughly 6–8%. (B) Group mean "attention effect" ratios plotted as a function of stimulus contrast. The attention effect was found to be constant across the range of contrasts tested (see text for details).

MAE produced by dynamic stimuli is mediated by directionally selective neurons at later stages of visual processing than the MAE produced by static stimuli. This possibility, in conjunction with the fact that the C_{50} is known to decrease through the motion pathway (Sclar, Maunsell, & Lennie, 1990, and see Thiele, Dobkins, & Albright, 2000), would lead one to predict that the asymptotic contrast value for the MAE should be lower in the dynamic test stimulus condition (see Nishida et al., 1997, for a similar suggestion).

The group mean attention effect is plotted as a function of contrast in Fig. 4B. Like subject group 1, subject group 2 demonstrated a roughly constant effect of attention across stimulus contrasts ($p = 0.34$), even over the range of contrasts where MAE duration had asymptoted. Averaged across contrasts, the effect of attention was 1.42-fold.

3.4. Model

In this section, we model our psychophysical results using known properties of directionally selective neurons in area MT. Because we have the widest range of data available for the *static* test stimulus, we present model results for this test stimulus condition only. Our model has three main features: (1) It assumes that the strength of the MAE (as measured via a duration assay) is based on the difference in signal strength between motion detectors tuned in the same (i.e., the "preferred" neuron) vs. opposite (i.e., the "anti-preferred" neuron) direction as the adapting stimulus. (2) It incorporates the effects that adaptation is known to have on the underlying contrast response functions of the preferred and anti-preferred motion detectors. (3) It introduces the concept of *adaptation gain*, which reflects the amount by which attention enhances the effects of adaptation. To our knowledge, this feature of the model has yet to be tested in MT neurons.

We begin by modeling psychophysical data obtained in the *poor*-attention condition, using contrast response functions (CRFs) described by the following formula:

$$R = R_{max} * (C^n / (C^n + C_{50}^n)) + m, \qquad (1)$$

where R is the neural response, R_{max} is the maximum response, C is the stimulus contrast, C_{50} is the semi-saturation point (i.e., the contrast yielding half the maximum response), n is the steepness of the function, and m represents baseline activity. Our model is based on the following assumptions.

(1) *Pre*-adaptation, both the "preferred neuron" and "anti-preferred" neuron exhibit CRFs with the following parameters: $R_{max} = 100$, $C_{50} = 10\%$, $n = 1.3$, and $m = 5$, which is depicted in Fig. 5A (*solid curve*). The C_{50} and m values were chosen to reflect those observed for MT neurons under anesthetized, and thus necessarily unattended, conditions (Kohn & Movshon, 2003). The slope value (n) was chosen based on mean values reported by Martinez-Trujillo and Treue (2002) for ignored stimuli under awake conditions, although the stimuli in their experiments were moving dots, rather than gratings.

(2) *Post*-adaptation, the C_{50} and R_{max} of the *anti-preferred* neuron's CRF are unaltered, i.e., contrast adaptation has no effect on the anti-preferred neuron, an assumption that is in line with the negligible effects of anti-preferred adaptation seen in MT (A. Kohn, personal communication; Kohn & Movshon, 2003; Van Wezel & Britten, 2002). Note, however, that the R_{max} of the post-adaptation CRF will only be unaltered if the post-adaptation stimulus is one moving in the preferred direction for that neuron. Because the test stimulus in our study was a *static* grating, which is less effective than a moving grating, we assume that post-adaptation responses produced by this static stimulus are a fraction of
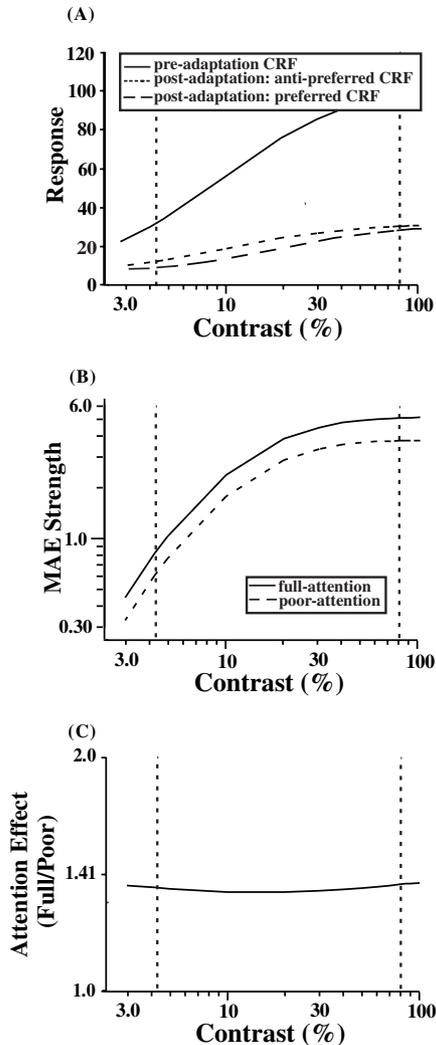
(A)

(B)

(C)

Fig. 5. *MAE model for static test stimuli.* (A) *Contrast response functions in the poor-attention condition.* The *solid curve* represents the CRF for the pre-adapted neuron presented with motion in its preferred direction under the poor-attention condition. After adapting to a stimulus moving in one direction (in this example, the contrast of the adapting stimulus is 50%), the CRF of the "preferred" neuron (i.e., adapting stimulus moves in its preferred direction,) gets shifted rightward by an amount proportional to the adapting contrast (*long-dashed curve*). By comparison, the post-adaptation CRF of the "anti-preferred" neuron (i.e., adapting stimulus moves in its anti-preferred direction) is unshifted (*short-dashed curve*). Note that for both the anti-preferred and preferred neuron, the post-adaptation responses to the test stimuli are scaled down to reflect the fact that motion detectors are less responsive to static vs. moving stimuli (see text for details). Under conditions of *full*-attention, the CRF of the preferred neuron gets shifted further to the right, which we refer to as "adaptation gain" (CRF not shown). Vertical dashed lines show the range of contrasts used for subject group 1. (B) *Predicted MAE strength for full- and poor-attention conditions.* For each test contrast (which is the same as the adapting contrast), the predicted MAE is calculated as the difference in response between the anti-preferred and preferred neuron. For both the poor-attention (*dashed curve*) and full-attention (*solid curve*) conditions, MAE strength increases with increasing contrast and reaches a maximum at roughly 25% contrast. (C) *predicted attention effect (MAE full-attention divided by MAE poor-attention) vs. contrast.* Over the range of contrasts used in the psychophysical experiment (vertical dashed lines), the effect of contrast is essentially constant.

those produced by a moving stimulus. Specifically, we used a value of 27% (i.e., $R_{max} = 27$) since previous data from MT neurons have shown that static stimuli produce 27% of the response produced by stimuli moving in a neuron's preferred direction (Albright, 1984). The actual scaling value used in the model does not alter the overall results. The post-adaptation CRF of the anti-preferred neuron is shown in Fig. 5A (*short-dashed curve*), and, accordingly, is a scaled-down version of the CRF that would be produced by a post-adaptation stimulus moving in the preferred direction for that neuron.

(3) *Post*-adaptation, the C_{50} of the *preferred* neuron's CRF is shifted rightward. As described in the *Introduction*, this is based on the finding by Kohn and Movshon (2003) that adapting MT neurons to gratings moving in their preferred direction produces a rightward shift in the C_{50} of the CRF, with little effect on the R_{max} (i.e., a contrast gain effect). For a 100% contrast moving adapting stimulus (the only contrast tested in their study), the average shift in MT neurons was 3.28-fold. In our model, we assume that the degree of rightward shift for the different adapting contrasts will be proportional to this value. An example for a 50% contrast adapting stimulus is provided in Fig. 5A. The CRF of the preferred neuron is shifted 1.64-fold rightward (Fig. 5A, *long-dashed curve*), which is 50% of the shift produced by a 100% contrast grating. This translates into a change in the C_{50} from 10% (the pre-adaptation value) to 16.8%. As for the case of the anti-preferred neuron (see above), because the test stimulus in our study was static rather than moving, the post-adaptation CRF of the preferred neuron is also scaled-down 27% relative to the CRF that would be produced by a post-adaptation stimulus moving in the preferred direction for that neuron.

(4) To compute the predicted MAE, we assume that the MAE strength (presumably reflected in the duration of the MAE) is equal to the linear difference between the response of the anti-preferred and preferred neuron elicited by a post-adaptation (i.e., test) stimulus of a given contrast (see Mather & Harris, 1998 for review of opponent motion models of MAE).

Fig. 5B shows the predicted MAE duration as a function of stimulus contrast (which was always the same for the adapting and test stimulus) under conditions of poor-attention (*dashed curve*). The model, just like the data shown in Fig. 3A, shows that MAE strength increases with contrast and reaches a maximum at ∼25% contrast. Unlike the data, in the model there is no tendency for MAE to decrease after this point. In addition, in the model, the increase in MAE across the range of

contrasts tested psychophysically (range depicted by *vertical dashed lines*) is larger than that observed in the data. These small differences between the model and the data can be remedied by changing the relation between the adapting contrast and the degree of shift in C_{50}. Nonetheless, the current model captures the most salient aspects of the data.

The next step in our model is to consider the effects of attention. In order to account for our psychophysical finding that the strength of the MAE is stronger in the full- vs. poor-attention condition and that this effect is constant across a wide rage of contrasts, we introduce a new concept—*adaptation gain*, whereby attention enhances the effects of adaptation. In our model, this adaptation gain is implemented as a multiplicative factor that shifts the C_{50} of the preferred neuron's CRF in the full-attention condition rightward as compared to that in the poor-attention condition (i.e., the *long-dashed curve* in Fig. 5A gets shifted further to the right, not shown in figure). When the adaptation gain is set to 1.4-fold, the model yields mean attention effects (i.e., *MAE for full-attention divided by MAE for poor-attention*) that mirror those observed psychophysically. Predicted MAE strength as a function of adapting/test contrast under the *full-attention* condition is shown in Fig. 5B (*solid curve*), and the predicted *attention effect* is shown in Fig. 5C (*solid curve*). The predicted attention effect varies negligibly over the range of contrasts employed in our psychophysical study (*vertical dashed lines*), and thus the model provides an adequate account of the constant effect of attention observed in our psychophysical study (see Fig. 3B).

It is important to point out, however, that adaptation gain effects of attention (which shift the CRF further to the right under adapting conditions) do not preclude the simultaneous existence of contrast gain effects of attention (which are known to shift the CRF leftward, Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000). As explained further in Section 4, adaptation gain effects of attention are distinctly different from contrast gain effects of attention, and importantly, the predicted effects of attention in our model are unaltered when we incorporate contrast gain effects of attention. In sum, this model accounts for our psychophysical data by incorporating the separate effects that adaptation and attention are known to have on the underlying CRF, with the crucial aspect that—in addition to these effects—an adaptation gain is imposed in which attention enhances the effects of adaptation.

4. Discussion

The results of our study demonstrate a constant effect of attention on the strength of motion processing (assessed by measuring the duration of the motion after-effect, MAE) across a wide range of stimulus contrasts (3.22–80.6%), including those contrasts for which the duration effect has asymptoted. Using an MAE model that incorporates the known properties of visual area MT neurons, we found that both the effect of contrast and attention on the MAE strength can be accounted for by assuming that attention *enhances* the effects of adaptation, by a mechanism we refer to as "adaptation gain". Specifically, attending to an adapting motion stimulus shifts the C_{50} of the CRF roughly 1.4-fold more to the right than does ignoring that same stimulus.

In the remainder of this *Discussion*, we first discuss the effects of variations in the assumptions of our model. Second, we address why contrast gain effects of attention (which shift the CRF leftward) cannot account for our results, making an important distinction between "contrast gain" vs. "adaptation gain" effects of attention. Third, we discuss the potential functional consequences of adaptation and attention, when they are manipulated separately as well as together.

4.1. Variations in the assumptions of the model

Because there are many assumptions in our model, not all of which can be based on known properties of MT neurons, we address whether the model is robust in the face of variations in these assumptions. First, our model assumes that the strength of the MAE is computed as the linear *difference* in response between the anti-preferred and preferred neuron elicited by the post-adaptation stimulus. However, if we instead compute a *ratio* of responses, we obtain very similar results. Second, our model assumes that the degree of rightward shift in the CRF due to adaptation is linearly proportional to the magnitude of the adapting contrast. We also tried a variation of the model where the shift resulting from a given adapting contrast was proportional to the effect that contrast had on the pre-adaptation response of the neuron (and thus the shift was *non-linearly* proportional to the magnitude of the adapting contrast). However, over the range of contrasts tested psychophysically, this model predicted substantial differences in the effects of attention, and thus was not consistent with the data. Third, our model assumes that adaptation has no effect on the R_{max} of the preferred neuron. If we instead assume a small decrease in R_{max} (20%), which is closer to actual data obtained in MT neurons (Kohn & Movshon, 2003), this does not change the main feature of the model, i.e., adaptation gain is still needed to create a constant attention effect across contrasts.

On the other hand, the particular value of C_{50} employed for the pre-adaptation CRF does affect the contrast where MAE strength is predicted to asymptote (in both the full- and poor-attention conditions). The value we used ($C_{50} = 10\%$) was based on data from Kohn and Movshon (2003), obtained from anesthetized monkeys.

As might be expected, lowering the C_{50} in the model lowers the asymptotic contrast value (and likewise, increasing the C_{50} value increases the asymptotic contrast value).

4.2. Can contrast gain effects of attention account for our results?

We have explained the enhanced effects of adaptation due to attention by postulating the existence of a mechanism that alters the gain of adaptation directly. Here, we address the possibility that contrast gain effects of attention (which shift the CRF leftward) might instead account for the enhanced effects of adaptation due to attention. One could argue that attending to an adapting stimulus produces a leftward contrast gain shift, which increases the overall neural response, in turn, leading to a greater degree of adaptation. However, contrast gain effects of attention can only increase neural responses at intermediate levels of contrast; there are no effects of attention in the asymptotic region of the CRF. Thus, according to this hypothesis, the predicted psychophysical effects of attention on MAE strength should *vary* as a function of contrast. In particular, there should be no effect at contrasts where MAE duration has asymptoted. This prediction is not in line with our psychophysical data. To state the case another way, consider the group mean data in Fig. 3A. Increasing the contrast in the poor-attention condition from 25% to 40% has very little effect on the MAE duration. However, attending to a 25% contrast grating greatly increases the MAE duration. This clearly demonstrates that, under these circumstances, the effect of attention is not equivalent to an increase in contrast. Hence, we feel confident that contrast gain effects of attention cannot account for our psychophysical results.

It is important to point out, however, that adaptation gain effects of attention are not inconsistent with the simultaneous existence of contrast gain effects of attention (the latter being known to exist in MT neurons, Martinez-Trujillo & Treue, 2002). The results of our model are unaltered if we allow attention to alter contrast gain during the adaptation phase, shifting the CRFs of the preferred and the anti-preferred neuron leftward. This is because the model assumes that the degree of rightward shift in the preferred neuron's CRF due to adaptation is proportional to the adapting contrast, not the response of the neuron. As a consequence, a leftward contrast gain in the model does not affect the adaptation. Hence, in the model, the attentional mechanisms of contrast gain and adaptation gain are entirely independent. This is unlikely to be exactly true, but given the absence of neurophysiological data that bear on this topic, is a reasonable working hypothesis. In sum, we believe that two distinct mechanisms underlie the effects of attention on motion processing. The first,

consistent with the neurophysiological findings in area MT, boosts the input to directionally selective neurons (contrast gain). The second, currently without neurophysiological support, boosts the effects of adaptation in these neurons (adaptation gain).

4.3. Functional consequences of adaptation and attention

Gain control has long been known to be essential in allowing the nervous system to optimally encode variations along a stimulus dimension. For example, without gain control, cells of the retina could only poorly signal changes in lightness across the vast range of light levels the visual system is exposed to throughout the day (see e.g., Normann & Werblin, 1974; Sakmann & Creutzfeldt, 1969). The same argument can be made for contrast, since this stimulus dimension can also vary greatly in the environment depending on, for example, atmospheric conditions. Thus, in the case of contrast coding, the result of shifting the CRF rightward is a closer alignment of the C_{50} point (which is the steepest portion of the CRF) with the prevailing contrast, which should improve contrast discrimination around that contrast. Contrast adaptation experiments in the laboratory setting, where subjects are exposed to a (typically) high contrast stimulus for an extended period of time, presumably invoke this same adaptive mechanism.

Attending to a stimulus, on the other hand, is thought to shift the CRF leftward, which is equivalent to boosting the effective contrast of a stimulus. At first glance, this may appear unbeneficial, since (for reasons explained above) it will lead to poorer contrast discrimination (at least for higher contrast stimuli). However, the main purpose of attention may be to improve overall detectability, rather than contrast discrimination. That is, attending to a given region in space is predicted to improve the chances for detecting the appearance of near threshold stimuli at that region of space. Psychophysical data demonstrates that this is, indeed, the case for static grating stimuli (e.g., Cameron, Tai, & Carrasco, 2002; Lu & Dosher, 1998, but see Lu, Liu, & Dosher, 2000 for results suggesting minimal effects of spatial attention on contrast sensitivity for luminance-defined moving stimuli). Also in line with contrast gain effects of attention, Carrasco and Read (2004) recently reported that attention increases the perceived contrast of stimuli more so at lower than at higher contrasts. A final benefit of contrast gain effects of attention is based simply on the fact that increased overall responses due to attention (specifically for stimuli of intermediate contrasts) are predicted to improve the overall signal to noise ratio in detectors, which, in turn, should enhance discrimination along stimulus dimensions (for example, direction) encoded by these detectors (see McAdams & Maunsell, 1999).

In the current study, our psychophysical data suggest that attending to an adapting stimulus shifts the CRF

further to the right than does ignoring that same stimulus, i.e., that attention enhances the effects of adaptation. Interestingly, a recent commentary by Boynton (2004) discussed this very possibility, which was offered up as an alternative account of fMRI results presented by Murray and Wojciulik (2004) (Murray and Wojciulik interpreted their results as attention narrowing tuning curves). This enhanced rightward shift of the CRF due to attention should make the C_{50} point more closely aligned with the adapting contrast, and therefore improve contrast discrimination around that contrast. It would be interesting to see whether adaptation gain effects of attention can also be found in other perceptual domains such as adaptation to orientation or color.

In conclusion, the psychophysical data of the current study show that attention increases the motion aftereffect duration by a factor of about 1.4 (for both static and dynamic test stimuli), which is independent of the contrast in the stimulus. A model based on MT neurons can explain this finding if we assume that attention enhances adaptability. This leads us to predict that the effects of adaptation on MT neurons should be larger when an animal attends vs. ignores a stimulus in the receptive field.

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