

Unseen complex motion is modulated by attention and generates a visible aftereffect

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The relationship between attention and awareness and the processing of visual information outside of attention and awareness remain controversial issues. We employed the motion aftereffect (MAE) illusion and continuous flash suppression (CFS) to study the behavioral effects of unseen and unattended visual motion. The main finding was that either withdrawal of attention or the lack of visual awareness on the adaptors did not eliminate the formation of translational MAEs, spiral MAEs, or the interocular transfer of the MAE. However, no spiral MAE was generated when attention was diverted from the unseen spiral adaptors. Interestingly, all MAEs that arose in the absence of awareness or in the absence of attention were reduced in size. The pattern of results is consistent with suggestions that the magnitude of visual motion adaptation depends on both attention and awareness.

Keywords: attention, binocular vision, motion—2D, masking

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Introduction

At any moment in time, we are only aware of a fraction of the information impinging on our senses. In order to understand the role of unconscious information in guiding action, it is critical to examine to what extent sensory stimuli are processed outside of awareness. A second, related question is how, and why, some stimuli gain access to awareness and how this access influences the way information about those stimuli is processed.

In the case of vision, it is generally agreed that a stimulus that falls on the retina may activate neural processing even when the participant is unaware of that stimulus (for review, see Kim & Blake, 2005; Koch, 2003). It has been proposed that visual information suppressed from awareness reaches subcortical areas (Haynes, Deichmann, & Rees, 2005; Schmid, Panagiotaropoulos, Augath, Logothetis, & Smirnakis 2009; Schmid et al., 2010), striate cortex (Blake & Logothetis, 2002; Crick & Koch, 1995; Keliris, Logothetis, & Tolia, 2010; Tong, 2003), and early extrastriate cortex (Rees, 2007; Sincich, Park, Wohlgenuth, & Horton, 2004; Vuilleumier et al., 2002). These claims are supported by neurophysiological, neuroimaging, and behavioral evidence. In the case of backward masking, there is evidence that information outside of awareness can travel beyond visual areas in order to influence language and decision-making processes in the parietal and frontal lobes (Dehaene et al., 2001; De Pisapia, Turatto, Lin, Jovicich, & Caramazza, 2011).

Visual motion provides a particularly interesting domain in which to study unconscious visual processing (Andrews & Blakemore, 1999; Blake, Ahlström, & Alais, 1999; Lehmkuhle & Fox, 1975; Melcher, Papathomas, & Vidnyánszky, 2005; Oshea & Crassini, 1981; Rajimehr, 2004; Wiesenfelder & Blake, 1990). One advantage of using moving stimuli is that even when motion stimuli are invisible they may still evoke a measurable motion aftereffect (MAE) or “waterfall illusion” (Mather, Verstraten, & Anstis, 1998). In the classic version of the waterfall illusion, staring at a pattern of downward movement for a period of seconds then causes a static pattern to appear to move upward. However, there are more complicated versions of the MAE for complex motion patterns such as expansion, contraction, or spiral motions. Since complex motion processing is thought to involve areas beyond primary visual cortex (V1), it is assumed that the presence of an MAE to complex motion reflects processing beyond early monocular cells in V1.

The current study fits into the tradition of studying aftereffects evoked by a non-conscious visual stimulus (for reviews, see Kim & Blake, 2005; Lin & He, 2009). Historically, many of the seminal studies on this issue used the method of binocular rivalry (BR) in which different and incompatible images are presented to the two eyes creating a conscious percept that alternates between the two images. Previous studies employing BR have shown that the duration of the MAE for simple linear motion was independent of the duration in which the adaptors were visible (Lehmkuhle & Fox, 1975; Oshea &

Crassini, 1981), while for the spiral MAE the magnitude was reduced as a function of the time of visibility of the adaptors (Van Der Zwan, Wenderoth, & Alais, 1993; Wiesenfelder & Blake, 1990). Based on these results, it has been proposed that the spiral MAE, but not the linear MAE, depends on visual awareness (Wiesenfelder & Blake, 1990). Models of binocular rivalry assume that rivalry suppression occurs prior to processing of such complex stimuli (Van Der Zwan et al., 1993; Wiesenfelder & Blake, 1990).

However, a reduction in size of the spiral MAE does not provide definite evidence of a complete abolishment of the MAE when generated with unseen adaptors: The behavioral effects of unseen stimuli can be reduced in magnitude (Blake, Tadin, Sobel, Raissian, & Chong, 2006) but still measurable. Moreover, binocular rivalry has some important methodological limitations (Kim & Blake, 2005) that should be taken into account when interpreting the prior results. In BR, switches in perceptual dominance occur randomly and the duration of the dominance phases is relatively short. Thus, adaptors cannot be rendered completely invisible for long periods of time. This means that it is possible to measure whether an adaptation aftereffect is independent of the time that a stimulus is visible, but it is not possible to conclusively state that an aftereffect cannot occur without awareness. For this reason, it is useful to test the MAE using continuous flash suppression (CFS), which is a variant of binocular rivalry in which a series of Mondrian images are presented in rapid succession to one eye causing the stimulus projected to the other eye to remain invisible for periods of seconds (Tsuchiya & Koch, 2005). With CFS, it is possible to directly test aftereffects evoked by a stimulus that never reaches awareness but is nonetheless shown long enough that it would evoke a strong aftereffect if visible.

The second aim of the present study is to investigate the role of inattention on the MAE. Given the complex nature of the relationship between attention and awareness (for reviews, see Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Lamme, 2003), it is useful first of all to compare the influences of adding or taking away these two factors on the same behavioral measure (in this case, the MAE). Using different MAE types, both simple and complex motion, allows us to test whether these two factors act at the same level of visual processing and whether their influence on the MAE is similar. Moreover, manipulating awareness and attention independently allows us to test the relative independence of these two variables (Kanai, Tsuchiya, & Verstraten, 2006; van Boxtel, Tsuchiya, & Koch, 2010).

It is well known that attention can influence the strength of adaptation aftereffects (Alais & Blake, 1999; Bahrami, Carmel, Walsh, Rees, & Lavie, 2008; Lankheet & Verstraten, 1995). Attention can, within certain limits, influence the phases of perceptual dominance during

binocular rivalry, meaning that subjects are able to exert some attentional control over what they perceive during rivalry (Meng & Tong, 2004; Mitchell, Stoner, & Reynolds, 2004; Ooi & He, 1999), in particular if they are given a visual task that requires focused attention to the stimuli in one eye (van Ee, van Dam, & Brouwer, 2005). Of particular relevance to the current study is the finding that inattention can reduce both the size of the MAE (Chaudhuri, 1990) and the responses of neurons coding motion stimuli (Rees, Frith, & Lavie, 1997). In addition, attention can influence the processing of both simple translational and spiral motion (S. M. Aghdaee, 2005; M. M. Aghdaee & Zandvakili, 2005).

The current study compared the effects of attention and of awareness on simple and complex motion. In the first three of our experiments, we measured the magnitude of MAEs for seen and unseen spiral and linear adaptors. In the fourth and fifth experiments, we investigated the effects of inattention on the generation of MAEs with seen and unseen adaptors. In this way, for the first time, we could directly compare the roles of attention and awareness on motion processing in a single study.

Methods

Subjects

Twenty-four subjects (11 males and 13 females, mean age = 27.5, $SD = 4.8$) participated in 5 experiments: six subjects per experiment with one subject (LK, one of the authors) participating in all experiments and AF (another author) participating in two. All had normal or corrected-to-normal vision and, except for LK and AF, were naive with respect to the purpose of the task. All participants gave informed consent according to the guidelines of the University of Trento Ethical Committee.

Stimuli

Stimuli were generated using the Matlab Psychtoolbox (Brainard, 1997) and displayed on a 21" Samsung SyncMaster 753 DF monitor (resolution = 1024×768 ; 85-Hz refresh rate; gamma corrected) at a viewing distance of 60 cm. Stimuli were presented against a light brown background (CIE coordinates: $X = 0.44$, $Y = 0.44$, $Z = 0.12$, luminance = 11 cd/m^2 , see Figure 1). For Experiments 1, 2, and 4, the adapting stimuli were Gabor patches of 2.5 by 2.5 degrees in size, with a spatial frequency of 4 cycles/deg, presented at a speed of 0.6 deg/s, yielding a temporal frequency of 2.4 Hz. The test probes were equal in every aspect to the adapting Gabors except that their speed was 0.02 deg/s and their temporal frequency was 0.08 Hz. For Experiments 3 and 5, sine-wave rotating

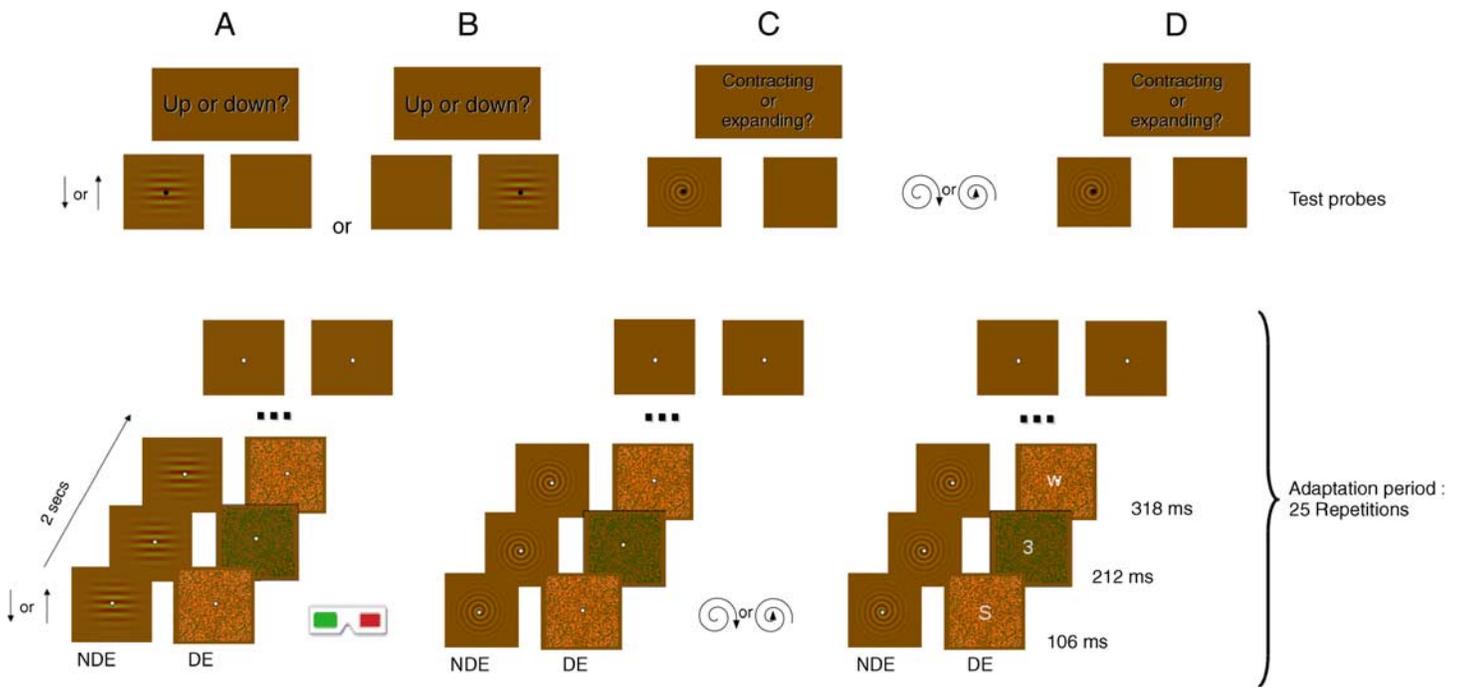


Figure 1. Top-up procedure. On each trial, the adaptation pattern was presented for 2 s, and after an interval of 753 ms, the test probe was displayed for 494 ms. The first trial of the block was preceded by an adaptation period of 68 s. The procedure was the same for all experiments. After the test probe disappeared, observers pressed one of two buttons to indicate the perceived direction (upward, downward, contracting, or expanding). The beginning of the test probes was signaled by a color change in the fixation dot. Only the invisible conditions are shown in the figure; for the conditions with visible adaptors, a blank screen was presented to the dominant eye instead of the Mondrians. Subjects performed the task wearing a pair of red–green anaglyph glasses. The colors and contrast of the stimuli in the figure resemble those colors presented on the screen. DE: dominant eye; NDE: non-dominant eye. (A) Monocular translational motion. (B) Interocular trials of translational motion. (C) Adaptation to spiral motion. (D) Spiral motion adaptors with the attentional task at fixation. The presentation rate of the letters varied for the high and low attentional tasks.

spirals were used as stimuli. The spirals were defined by $\sin(r + \theta)$, where r is the distance from the origin to a point in the x - y plane and θ is the angular displacement in radians from the positive x -axis. The adaptation spirals were rotated at 67 revolutions per minute (rpm) and the test spirals at 6.7 rpm.

A total of 20 pairs of masks were created for each experiment and one pair was randomly selected for each trial. They had a size of 4×4 degrees of visual angle and were constructed by assigning each dot of the image (2 pixels each, 4.8-arcmin size) either a light or a dark luminance value (Figure 1). Each trial in the unseen condition began with the presentation of a mask that had been randomly assigned with dots in the luminance range of 0–0.3 (where 0 means black pixels and 1 means white). This mask was replaced 106 ms later by a second mask, which had the exactly same dot distribution with the only difference that the values of 75% of its dots were changed to a luminance range between 0.8 and 1. The masks alternated on the screen every 106 ms (9.4 Hz) and the 75% of dots that changed luminance were always the same throughout the trial. In this way, only luminance

changes were perceived and no first-order motion was present from adjacent pixels in the masks.

Experimental procedures

All subjects viewed the stimuli through a pair of red–green anaglyph glasses. Before starting the experiments, eye dominance was assessed for each subject (<http://www.archeryweb.com/archery/eyedom.htm>). The adapting stimuli were always presented in the green channel to the non-dominant eye (NDE) and the masks on the red channel to the dominant eye (DE). Adaptors were never presented to both eyes. In the first experiment, we used contrast-modulated Gabor patches to measure MAEs under monocular conditions. The same stimuli were adopted also for Experiment 2, testing the MAE interocular transfer, presenting test probes to the non-adapted eye. The third experiment evaluated the spiral MAE again under monocular conditions. Finally, in Experiments 4 and 5, we tested translational and spiral MAEs while manipulating subjects' attention.

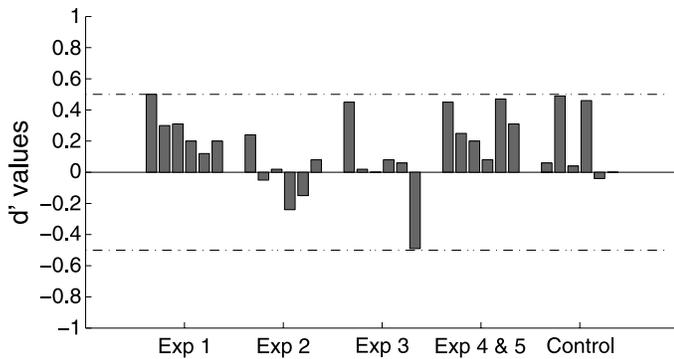


Figure 2. Objective measure of visibility. d' values of participants for each of the experiments ($N = 6$ for each experiment, mean d' value = 0.14, $SD = 0.23$). For each participant, we ran a visibility detection task prior to the adaptation task and selected a contrast for the adaptors that yielded a d' between -0.5 and 0.5 . In addition to these objective measures, subjects reported being completely unaware of the presence or absence of the stimuli when the Mondrians were displayed on the screen. The same 6 subjects participated in Experiments 4 and 5 (low and high attentional load), and for this reason, we only report one d' (the same contrast value was used for adaptors in both experiments). The final condition shows the results of a control experiment to test for leakage between the eyes. Subjects were unable to detect with their dominant eye the stimuli presented in the green channel even when the Mondrians were not displayed on the screen (see [Methods](#) section for details).

Top-up adaptation procedure. Each run of the adaptation experiments began with a 1-min period of adaptation in which the adapting stimuli were presented for 2 s interspaced with 750 ms of a blank screen (Figure 1). After the initial adaptation period, subjects were presented repeatedly with 2 s of adaptation followed by the presentation of a test probe (Figure 1). The participants' task was to respond whether the test probes were moving upward or downward (Experiments 1, 2, and 4) or whether they were expanding or contracting (Experiments 3 and 5). Test probes moved half of the time in the direction of the adaptor and half of the trials in the opposite direction of the adaptor. Subjects responded by pressing two keyboard keys, with their index and middle fingers. To avoid finger biases, we counterbalanced the order of the responses. As an example, for each block of trials in Experiments 1 and 2 on half of the trials, the index finger presses corresponded to "up" and the middle finger presses to "down," and on the other half of the trials, the index finger presses corresponded to "down" and the middle finger presses to "up." No feedback was given to subjects after the response.

Experiments 1 (Figure 1A), 2 (Figure 1B), and 4 comprised 4 conditions: seen adaptor moving up, seen adaptor moving down, unseen adaptor moving up, and unseen adaptor moving down. For Experiments 3 (Figure 1C) and 5, the conditions were the same except that the adaptors

were spirals moving clockwise (expanding) or counter-clockwise (contracting). Experiments 4 and 5 were equal to Experiments 1 and 3 (respectively) except for the addition of an attentional task at fixation (Figure 1D). A stream of letters (all of the letters of the alphabet) and numbers (from 1 to 4 and from 6 to 9) of 1.5 degrees in size was continuously presented to the dominant eye during the adaptation period and prior to the test probe presentation on the fixation point (Figure 1D). The presentation rate of digits (letters and numbers) was 2.85 HZ: They appeared for 250 ms on the screen interleaved with 106 ms with no numbers/digits. Subjects were told to consider numbers as targets and letters as distractors and to respond as fast as possible whether the targets were numbers bigger or smaller than "5," while adaptors were presented to the other eye. Letters and numbers were randomly chosen but with the restriction that two consecutive numbers were never presented. To vary the attentional load of the task, we used two rates of number presentation (numbers presented over letters presented). In Experiments 4 and 5, the rate of appearance of numbers among letters was of 1/8 (low attentional load task) or of 1/3 (high attentional load task). The rate of appearance of numbers for the high and low attentional load was obtained in previous pilot studies (see [Methods](#) section). For all five experiments, we ran each condition separately in blocks of 6 consecutive top-up runs, each one containing 20 trials, totaling 120 trials per condition per subject. Test probes were pseudorandomly distributed inside each run, with the same amount of test probes moving in both directions. Half of the subjects performed first the conscious conditions and, on a separate day, the unconscious conditions, and half of the subjects performed it the other way around.

Stimuli invisibility assessment. Prior to the start of each experiment, we ran a staircase procedure (a one-down, one-up procedure leading to 50% correct performance; Levitt, 1971) to determine each subject's invisibility contrast threshold. "Throughout the experiments, contrast was measured employing the Michelson contrast, defined as $[L_{MAX} - L_{MIN}] / [L_{MAX} + L_{MIN}]$. Once this threshold was estimated, we tested subjects with a detection task using contrast values below the estimated invisibility contrast threshold (80 trials, with 40 moving and 40 static stimuli). Subjects responded whether the masked target grating was either moving or static (2AFC). We calculated the d' for each of these contrast values, and for each subject, we selected a final contrast value that yielded a d' between -0.5 and 0.5 (Figure 2). This contrast value was finally used in the adaptation experiments. In all cases, subjects reported to be unable to perceive whether a grating had been presented to them or not under the masked conditions.

We ran a control experiment to rule out the possibility of leakage between the eyes. We checked to be sure that the visual stimulus presumed to be suppressed were not visible to the other eye (Figure 2, control condition). We

tested 6 subjects with a simple detection task consisting of 60 trials: 30 with a moving Gabor presented on the screen for 2 s at fixation and 30 with a blank screen of background color. Subjects had to detect whether a moving Gabor was present or absent on the screen. Gabors had a Michelson contrast value of 5% (the highest contrast value employed throughout the experiments across subjects) and a speed of 0.6 deg/s. Subjects wore anaglyph glasses during the task and they were requested to close the eye that corresponded to the green filters of the anaglyph glasses. Therefore, only the eye wearing the red filter of the anaglyph glasses was used for this experiment. No Mondrians were displayed during this task. The results of this control experiment showed that subjects could not detect the presence or absence of the Gabors with the non-dominant eye. We found no evidence of leakage between the eyes for the adapting stimuli with these contrast values.

Results

In each experiment, we measured the MAE by assessing the proportion of responses opposite to the direction of the adaptor (up–down or expanding–contracting). For each subject, this proportion was averaged across the two different adaptor directions (e.g., the average of the responses up for a downward motion adaptor and responses down with an upward moving adaptor). For each condition, we assessed whether the proportion of responses opposite to the adaptor direction across subjects was above chance level (one-tailed t -test against a mean of 0.5). We estimated the MAE size for each condition by subtracting 0.5 (chance level) to the proportion of responses contrary to the MAE. To compare across conditions, we calculated the rate between MAE sizes.

Initially, we examined whether linearly moving Gabors that had been completely rendered invisible would still produce an MAE on visible test probes (Figure 3, monocular). We observed, as expected, a strong MAE for the seen adaptors (one-tailed t -test, $t = 9.0461$, $df = 5$, $p < 0.001$). Likewise, in line with previous studies that made use of binocular rivalry (Wiesenfelder & Blake, 1992) and CFS (Maruya, Watanabe, & Watanabe, 2008), we found an MAE for the unseen adaptors with translational motion. The effect of the unseen adaptors, though reduced to half the size of the seen MAE, was consistent and statistically different from chance level (one-tailed t -test, $t = 2.3403$, $df = 5$, $p < 0.05$). In our second experiment, we measured the interocular transfer of the MAE. Test probes were presented to the eye that was not stimulated by the adapting Gabors (Figure 1B). We found interocular transfer of the MAE using both seen (one-tailed t -test, $t = 7.4649$, $df = 5$, $p < 0.001$) and unseen adaptors (one-tailed t -test, $t = 3.3113$, $df = 5$, $p < 0.05$, Figure 3, interocular). The third experiment evaluated

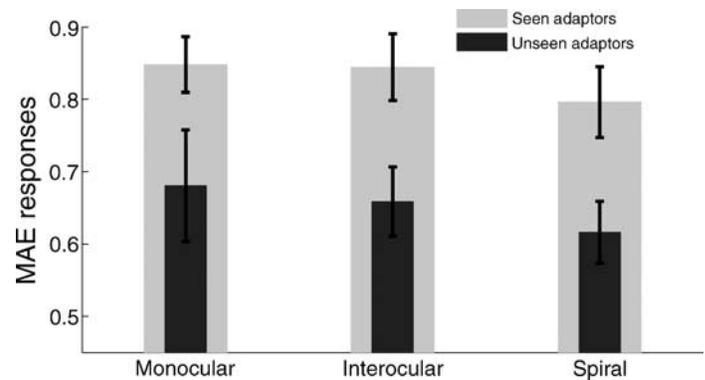


Figure 3. MAE with seen and unseen adaptors. The proportion of responses contrary to the adaptor direction is plotted for the first three experiments. We compared the generation of MAEs when adaptors were visible with the conditions in which adaptors were invisible to participants. Though reduced in size, monocular, interocular, and spiral MAEs were found using unseen adaptors. Error bars represent 1 SEM.

the spiral motion aftereffect (Figure 3, spiral). As in Experiments 1 and 2, we could observe an MAE both with seen (one-tailed t -test, $t = 6.0507$, $df = 5$, $p < 0.001$) and unseen adaptors (one-tailed t -test, $t = 2.7143$, $df = 5$, $p < 0.05$). The MAEs obtained under suppressed visual awareness were reduced on average to 45% for our first 3 experiments as compared to MAEs obtained under the visible conditions (reduced by 52% for the translational motion, 44% for the interocular transfer, and 40% for the spiral motion). A 2×3 ANOVA with visibility (seen and unseen) and experimental condition (monocular, interocular, and spiral) as factors revealed a main effect for visibility ($F(1,30) = 17.65$, $p < 0.001$) but no effect for experimental condition ($F(2,30) = 0.69$, $p = 0.5$) nor for an interaction between the factors ($F(2,30) = 0.01$, $p = 0.98$).

Our fourth and fifth experiments studied the influence of attention on the generation of translational and spiral MAEs (Figure 4). Accuracy in the secondary task (discriminating the numbers as bigger or smaller than 5) was on average 93% across participants ($SD = 2\%$) for the low attentional load task and 76% ($SD = 3\%$) for the high attentional load task. Subjects were more accurate on the low attentional task compared to the high attentional task (two-tailed t -test, $t = -21.44$, $df = 9$, $p < 0.001$). In the case of translational motion (Figure 4A), between-subjects ANOVA with visibility as a categorical variable (seen and unseen) and attentional level as linear predictor (no task, low load, high load) showed main effects of visibility ($F(1,32) = 12.33$, $p < 0.01$) and attentional level ($F(1,32) = 5.64$, $p < 0.05$) but no interaction ($F(1,32) = 0.05$, $p = 0.81$). Unseen adaptors were able to generate an MAE with a low attentional load task (one-tailed t -test, $t = 2.0462$, $df = 5$, $p < 0.05$) and with a high attentional load task (one-tailed t -test, $t = 2.8465$, $df = 5$, $p < 0.05$). In the seen conditions, allocating attention away from the

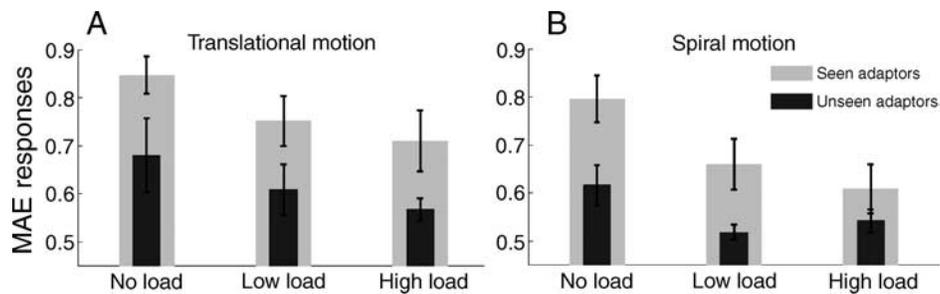


Figure 4. The motion aftereffect, awareness, and attention. The proportion of responses contrary to the adaptor direction is plotted as a function of 3 tasks with varying levels of attentional load and 2 types of adaptors. Either the lack of attention (high load, light gray bars) or visual awareness (no load, black bars) did not impede the formation of translational and spiral MAEs. However, unseen and unattended adaptors generated a reduction of 50% of the MAE size as compared to the fully seen and attended adaptors (no load, light gray bars). Both visibility and attention consistently modulated the magnitude of the (A) linear and (B) spiral MAEs. However, under conditions of inattention and CFS (low load and high load, black bars), only the responses to the linear adaptors (A) were above chance level and generated an MAE (see Results section). Error bars represent 1 SEM.

adaptor reduced the linear MAEs by 27% in the low attentional task and by 40% in the high attentional task compared to the no load task.

Employing spiral motion adaptors (Figure 4B), between-subjects ANOVA with visibility (seen and unseen) and attentional level as a linear predictor (no task, low load, high load) revealed main effects of visibility ($F(1,32) = 14.36, p < 0.001$) and attentional level ($F(1,32) = 9.75, p < 0.01$) but no interaction ($F(1,32) = 0.19, p = 0.4$). We observed an MAE with seen adaptors for the low attentional load task (one-tailed t -test, $t = 3.02, df = 5, p < 0.05$) and for the high attentional load task (one-tailed t -test, $t = 2.1071, df = 5, p < 0.05$). However, no MAE was found with unseen adaptors, both for low and high attention tasks (two one-tailed t -tests, $t = 1.12, df = 5, p > 0.05$ and $t = 1.6992, df = 5, p > 0.05$, respectively). In the seen conditions, allocating attention away from the adaptor reduced the spiral MAEs by 47% in the low attentional task and by 67% in the high attentional task compared to the no load task.

Discussion

The two main findings of our experiments were that a spiral MAE was found even with stimuli suppressed from awareness and that attention and awareness had similar, but independent, effects on reducing the magnitude of both linear and spiral MAEs. The first finding, that invisible spiral motion was able to generate a visible MAE during interocular suppression, differs from prior reports (Wiesenfelder & Blake, 1990). As described in the Introduction section, this may reflect methodological differences in the two designs, as we used continuous flash suppression of the adaptor rather than inferring the influence of suppression based on binocular rivalry durations.

Our data suggest, in agreement with previous studies (Macknik & Martinez-Conde, 2004; Meng, Chen, & Qian, 2004; van Boxtel, Knapen, Erkelens, & van Ee, 2008), that both monocular and binocular channels are involved during interocular suppression. Our results show the interocular transfer of an MAE generated with unseen adaptors and that the magnitude of the MAE is dependent on the awareness of the adaptor. Extensive evidence favors the idea that some type of degraded motion information can be processed from V1 to MT under interocular suppression (Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997) or in the absence of striate cortex (Schmid et al., 2010; Weiskrantz, 1997). The MAE with unseen adaptors reported in our experiments could be explained either by local gains at the level of V1, by adaptation of neurons from V1 up to area MT, or perhaps by a modulation of a subpopulation of neurons in MT that respond to the physical retinal stimulation (Logothetis & Schall, 1989). Our data do not allow us to infer the site of suppression of unseen spiral or linear motion. Further physiological experiments should be conducted to test these possibilities. To the best of our knowledge, no neurophysiological experiment has been conducted in non-human primates combining binocular rivalry or CFS with spiral motion.

We were able to directly compare the influences of attention (via a distractor task) and awareness (via CFS) on the formation of motion aftereffects. This direct comparison within a single experiment is relevant to the current debate over the relationship between these two factors (Dehaene et al., 2006; Lamme, 2003). Moreover, by including both simple and complex motion stimuli, we were able to see if there was any dissociation/interaction between the two factors. Our results are consistent with additive effects with no interaction between attention and awareness. Both inattention and suppression from awareness led to a similar reduction in the MAE. In the case of

unseen adaptors, reducing attention to the adaptor region of the display reduced the magnitude of the MAEs.

This result is consistent with previous reports that attention can modulate unseen visual motion (S. M. Aghdaee, 2005; Melcher et al., 2005). Interestingly, the effect of diverting attention was qualitatively similar to the effect of interocular suppression. Both attention and awareness were necessary to have the maximum MAE, indicating that both factors contributed separately to the degree to which motion stimuli were processed.

Diverting visual selective attention from the adaptor reduced the magnitude of both the linear and spiral MAEs (Figure 4). However, under conditions of inattention and CFS, only the responses to the linear adaptors were still above chance level and generated an MAE. We can speculate that these small but statistically significant differences in the changes due to inattention may be due to these two types of motion being processed at different levels of the visual system. Presumably, linear motion is processed at earlier stages and, therefore, is more resistant to inattention and interocular suppression. Rotational, radial, spiral, and plaid motion patterns are thought to be processed mainly in the complex MT/MST (Morrone, Burr, & Vaina, 1995; Rodman & Albright, 1989; Tanaka, Fukada, & Saito, 1989). Visual information in the ventral stream is known to suffer from increased inhibition in higher areas of the visual processing (Sheinberg & Logothetis, 1997). Similarly, it has been suggested that the interocular suppression mechanisms of motion perception operate at multiple areas of the visual cortex (Blake & Logothetis, 2002), perhaps with deeper suppression at higher levels of processing (Alais & Melcher, 2007). Our results cannot confirm or refute this depth-of-suppression hypothesis since both linear and spiral MAEs were reduced by CFS in this study.

Overall, the strength of the MAEs obtained with invisible or unattended stimuli were reduced, on average, to *around half the size* of the MAEs with full visible adaptors, a decrease in magnitude that is in accordance with recent studies (Blake et al., 2006; Maruya et al., 2008) but challenges the results of early binocular rivalry reports (Lehmkühle & Fox, 1975; Oshera & Crassini, 1981). The fact that smaller MAEs emerge with unseen adaptors raises the question about the role of visual awareness and attention on visual motion processing. While orientation aftereffects are relatively unaffected by the lack of awareness (He, Cavanagh, & Intriligator, 1996), face adaptation aftereffects are effectively eliminated by suppression (Alais & Melcher, 2007; Amihai, Deouell, & Bentin, 2011). This transition from relatively bottom-up processing of orientation, independent of attention or awareness, to perception of complex objects, which is attention- and awareness-dependent, remains a key issue in the attempts to understand the nature of conscious awareness. Our current results add to this literature by showing that the magnitude of adaptation to visual motion depends on both attention and awareness

and that the neural mechanisms that operate outside of visual awareness are not sufficient to account for normal visual motion adaptation.

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References

- Aghdaee, M. M., & Zandvakili, A. (2005). Adaptation to spiral motion: Global but not local motion detectors are modulated by attention. *Vision Research*, *45*, 1099–1105.
- Aghdaee, S. M. (2005). Adaptation to spiral motion in crowding condition. *Perception*, *34*, 155–162.
- Alais, D., & Blake, R. (1999). Neural strength of visual attention gauged by motion adaptation. *Nature Neuroscience*, *2*, 1015–1018.
- Alais, D., & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Research*, *47*, 269–279.
- Amihai, I., Deouell, L., & Bentin, S. (2011). Conscious awareness is necessary for processing race and gender information from faces. *Consciousness and Cognition*, *20*, 269–279.
- Andrews, T. J., & Blakemore, C. (1999). Form and motion have independent access to consciousness. *Nature Neuroscience*, *2*, 405–406.
- Bahrami, B., Carmel, D., Walsh, V., Rees, G., & Lavie, N. (2008). Unconscious orientation processing depends on perceptual load. *Journal of Vision*, *8*(3):12, 1–10, <http://www.journalofvision.org/content/8/3/12>, doi:10.1167/8.3.12. [PubMed] [Article]
- Blake, R., Ahlström, U., & Alais, D. (1999). Perceptual priming by invisible motion. *Psychological Science*, *10*, 145–150.
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, *3*, 13–21.
- Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proceedings*

- of the National Academy of Sciences of the United States of America, 103, 4783–4788.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature*, 344, 60–62.
- Crick, F., & Koch, C. (1995). Are we aware of neural activity in primary visual cortex? *Nature*, 375, 121–123.
- Dehaene, S., Changeux, J., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences*, 10, 204–211.
- Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J.-F., Poline, J.-B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, 4, 752–758.
- De Pisapia, N., Turatto, M., Lin, P., Jovicich, J., & Caramazza, A. (2011). Unconscious priming instructions modulate activity in default and executive networks of the human brain. *Cerebral Cortex*.
- Haynes, J.-D., Deichmann, R., & Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature*, 438, 496–499.
- He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, 383, 334–337.
- Kanai, R., Tsuchiya, N., & Verstraten, F. (2006). The scope and limits of top-down attention in unconscious visual processing. *Current Biology*, 16, 2332–2336.
- Keliris, G. A., Logothetis, N. K., & Tolias, A. S. (2010). The role of the primary visual cortex in perceptual suppression of salient visual stimuli. *The Journal of Neuroscience*, 30, 12353–12365.
- Kim, C.-Y. Y., & Blake, R. (2005). Psychophysical magic: Rendering the visible ‘invisible’. *Trends in Cognitive Sciences*, 9, 381–388.
- Koch, C. (2003). *The quest for consciousness: A neurobiological approach*. Englewood, Colorado: Roberts & Company Publishers.
- Lamme, V. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, 7, 12–18.
- Lankheet, M. J., & Verstraten, F. A. (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Research*, 35, 1401–1412.
- Lehmkuhle, S. W., & Fox, R. (1975). Effect of binocular rivalry suppression on the motion aftereffect. *Vision Research*, 15, 855–859.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *The Journal of the Acoustical Society of America*, 49, 467–477.
- Lin, Z., & He, S. (2009). Seeing the invisible: The scope and limits of unconscious processing in binocular rivalry. *Progress in Neurobiology*, 87, 195–211.
- Logothetis, N. K., & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science*, 245, 761–763.
- Macknik, S. L., & Martinez-Conde, S. (2004). Dichoptic visual masking reveals that early binocular neurons exhibit weak interocular suppression: Implications for binocular vision and visual awareness. *Journal of Cognitive Neuroscience*, 16, 1049–1059.
- Maruya, K., Watanabe, H., & Watanabe, M. (2008). Adaptation to invisible motion results in low-level but not high-level aftereffects. *Journal of Vision*, 8(11):7, 1–11, <http://www.journalofvision.org/content/8/11/7>, doi:10.1167/8.11.7. [PubMed] [Article]
- Mather, G., Verstraten, F., & Anstis, S. (1998). *The motion aftereffect: A modern perspective*. Cambridge, MA: MIT Press.
- Melcher, D., Papathomas, T. V., & Vidnyánszky, Z. (2005). Implicit attentional selection of bound visual features. *Neuron*, 46, 723–729.
- Meng, M., & Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *Journal of Vision*, 4(7):2, 539–551, <http://www.journalofvision.org/content/4/7/2>, doi:10.1167/4.7.2. [PubMed] [Article]
- Meng, X., Chen, Y., & Qian, N. (2004). Both monocular and binocular signals contribute to motion rivalry. *Vision Research*, 44, 45–55.
- Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. *Nature*, 429, 410–413.
- Morrone, M. C., Burr, D. C., & Vaina, L. M. (1995). Two stages of visual processing for radial and circular motion. *Nature*, 376, 507–509.
- Ooi, T. L., & He, Z. J. (1999). Binocular rivalry and visual awareness: The role of attention. *Perception*, 28, 551–574.
- Oshea, R., & Crassini, B. (1981). Interocular transfer of the motion aftereffect is not reduced by binocular rivalry. *Vision Research*, 21, 801–804.
- Rajimehr, R. (2004). Unconscious orientation processing. *Neuron*, 41, 663–673.
- Rees, G. (2007). Neural correlates of the contents of visual awareness in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 877–886.
- Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science*, 278, 1616–1619.

- Rodman, H. R., & Albright, T. D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Experimental Brain Research*, *75*, 53–64.
- Schmid, M. C., Mrowka, S. W., Turchi, J., Saunders, R. C., Wilke, M., Peters, A. J., et al. (2010). Blindsight depends on the lateral geniculate nucleus. *Nature*, *466*, 373–377.
- Schmid, M. C., Panagiotaropoulos, T., Augath, M. A., Logothetis, N. K., & Smirnakis, S. M. (2009). Visually driven activation in Macaque areas V2 and V3 without input from the primary visual cortex. *PLoS ONE*, *4*, e5527+.
- Sheinberg, D. L., & Logothetis, N. K. (1997). The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences*, *94*, 3408–3413.
- Sincich, L. C., Park, K. F., Wohlgenuth, M. J., & Horton, J. C. (2004). Bypassing V1: A direct geniculate input to area MT. *Nature Neuroscience*, *7*, 1123–1128.
- Tanaka, K., Fukada, Y., & Saito, H. A. (1989). Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, *62*, 642–656.
- Tong, F. (2003). Primary visual cortex and visual awareness. *Nature Reviews Neuroscience*, *4*, 219–229.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*, 1096–1101.
- van Boxtel, J. J., Tsuchiya, N., & Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 8883–8888.
- van Boxtel, J. J. A., Knapen, T., Erkelens, C. J., & van Ee, R. (2008). Removal of monocular interactions equates rivalry behavior for monocular, binocular, and stimulus rivalries. *Journal of Vision*, *8*(15):13, 1–17, <http://www.journalofvision.org/content/8/15/13>, doi:10.1167/8.15.13. [PubMed] [Article]
- Van Der Zwan, R., Wenderoth, P., & Alais, D. (1993). Reduction of a pattern-induced motion aftereffect by binocular rivalry suggests the involvement of extrastriate mechanisms. *Visual Neuroscience*, *10*, 703–709.
- van Ee, R., van Dam, L. C., & Brouwer, G. J. (2005). Voluntary control and the dynamics of perceptual bi-stability. *Vision Research*, *45*, 41–55.
- Vuilleumier, P., Armony, J. L., Clarke, K., Husain, M., Driver, J., & Dolan, R. J. (2002). Neural response to emotional faces with and without awareness: Event-related fMRI in a parietal patient with visual extinction and spatial neglect. *Neuropsychologia*, *40*, 2156–2166.
- Weiskrantz, L. (1997). *Consciousness lost and found: A neuropsychological exploration*. USA: Oxford University Press.
- Wiesenfelder, H., & Blake, R. (1990). The neural site of binocular rivalry relative to the analysis of motion in the human visual system. *The Journal of Neuroscience*, *10*, 3880–3888.
- Wiesenfelder, H., & Blake, R. (1992). Binocular rivalry suppression disrupts recovery from motion adaptation. *Visual Neuroscience*, *9*, 143–148.