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


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, & Tolas, 2010; Tong, 2003), and early extrastriate cortex (Rees, 2007; Sincich, Park, Wohlgemuth, & 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 after-effect (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, Raisssian, & 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 (Tschiya & 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, Tschiya, & Verstraten, 2006; van Boxtel, Tschiya, & 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/m², 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
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 \( \theta \) 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.
The response. Presses to “up.” No feedback was given to subjects after and on the other half of the trials, the index finger responded to “up” and the middle finger presses to “down,” 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 counterclockwise (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 \( \frac{L_{\text{MAX}} - L_{\text{MIN}}}{L_{\text{MAX}} + L_{\text{MIN}}} \). 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

![Figure 2](image-url)
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 of 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 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
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.

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

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.
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 (Lehmkuhle & Fox, 1975; Oshea & 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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