

The role of stationary and dynamic test patterns in rapid forms of motion after-effect

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Subsecond adaptation to directional motion can induce a rapid form of motion after-effect (rMAE). Unlike the characteristics of the classic motion after-effect (MAE), produced by adaptation of several seconds or minutes, the properties of the rMAE have been less well explored. In a series of experiments, we assessed the role of stationary and dynamic test patterns (counterphase flickering gratings) in generating rMAE. In particular, we varied the duration, temporal frequency, and spatial phase of the adapting stimuli. Our results show that rMAE is only generated by dynamic test patterns, exhibiting a strong dependence on the adaptation duration and temporal frequency but not on the spatial phase. Similarly to the classic dynamic MAE, the temporal frequency tuning of the dynamic rMAE suggests the involvement of both low-pass and band-pass visual channels. Unexpectedly, our results do not show evidence for static rMAE. We speculate that a stationary test pattern presented immediately (or very soon) after the adapting pattern could interfere with the effects of adaptation by disrupting weak motion signals that arise from adapted and unadapted motion detectors (Ledgeway & Smith, 1994a, 1994b).

Keywords: brief (subsecond) adaptation, stationary test pattern, dynamic test pattern, motion after-effect (MAE), rapid motion after-effect (rMAE), phase shift, temporal frequency selectivity

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Introduction

The classic motion after-effect involves an observer viewing unidirectional motion for a prolonged period of time (adaptation) after which a stationary test pattern appears to move in the opposite direction to that of the adaptation. This effect is known as static MAE (SMAE). Another form of MAE is the dynamic MAE (DMAE), which is obtained by using dynamic test patterns such as dynamic visual noise or counterphase flickering gratings. Motion adaptation and MAEs have been used extensively to investigate the spatiotemporal tuning, interactions, and the neural substrates of channels involved in motion perception (Bex, Verstraten, & Mareschal, 1996; Ledgeway & Hutchinson, 2009; Mareschal, Ashida, Bex, Nishida, & Verstraten, 1997; Nishida & Sato, 1995).

The properties of DMAEs are different from those of SMAEs and have led to the conclusion that the two after-effects are mediated by different populations of cells. In particular, the use of dynamic and static test patterns has allowed the exploration of whether MAE depends on a single source of adaptation or if it reflects adaptation at several sites along the motion processing pathway. Verstraten, van der Smagt, Fredericksen, and

van de Grind (1999) found that the same adaptation pattern produced a MAE in different directions depending on whether dynamic or static test patterns were used. Their participants adapted to transparent motion stimuli (Verstraten, Fredericksen, & van de Grind, 1994), i.e., two superimposed fields of noise (random pixel arrays [RPAs]) that move transparently in orthogonal directions. The results showed that the SMAE was opposite to the direction of the slower speed component, whereas the DMAE was mostly opposite to the direction of the fastest component. Further studies have shown that the MAE, obtained by adapting to moving random textures, random dots, or RPAs and testing with dynamic noise, peaks at higher speeds than the SMAE with an upper cut-off speed of $\sim 100^\circ/\text{s}$ (van de Grind, van Hof, van der Smagt, & Verstraten, 2001). Taken together these results suggest the presence of detectors that encode high velocities and support short temporal delays (a transient channel) and detectors for slower velocities that support longer temporal delays (a sustained channel).

Furthermore, the temporal characteristics of DMAE may vary depending on the test stimulus used. For example, van der Smagt (1999) and van der Smagt, Verstraten, and van de Grind (2000) adapted to moving RPAs and investigated the effect of test stimulus speed

on the duration of MAE. Three different test patterns were used: a static noise test to measure the SMAE, a dynamic noise test to measure the DMAE, and a counterphase flickering RPA. Results showed that both SMAE and DMAE obtained with dynamic noise were compatible with the involvement of slow and fast motion sensors, respectively. The DMAE obtained with counterphase flickering RPA, however, exhibited mixed properties, which suggests that the DMAE seen in dynamic noise and counterphase flickering RPA may have partly different origins, while still reflecting the activity of both slow and fast motion sensors (Tao, Lankheet, van de Grind, & van Wezel, 2003).

Since, in general, SMAEs and DMAEs reveal the presence of two distinct and separable temporal channels, this might imply that adaptation occurs at different levels along the motion processing pathway. Further evidence of the multiplicity of the MAE mechanisms arises from studies that measured the degree of interocular transfer (IOT) of the two after-effects (Nishida & Ashida, 2000; Nishida, Ashida, & Sato, 1994), and studies that employ second-order motion stimuli (i.e., moving stimuli defined by modulations of features like contrast, texture, or disparity; Cavanagh & Mather, 1989; Derrington, Badcock, & Henning, 1993; Ledgeway & Smith, 1994a, 1994b; McCarthy, 1993; Pantle & Turano, 1992). Based on these results Mather, Pavan, Campana, and Casco (2008) argue that at least three populations of cells are required to explain the diverse empirical properties of the motion after-effect: (a) one low-level population mediates the classic SMAEs and DMAEs seen in very low temporal frequency dynamic test patterns; (b) a second low-level population mediates DMAEs seen using high temporal frequency test patterns; and (c) a third, “higher-level” population mediates DMAEs from second-order motion seen using low temporal frequency test patterns. Thus, DMAEs do not tap a single population of cells, but different populations depending on the properties of both adapting and test stimuli (Bex & Baker, 1999; Cavanagh & Favreau, 1980; Maruya, Watanabe, & Watanabe, 2008; Smith, Scott-Samuel, & Singh, 2000).

The effects of adaptation and the role of stationary and dynamic test patterns as those reported so far have been investigated using long adaptation durations (from seconds up to minutes). There is, however, neurophysiological evidence that even a few milliseconds of stimulus presentation can produce adaptation (Chance, Nelson, & Abbott, 1998; Glasser, Tsui, Pack, & Tadin, 2011; Nordström, Moyer de Miguel, & O’Carroll, 2011; Priebe, Churchland, & Lisberger, 2002; Priebe & Lisberger, 2002; Varela et al., 1997; Varela, Song, Turrigiano, & Nelson, 1999). Glasser et al. (2011), for example, found that in the cortical area MT of macaque monkeys, a very brief exposure to directional motion (67 ms) produced direction-selective

responses to subsequently presented stationary test stimuli; this is compatible with a short-term adaptation and, consequently, with a rapid form of (stationary) motion after-effect (SrMAE). There is recent psychophysical evidence indicating a possible relationship between these short-term forms of neural adaptation and patterns of psychophysical behavior. Kanai and Verstraten (2005) and Pavan and colleagues showed that after adapting to a drifting Gabor for 320 ms, a counterphase flickering Gabor patch presented after a blank interval of a few tens of milliseconds (e.g., 40 or 120 ms), was perceived as moving in the opposite direction with respect to that of the adapting stimulus, compatible with a rapid form of (dynamic) motion after-effect (DrMAE) (Pavan, Campana, Guerreschi, Manassi, & Casco, 2009; Pavan, Campana, Maniglia, & Casco, 2010).

From here we will refer to rMAE for the rapid MAE in general, SrMAE for rMAE obtained using a stationary test, and DrMAE for rMAE obtained using a dynamic test (i.e., counterphase flickering grating).

Given the existence of different channels for motion processing revealed by the spatiotemporal properties of SMAE and DMAE, the characteristics of rMAEs have still not been fully understood and investigated. Though the DrMAE has been demonstrated for brief (subsecond) adapting stimuli, the evidence for the existence of SrMAE generated by even shorter adapting stimuli (e.g., 67 ms) is equivocal. Glasser et al. (2011) found that 67 ms of adaptation in both humans and monkeys was sufficient to induce SrMAE when testing immediately or very soon (e.g., 0 to 150 ms) after the adaptation stimulus. To date, however, there are no other studies that have systematically investigated and characterized the presence of SrMAE. The investigation of the properties of rMAEs could represent an important advance in the comprehension of the fine-tuned mechanisms underlying motion perception and in understanding whether classic MAE and rMAE rely on the same temporal channels or reflect the activity of different channels with different spatiotemporal properties.

In the present study we performed a series of experiments to assess the role and the characteristics of stationary and dynamic test patterns in generating rMAE. In [Experiment 1](#) we assessed the presence of rMAE using both stationary and dynamic (counterphase flicker) test patterns. We adapted to drifting Gabors for a range of subsecond durations and tested two adapting temporal frequencies (i.e., 7.5 and 15 Hz); in [Experiment 2](#) we investigated the role of the adapting phase shift, test duration, test contrast, and adaptation-test blank interval (i.e., interstimulus interval [ISI]) in generating SrMAE; in [Experiment 3](#) we investigated the role of adapting duration and phase shift in DrMAE; finally, in [Experiment 4](#) we investigated the temporal

frequency tuning of the DrMAE to assess whether fast and slow motion sensors as those implicated in the classic DMAE are also involved in DrMAE.

General method

Apparatus

Stimuli were displayed on a 22" LCD SAMSUNG Syncmaster 2233RZ monitor with a refresh rate of 120 Hz (Wang & Nikolić, 2011). We generated the stimuli with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1680×1050 pixels. Each pixel subtended ~ 1.7 arcmin. The minimum and maximum luminance of the screen were 0.19 and 134 cd/m^2 , respectively, and the mean luminance was 66.24 cd/m^2 . Luminance was measured with a Minolta LS-100 photometer. A gamma-corrected lookup table (LUT) was used so that luminance was a linear function of the digital representation of the image.

Observers

Eight observers (six naïve participants and the two authors) participated in Experiments 1, 2A, 3, and 4, whereas in Experiment 2B a new set of eight naïve observers was recruited. Observers sat in a dark room at a distance of 57 cm from the screen. Viewing was binocular. They were instructed to fixate the center of the patterns. All observers had normal or corrected-to-normal visual acuity. All participants gave their informed written consent, participated voluntarily, and except for the two authors, received monetary compensation.

Stimuli

Stimuli were vertically oriented Gabor patterns with a full width of 8° at half maximum amplitude (FWHM) and a spatial frequency of 1 c/deg (Kanai & Verstraten, 2005, 2006; Pavan et al., 2009). For the adapting stimulus, the Gaussian envelope was always stationary, whereas the sine-wave carrier drifted either leftward or rightward. The Michelson contrast of the adapting stimulus was always constant at 0.9. Test stimuli consisted of stationary and dynamic test patterns. For dynamic (i.e., counterphase flickering) test patterns, the spatial phase of the Gabor's carrier was reversed by 180° every 66.7 ms in the case of 7.5 Hz, and every 33.3 ms in the case of 15 Hz. The initial spatial phase of both adapting and test patterns was randomized across trials. Figure 1 shows a space–time representation of a subsample of the stimuli used in the study.

General procedure

Direction discrimination (Step 1)

Before and after the main experiment observers performed a direction discrimination task in which they had to judge whether the adapting gratings moved leftward or rightward (two-alternative forced choice: 2AFC). To aid fixation, the central part of the Gabor was replaced by a gray disk (0.32° in diameter) with the same mean luminance as the background (66.24 cd/m^2), and a white fixation point (0.2°) was present at the center of the gray disk for the entire stimulus duration. To avoid any cumulative effect of adaptation, we randomized the motion direction trial-by-trial and set an intertrial interval of 2 s, since Kanai and Verstraten (2005) and Pavan et al. (2009) have shown a full recovery from brief motion adaptations after an ISI of this duration.

Contrast threshold (Step 2)

A two-interval forced-choice (2IFC) procedure was used to estimate the observers' contrast detection threshold (CDT) for each type of test pattern. The CDT corresponded to 84% correct responses. CDTs were estimated in separate blocks for each type of test pattern. The contrast of the test Gabor was varied adaptively using a 1 up-4 down staircase (Levitt, 1971). The adaptive staircase was terminated after either 120 trials or 16 reversals. The initial step size of the staircase was set at 0.089; then after each reversal the step size was decreased until a minimum value of 0.001. Observers indicated whether the Gabor patch was present in the first or the second interval by pressing one of the two response keys. Each trial consisted of two intervals separated by 1 s. The duration of each interval depended on the relative duration of the test pattern. During the interinterval period the screen was set at the mean luminance and the white fixation point was also present. A pure tone of 16 ms marked the start of the first and second interval, whereas another pure tone of 16 ms, one octave higher, marked the end of the second interval. At the end of the procedure, the threshold was calculated by averaging the modulation values of the last eight reversals. Estimating the 84% correct responses for stationary and dynamic test stimuli ensured that they were matched for salience (Hutchinson & Ledgeway, 2004). In addition, the detection thresholds were multiplied by 3 or 10 (depending on the experiment) and the resulting values were used in the main experiment. The resulting contrast of the test patterns was always lower than the adapting contrast; this has been shown to increase the duration and strength of the classic MAE (Keck, Palella, & Pantle, 1976; Mather, Verstraten, & Anstis, 1998; Nishida, Ashida, & Sato, 1997). Stationary and

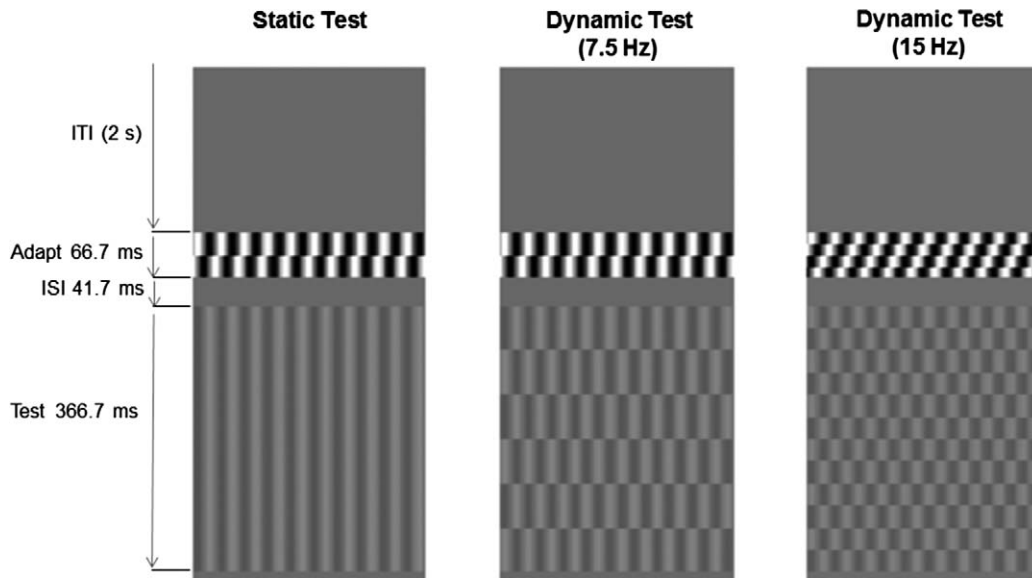


Figure 1. Space-time (xt) representation of the stimuli and the task used. Shown are example values from [Experiment 1](#), but the general trial sequence holds across all the experiments. On each trial a high-contrast adapter (0.9) was presented for a variable duration and at different temporal frequencies. The adapting pattern was followed by a low-contrast test stimulus with variable ISIs (depending on the experiment). Test stimuli could be either stationary or dynamic (counterphase flickering). Ambiguous motion was obtained by shifting the spatial phase of the sinusoidal modulation by 180° (Panels B and C). The duration of the test stimulus was varied in different experiments as well. In [Experiments 1, 2, and 3](#) the temporal frequency of the test pattern always matched that of the adapting pattern. At the end of each trial observers had to indicate the perceived motion direction of the test stimulus. Panel A: adaptation of 66.7 ms (7.5 Hz), phase shift 90° , stationary test pattern of 366.7 ms. Panel B: adaptation of 66.7 ms (7.5 Hz), phase shift 90° , temporal frequency of the dynamic test stimulus 7.5 Hz (366.7 ms). Panel C: adaptation of 66.7 ms (15 Hz), phase shift 90° , temporal frequency of the dynamic test stimulus 15 Hz (366.7 ms).

dynamic test patterns were presented in separate blocks and in randomized order across observers.

Measuring directional biases (Step 3)

In Step 3, which was the main part of the experiment, we assessed the presence of stationary and dynamic rapid motion aftereffects. Temporal frequencies and different types of test patterns were always presented in separate blocks. In the case of dynamic test stimuli, the temporal frequency of the test pattern always matched that of the adapting pattern, with the exception of [Experiment 4](#), in which we assessed the temporal frequency tuning of the DrMAE combining different adapting/test temporal frequencies. The motion direction of the adapting pattern was balanced and randomized across trials. On each trial after an initial adaptation period and an ISI of variable duration (depending on the experiment), a stationary or a directionally ambiguous (dynamic) test pattern was presented. During the ISI the display was blank except for the fixation point, which was always present. Observers judged whether the test stimulus was moving leftward or rightward (2AFC) by pressing one of two response keys. The intertrial interval was set at 2 s.

Experiment 1: The role of stationary and dynamic test patterns in rMAE

Method

Adapting stimuli were displayed for 66.7, 100, 166.7, and 366.7 ms and drifted either at 7.5 or 15 Hz. The adapter phase shift was 90° . The ISI was constant at 41.7 ms. Three types of test patterns were used: stationary, dynamic (counter-phase flicker) at 7.5 Hz, and dynamic at 15 Hz. CDTs were multiplied by 10. The duration of the test pattern was constant at 366.7 ms. There were 12 conditions (i.e., 4 Adaptation Durations \times 3 Test Patterns) with 28 trials for each condition.

Results and discussion

The results of the direction discrimination task conducted before and after the main experiment showed that for adapting patterns of 66.7 ms, the performance did not differ from chance (0.5) for both temporal frequencies employed. The estimated contrast

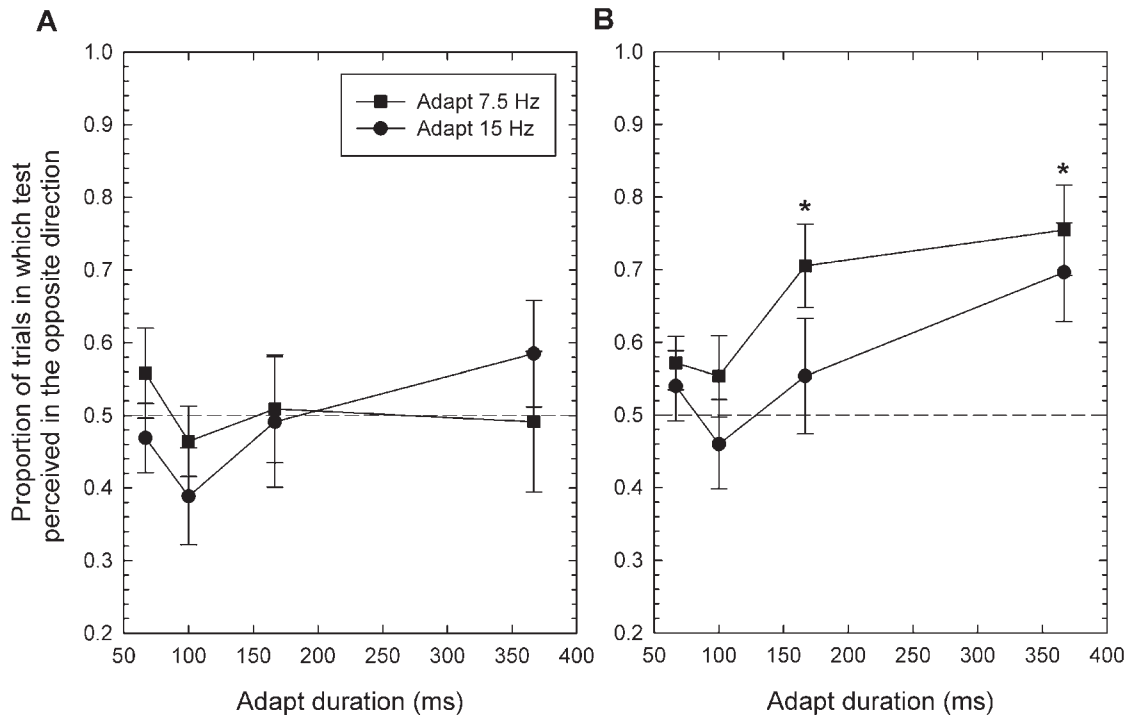


Figure 2. Results from [Experiment 1](#) ($N = 8$). The mean proportion of trials in which observers judged the test stimulus as drifting in the opposite direction with respect to the adaptation stimulus (i.e., rMAE) is shown as a function of the adaptation duration. The results are shown for 7.5 and 15 Hz temporal frequencies of the adapter for both stationary (Panel A) and dynamic (Panel B) test patterns. The asterisks mark the significant (rMAE) effects, which correspond to the longer adaptation durations for the 7.5 Hz dynamic test patterns (corrected critical p -value = 0.0125). Error bars \pm SEM.

thresholds for the three types of test patterns (i.e., stationary, dynamic 7.5 Hz, and dynamic 15 Hz) were 0.168 (SE : 0.016), 0.167 (SE : 0.015), and 0.151 (SE : 0.008) (Michelson contrast), respectively.

[Figure 2](#) shows the results for stationary and dynamic rMAEs. We plotted the proportion of trials in which the test pattern was perceived to drift in the opposite direction to that of the adaptation pattern as a function of the adapter duration. A repeated measures ANOVA performed, including as factors the Test Type, the Temporal Frequency, and the Adapter Duration, did not report an effect of the Test Type, $F(1, 7) = 3.17$, $p = 0.12$, $\eta^2 = 0.31$, nor a significant effect of the Temporal Frequency, $F(1, 7) = 1.79$, $p = 0.22$, $\eta^2 = 0.20$, but pointed out a significant effect of the Adapter Duration, $F(3, 21) = 3.45$, $p = 0.035$, $\eta^2 = 0.33$. Bonferroni corrected pairwise comparisons revealed only a significant difference between 100 ms and 366.7 ms adaptation ($p = 0.005$).

In order to investigate in detail the characteristics of SrMAE and DrMAE, we performed separate analyses on the results obtained with stationary and dynamic test patterns. In particular, we used a series of Bonferroni corrected one-sample t tests to assess whether each combination of adapter duration and temporal frequency was significantly different from chance level.

For stationary test patterns ([Figure 2A](#)), Bonferroni corrected one-sample t tests did not point out any significant effect across all the adaptation durations and temporal frequencies employed.

For dynamic test patterns ([Figure 2B](#)), Bonferroni corrected one-sample t tests with respect to the chance level pointed out significant DrMAEs after 166.7 ms ($p = 0.048$) and 366.7 ms ($p = 0.024$) of adaptation, but only for the lower temporal frequency used (i.e., 7.5 Hz). No significant effects were found for the 15 Hz adapting and test patterns.

The results of [Experiment 1](#) showed that a stationary test pattern presented 41.7 ms after the offset of the adapting pattern did not produce rMAE with either of the temporal frequencies employed. In the case of dynamic test patterns we found significant effects (DrMAEs) only for the lower temporal frequency (i.e., 7.5 Hz), and for the longer adaptation durations employed (i.e., 166.7 and 366.7 ms), despite the higher temporal frequency (i.e., 15 Hz) we found only a weak rMAE in correspondence to the longer adaptation duration, though it was not significant.

Thus, it seems that a stationary test pattern of 366.7 ms presented after a variable adaptation period is not able to capture any directional bias induced by the adaptation. Recently, [Glasser et al. \(2011\)](#) found that when observers were adapted for 66.7 ms to directional

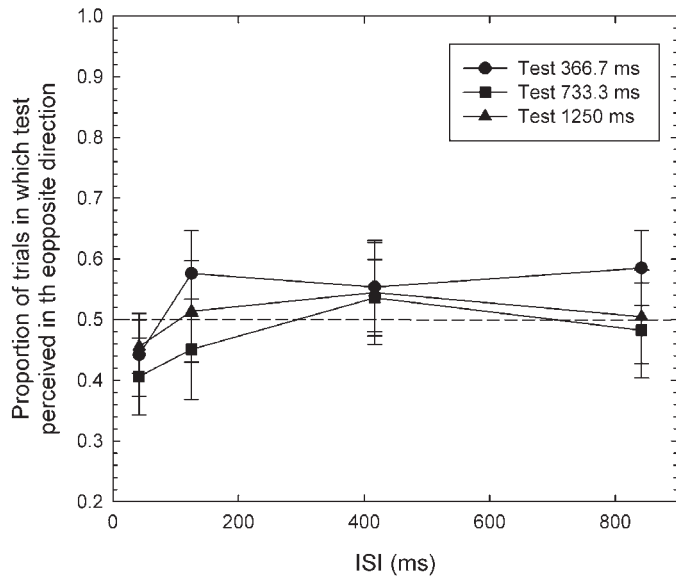


Figure 3. Results from [Experiment 2A](#) ($N = 8$). The mean proportion of trials in which observers judged the test stimulus as drifting in the opposite direction with respect to the adaptation stimulus is shown as a function of the ISI. The results are shown for the three durations of the stationary test pattern (i.e., 366.7, 733.3, and 1250 ms). Error bars $\pm SEM$.

motion, a stationary test pattern presented immediately or up to 150 ms after the adapting stimulus induced SrMAE. However, it should be noted that their stationary test pattern was presented until response. It could be possible that SrMAE needs more time to arise, and 366.7 ms of test pattern presentation is not sufficient to allow a complete deployment of the effect. Indeed, a stationary test pattern presented immediately (or very soon) after the adapting pattern could interfere with the effects of adaptation; that is, the stationary test pattern might disrupt weak motion signals that arise from adapted and unadapted motion detectors (Ledge-way & Smith, 1994a, 1994b). In [Experiment 2](#) we further investigated the role of stationary test stimuli in rMAE using longer adaptation duration (i.e., 733.3 ms) to ensure stronger adaptation, three durations of the stationary test pattern, and four ISI levels. This is to assess the temporal deployment of SrMAE and, if it exists, its recovery from (brief) adaptation.

Experiment 2A: The role of the test duration in stationary rMAEs

Method

Adapting duration of 733.3 ms, adapter temporal frequency at 7.5 Hz, and adapter phase shift of 90° . Four

levels of ISI: 41.7, 125, 416.7, 841.6 ms, and three test durations: 366.7, 733.3, and 1250 ms were used. CDTs were multiplied by 10. There were 12 conditions (i.e., 4 ISIs \times 3 Test Durations), with 28 trials per condition. Different test durations were presented in separate blocks, whereas ISI levels were randomized across trials.

Results and discussion

The proportion of correct answers for the direction discrimination of 733.3 ms adapting stimuli was one both before and after the rMAE experiment. Contrast thresholds (Michelson contrast) were on average 0.190 ($SE: 0.009$), 0.197 ($SE: 0.018$), and 0.191 ($SE: 0.011$) for 366.7, 733.3, and 1250 ms test patterns, respectively.

[Figure 3](#) shows the results of [Experiment 2A](#). A repeated measures ANOVA including as factors the Test Duration and the ISI did not reveal any significant effect, $F(2, 14) = 1.95$, $p = 0.18$, $\eta^2 = 0.22$; $F(3, 21) = 1.82$, $p = 0.17$, $\eta^2 = 0.21$; for Test Duration and ISI respectively, nor any significant interaction, $F(6, 42) = 0.77$, $p = 0.60$, $\eta^2 = 0.09$. Bonferroni corrected one-sample t tests performed for each stimulus condition with respect to the chance level again did not point out any significant SrMAE.

It should be noted that some combinations of test duration and ISI we used were similar to those used by Kanai and Verstraten (2005, 2006) and Pavan et al. (2009). These authors found that adapting for 640 ms and after an ISI of 1000 ms the rMAE obtained using counterphase flickering test patterns (i.e., DrMAE) had almost recovered. If SrMAE is a slower process and takes time to arise, 1250 ms of test pattern in combination with an ISI of 841.6 ms should still be sufficient to tap the effect. This is because the combination of these two parameters exceeds the time window for which DrMAE arises and decays, and to date there is no evidence that SrMAE ought to exist within a radically different time window.

However, Glasser et al. (2011) showed consistent SrMAE using a different stimulus configuration. In particular, the duration of their adapting stimulus was always 66.7 ms, the phase shift of the adapting sinewave carrier was 45° , and its temporal frequency was 15 Hz. In addition, a low contrast (i.e., three times the 82% contrast threshold) and large radius (8°) test pattern was used. The authors also ensured that each observer was familiar with MAE by training the observers with MAEs generated by prolonged adapting stimuli, whose duration was gradually decreased until it reached 66.7 ms. Importantly, the authors chose only the observers who were not able to discriminate the motion direction of the adapting pattern. In [Experiment 2B](#) we employed a similar stimulus configuration and procedure to further assess the presence of SrMAE. In particular,

we used two phase shifts of the adapting grating (45° and 90°), two temporal frequencies (i.e., 7.5 and 15 Hz), and two test pattern contrasts (i.e., 3 and 10 times the 84% test CDT). Similarly to Glasser et al. we only kept those observers who performed the direction discrimination task for the 66.7 ms adaptation at chance for the two phase shifts both before and after the main experiment. However, differently from Glasser et al. (2011): (a) we did not train observers with MAEs generated by prolonged adapting stimuli. This is because we aimed to avoid any perceptual learning effect and thus any possible *implicit* directional bias towards the opposite direction of the adapting pattern, (b) we did not use infinite test duration since rapid adaptation is expected to rise and decay over a short timescale (Kanai & Verstraten, 2005, 2006; Pavan et al., 2009; Pavan et al., 2010), (c) we kept constant the stimulus size at 8° (FWHM) since Glasser et al. showed strong SrMAE for such stimulus size when using a speed nulling technique.

Experiment 2B: The role of awareness of adapter direction and of test contrast in SrMAE

Method

Adapting duration of 66.7 ms, two adapter temporal frequencies: 7.5 and 15 Hz, two adapter phase shifts: 45° and 90°, one ISI at 41.7 ms, a stationary test pattern of 1250 ms, two levels of contrast of the test pattern: 3 and 10 times the 84% CDT. This gave a total of eight conditions (i.e., 2 Adapter Temporal Frequencies × 2 Adapter Phase Shifts × 2 Test Contrasts), which were presented in separate blocks (28 trials for each condition). Observers who exhibited above chance performance in either of the pre- or postexperiment direction discrimination tasks were excluded from the final data sample. It should be noted that the number of motion steps is different across the conditions employed. In particular, a phase shift of ±45° generates three motion steps in the case of 7.5 Hz patterns and seven motion steps in the case of 15 Hz patterns, whereas a phase shift of ±90° generates a single motion step in the case of 7.5 Hz patterns and three motion steps in the case of 15 Hz patterns.

Results and discussion

Contrast thresholds for the test pattern were on average 0.044 (*SE*: 0.002) in the case of low-contrast condition and 0.146 (*SE*: 0.007) in the case of high-contrast condition (i.e., 3 and 10 times the 84% threshold, respectively).

Figure 4 shows the results of Experiment 2B. Panel A shows the results for the 45° phase shift, panel B for the 90° phase shift. A repeated measures ANOVA including as factors the Phase Shift, the Temporal Frequency, and the Test Contrast did not reveal any significant effect, $F(1, 7) = 0.025$, $p = 0.88$, $\eta^2 = 0.004$; $F(1, 7) = 0.007$, $p = 0.94$, $\eta^2 = 0.001$; $F(1, 7) = 0.092$, $p = 0.77$, $\eta^2 = 0.013$; for Phase Shift, Temporal Frequency, and Test Contrast, respectively, nor any significant interactions. Bonferroni corrected one-sample *t* tests performed for each condition with respect to the chance level did not report any significant differences.

The results showed no SrMAE across all the conditions tested. Stimulus configuration and procedure were very similar to those used by Glasser et al. (2011); however, a key difference is that our observers were not trained with MAEs seen using prolonged adaptation duration. It is possible that the initial training can generate an *implicit* bias towards the opposite direction with respect to the *implicit* motion direction of the adapting stimulus.

Experiment 3: The role of phase shift in DrMAE

In Experiment 3 we investigated the role of phase shift in DrMAEs using two adaptation durations (66.7 and 733 ms) and a temporal frequency of 7.5 Hz. In addition, we also used stationary test patterns to partially replicate the findings of Experiment 2B, but using observers that performed the direction discrimination task significantly above chance for adapting stimuli with 45° phase shift. In particular, we used phase shifts of 45° and 90° to assess the optimal displacement for DrMAE. The rationale was based on previous psychophysical studies that investigated the dependence of SMAE on the spatial displacement of the adapting grating. Baker, Baydala, and Zeitouni (1989) used jumping gratings with exposure durations that precluded correlations by the short-range process over multiple jumps (i.e., 68 ms). The displacement producing the largest aftereffect was expressed as a fraction of the spatial period of the grating (D_{opt}). The authors found that for spatial frequencies ranging between 0.21 and 4.8 c/deg, the D_{opt} was slightly less than one fourth of the spatial period (see also Nakayama & Silverman, 1985; Turano & Pantle, 1985). This result supports quadrature models of motion sensing, in which direction selectivity is produced by the combination of receptive fields in spatial and temporal quadrature phase (Adelson & Bergen, 1985; van Santen & Sperling, 1984, 1985; Watson & Ahumada, 1983, 1985; Watson, Ahumada & Farrell, 1986). We chose to test 45° and 90° phase shifts also because Pinkus and Pantle (1997)

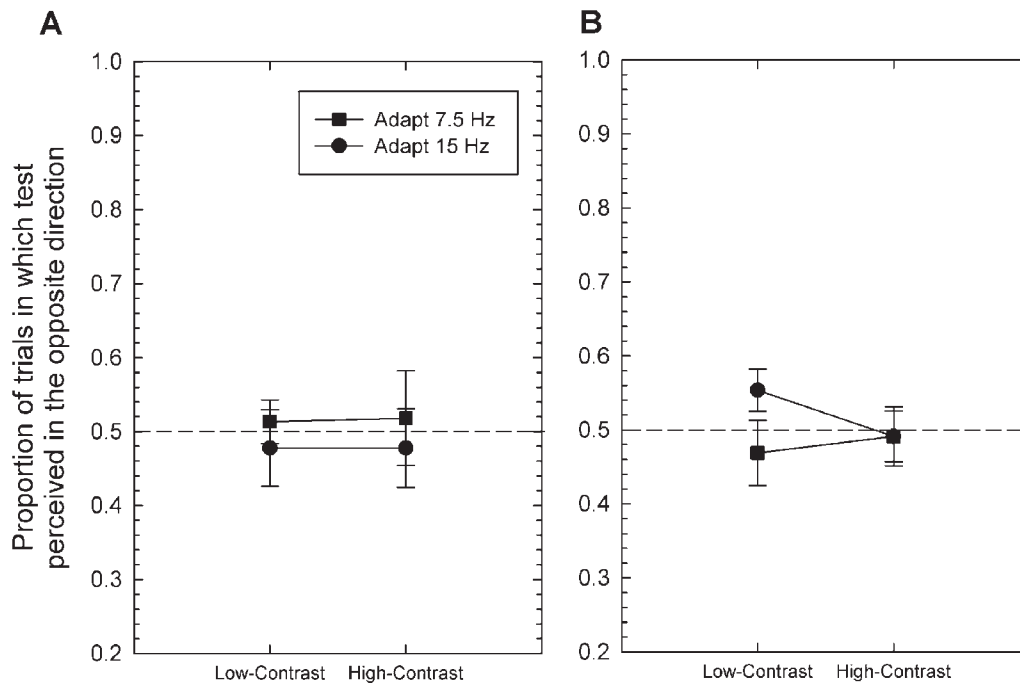


Figure 4. Results from Experiment 2B ($N = 8$). The proportion of trials in which observers judged the test stimulus as drifting in the opposite direction with respect to the adaptation stimulus is shown as a function of the test contrast. Panels A and B show data obtained for 45° and 90° phase shifts, respectively. Separate curves for temporal frequencies. Error bars $\pm SEM$.

showed that rapid visual motion priming (rVMP: a mirror-symmetric effect of rapid adaptation in which the test pattern is perceived as drifting in the same direction as the adapting pattern; Kanai & Verstraten, 2005; Pavan et al., 2009) seen in a two-frame sequence (i.e., single motion step) peaked when using 90° phase shift and was drastically reduced when using a 45° phase shift. We also tested two ISI durations (41.7 and 125 ms) for which brief adaptations have been shown to generate stronger rMAEs (Kanai & Verstraten, 2005, 2006; Pavan et al., 2009; Pavan et al., 2010).

Method

Two adapting durations: 66.7 and 733 ms, adapter temporal frequency at 7.5 Hz, two adapter phase shifts: 45° and 90° , two ISIs: 41.7 and 125 ms, test duration of 366.7 ms, two types of high-contrast (CDT \times 10) test patterns: stationary and dynamic at 7.5 Hz. This gave a total of 16 conditions (28 trials per condition). Adapting durations and phase shifts were presented in separate blocks, whereas ISIs were randomized across trials.

Results and discussion

Observers performed the direction discrimination task above chance for adapting stimuli of 66.7 ms with 45° phase shift, but not for those with 90° phase shift

(i.e., with a single motion step). Bonferroni corrected one-sample t tests reported that the direction discrimination of the adapting pattern of 66.7 ms with 90° phase shift did not differ from chance level ($p = 0.56$ and $p = 0.78$, for direction discrimination before and after the main experiment, respectively).

The estimated contrast thresholds were 0.189 (SE : 0.025) and 0.155 (SE : 0.011) (Michelson contrast) for the stationary and dynamic test patterns, respectively.

Figure 5 shows the results of the main experiment. Different curves show the results for each combination of adapting duration and phase shift. A repeated measures ANOVA including as factors the Test Type, Phase Shift, Adaptation Duration, and ISI revealed a significant effect of the Test Type, $F(1, 7) = 23.26$, $p = 0.002$, $\eta^2 = 0.77$, a significant effect of the Adaptation Duration, $F(1, 7) = 26.01$, $p = 0.001$, $\eta^2 = 0.79$, but not a significant effect of the Phase Shift, $F(1, 7) = 2.16$, $p = 0.18$, $\eta^2 = 0.24$. Moreover, we found a significant interaction between Test Type and Adaptation Duration, $F(1, 7) = 9.26$, $p = 0.019$, $\eta^2 = 0.57$. Bonferroni corrected pairwise comparisons pointed out a significant difference between the two test types for each of the adaptation durations.

Bonferroni corrected one-sample t tests with respect to the chance level pointed out a significant rMAE only with dynamic test patterns following 733.3 ms of directional adaptation for both 45° and 90° phase shifts (Figure 5).

We found that 66.7 ms of adaptation was not sufficient to generate DrMAE. However, we obtained

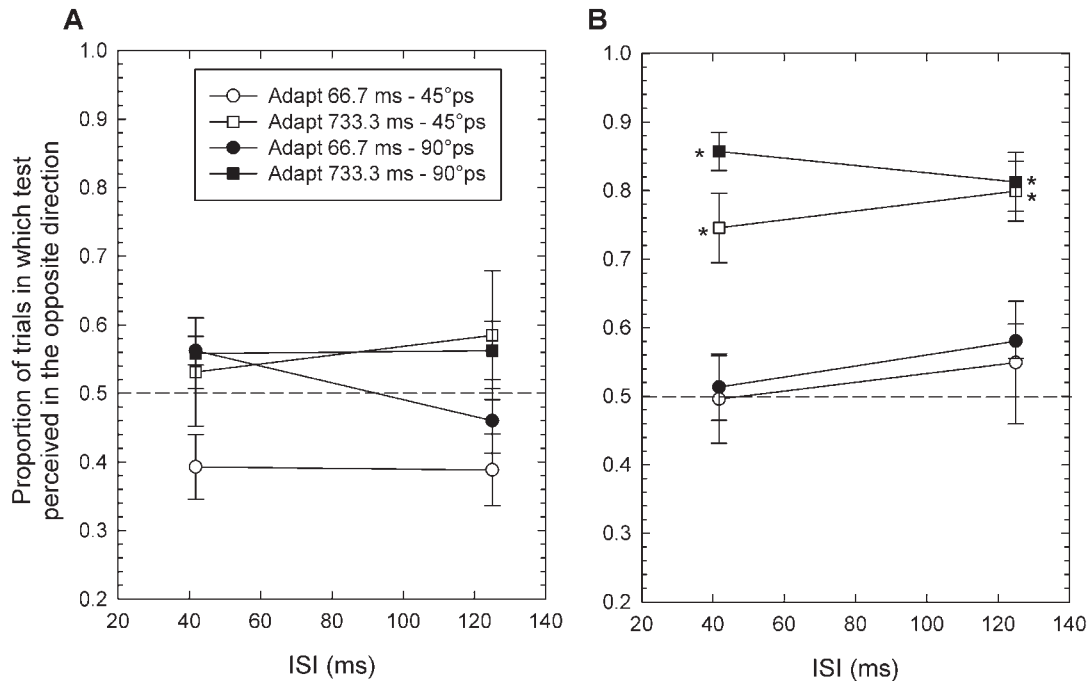


Figure 5. Results from [Experiment 3](#) ($N=8$). The proportion of trials in which observers judged the test stimulus as drifting in the opposite direction with respect to the adaptation stimulus is shown as a function of the ISI. Each panel shows data obtained with stationary (Panel A) and dynamic (Panel B; 7.5 Hz) test patterns. Separate curves for different combinations of adaptation duration and phase shift. The asterisks mark the conditions that were significantly above the chance level: Bonferroni corrected one-sample t tests with respect to the chance level (0.5) separately for dynamic and stationary test patterns (corrected critical p -value = 0.0063). Error bars \pm SEM.

significant DrMAEs when adapting for 733.3 ms. Moreover, for this adaptation duration we found no significant differences between 45° and 90° phase shifts. This result will be discussed in the [General discussion](#) section. For stationary test patterns we confirmed the results of the [Experiment 2B](#). While for 45° phase shift observers could discriminate the motion direction of the adapting pattern, we still did not observe any SrMAE. The same pattern of results was observed when using adapting patterns with 90° phase shift. It is worthwhile to note that when observers were adapted for 66.7 ms with a phase shift of 45° we observed a weak though not significant rVMP (Kanai & Verstraten, 2005, 2006; Pavan et al., 2009; Pinkus & Pantle, 1997) for both ISIs employed. Taken together, these results suggest that under the stimulus conditions tested SrMAE does not exist.

Experiment 4: The temporal frequency tuning of DrMAE

DrMAE was found for adapting patterns equal to or longer than 166.7 ms with a peak at a temporal frequency of 7.5 Hz, i.e., close to the peak sensitivity of the transient channel (Hess & Snowden, 1992), and seemed to be independent of the spatial phase (at least

for the range tested in the present study). Bex, Verstraten, and Mareschal (1996) found that the largest (classic) DMAE was found with slow counterphasing test gratings (i.e., at 0.125–0.25 Hz). The largest DMAEs were also found when the test grating was of similar spatial frequency to that of the adapting grating, even at a very low spatial frequency (e.g., 0.125 c/deg). Overall, these findings suggest that DMAE is dominated by a single low-pass temporal frequency mechanism. However, as stated in the [Introduction](#), depending on the test pattern, DMAE can tap motion systems sensitive to relatively low or high temporal frequencies (Alais, Verstraten, & Burr, 2005; Bex et al., 1996; Mareschal et al., 1997; Verstraten, van der Smagt, & van de Grind, 1998). Shioiri and Matsumiya (2009), for example, found that DMAE taps a motion system with low spatial frequency tuning and high temporal frequency tuning (i.e., transient motion detectors). In [Experiment 4](#) we investigated the temporal frequency tuning of the DrMAE to assess whether subsecond stimulus presentations are likely to adapt both sustained and transient channels.

Method

Adapting duration of 733.3 ms, adapter phase shift of 90°, ISI of 41.7 ms, high-contrast (CDT \times 10)

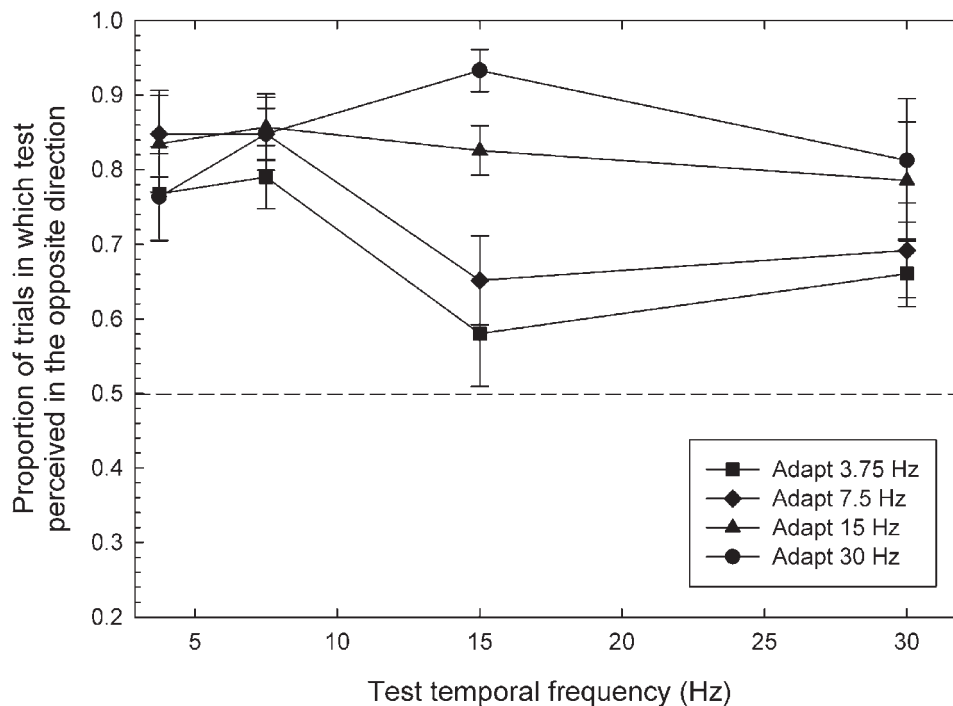


Figure 6. Results from Experiment 4 ($N=8$). The proportion of trials in which observers judged the test stimulus as drifting in the opposite direction with respect to the adaptation stimulus is shown as a function of the temporal frequency of the dynamic test pattern with separate curves for different adapting temporal frequencies. Error bars $\pm SEM$.

dynamic test pattern with a duration of 366.7 ms. We varied the temporal frequencies of the adapting and test patterns from 3.75 to 30 Hz (one octave step). This resulted in a total of 16 conditions (28 trials for each condition). Each of the combinations of adaptation-test temporal frequency was presented in a separate block and the sequence of combinations was randomized across observers.

Results and discussion

The proportion of correct answers for direction discrimination of the 733.3 ms adapting stimulus was one for all adapter temporal frequencies. The estimated contrast thresholds for the test patterns were 0.14 ($SE: 0.015$), 0.14 ($SE: 0.021$), 0.16 ($SE: 0.028$), and 0.25 ($SE: 0.042$) (Michelson contrast) for 3.75, 7.5, 15, and 30 Hz, respectively.

Figure 6 shows the results of Experiment 4. A repeated measures ANOVA revealed a significant effect of the Adapter Temporal Frequency, $F(3, 21) = 5.39$, $p = 0.007$, $\eta^2 = 0.44$, but not a significant effect of the Test Temporal Frequency, $F(3, 21) = 2.45$, $p = 0.092$, $\eta^2 = 0.26$. However, we found a significant interaction between Adapter and Test Temporal Frequency, $F(9, 63) = 3.74$, $p = 0.001$, $\eta^2 = 0.35$. Bonferroni corrected pairwise comparisons pointed out for Test Temporal Frequency of 15 Hz a significant difference between

adaptation at 3.75 Hz and 30 Hz ($p = 0.010$) and between adaptation at 7.5 Hz and 30 Hz ($p = 0.028$). Table 1 reports the results of the Bonferroni corrected one-sample t tests for each combination of adapting/test temporal frequency with respect to the chance level.

Overall, the results of Experiment 4 showed that for the lower adapting temporal frequencies (i.e., 3.75 and 7.5 Hz), the DrMAE was strongest when testing with the lower temporal frequencies (i.e., 3.75 and 7.5 Hz), while showing a strong reduction when testing with the higher temporal frequencies (i.e., 15 and 30 Hz). However, when adapting to the higher temporal frequencies (i.e., 15 and 30 Hz), we observed DrMAE across all the test temporal frequencies, suggesting the presence of a broadband tuning mechanism. These results suggest that brief (subsecond) adaptations could tap both sustained and transient motion detectors (Alais et al., 2005; Bex et al., 1996; Shioiri & Matsumiya, 2009; Verstraten et al., 1998).

General discussion

The use of stationary and dynamic test patterns in classic MAE has revealed the presence of channels with specific spatiotemporal characteristics that might be implemented at different stages along the motion processing pathway. There is now a growing interest

in MAEs that build up after very brief (subsecond) exposures to directional motion. The present study focused first on the presence of rMAE when testing with stationary test patterns, and second, on the spatiotemporal characteristics of the DrMAE and whether it relies on the same neural mechanisms as the classic DMAE.

The lack of SrMAE

Overall, we were not able to report any SrMAE for either of the temporal frequencies tested despite employing a variety of adapter durations, ISIs, and test durations. Some of the stimulus parameter configurations tested were similar to those from a previous work by Glasser et al. (2011) that consistently found SrMAE. A key difference with respect to Glasser et al.'s work was in the procedure we employed. Initially the authors trained their observers with the classic (long) MAE and progressively shortened the adapting time to 66.7 or 25 ms. Petrov and Van Horn (2012) showed that training with a direction discrimination task improved the sensitivity for motion direction but not the relative duration of stationary or dynamic MAEs tested prior and after the training. In the case of Glasser et al., the initial training with progressively decreasing adaptation durations and MAE could have substantially contributed to building up implicit representations of the adapting direction and MAE, sufficient to systematically bias the decision of the observers to be the opposite of the (implicit) direction of the adapting pattern, regardless of adapter's duration. However, further experiments are necessary to test the effect of training on the build-up of the MAE.

DrMAE: Spatiotemporal characteristics and neural mechanisms

In our study the only rMAEs were observed using dynamic (counterphase flickering) test patterns. The reported DrMAEs show: (a) a dependency on the adapting duration, progressively increasing from 166.7 to 733 ms, (b) an independence from the spatial phase of the sinewave carrier, and (c) a temporal frequency tuning compatible with the involvement of sustained and transient channels.

Dependency on the adapting duration

Concerning the dependence of the aftereffect on the adaptation duration, we found that quite long (i.e., 366.7 or 733.3 ms) adapting durations were required to observe DrMAE. Previous studies on rapid/brief adaptations have reported a mirror-symmetrical effect

Dynamic test temporal frequency (Hz)	Bonferroni corrected one-sample t tests
Adapt 3.75 Hz	
3.75	$T_7 = 4.25, p = 0.004^*$
7.5	$T_7 = 6.84, p = 0.0001^*$
15	$T_7 = 1.13, p = 0.29$
30	$T_7 = 3.63, p = 0.008^*$
Adapt 7.5 Hz	
3.75	$T_7 = 6.01, p = 0.001^*$
7.5	$T_7 = 10.17, p = 0.0001^*$
15	$T_7 = 2.55, p = 0.038$
30	$T_7 = 3.03, p = 0.019$
Adapt 15 Hz	
3.75	$T_7 = 5.17, p = 0.001^*$
7.5	$T_7 = 7.98, p = 0.0001^*$
15	$T_7 = 9.77, p = 0.0001^*$
30	$T_7 = 3.64, p = 0.008^*$
Adapt 30 Hz	
3.75	$T_7 = 4.54, p = 0.003^*$
7.5	$T_7 = 7.10, p = 0.0001^*$
15	$T_7 = 15.36, p = 0.0001^*$
30	$T_7 = 3.78, p = 0.007^*$

Table 1. Each panel shows the one-sample t test for a specific temporal frequency of the adapting pattern in combination with each temporal frequency of the test pattern. The second column reports the results of the Bonferroni corrected one-sample t tests (critical $p = 0.0125$). Note: Significant p -values are marked with asterisk.

of DrMAE known as rapid visual motion priming (rVMP; Kanai & Verstraten, 2005, 2006; Pavan et al., 2009; Pinkus & Pantle, 1997). That is, adaptation durations <100 ms (e.g., 80 ms) biased the perceived direction of a counterphase flickering test pattern in the same direction as that of the adaptation. This form of facilitation has been attributed to the influence of attention, generating high-level priming (Kanai & Verstraten, 2005, 2006; Pavan et al., 2010). The fact that in the present and previous studies DrMAE has been observed after an adapting duration ≥ 166 ms suggests that the susceptibility of directionally ambiguous stimuli to high-level facilitation/priming precludes observations of adaptation effects following very short stimulus exposures.

Additionally, there is physiological evidence that excitatory and inhibitory synapses in many cortical circuitries exhibit a mixture of facilitation and suppression (Tarczy-Hornoch, Martin, Jack, & Stratford, 1998; Thomson, 1997; Varela et al., 1997; Varela, Song, Turrigiano, & Nelson, 1999). Varela et al. (1997) recorded synaptic responses in layer 2/3 of rat primary visual cortex following transient electrical stimulation. Responses exhibited complex dynamics that were well described by a three-component model consisting of initial facilitation and two forms of depression/sup-

pression: a stronger form that decayed exponentially with a time constant of several hundred milliseconds and a subsequent weaker form that decayed with a time constant of several seconds. Because of the coexistence of facilitation and suppression at the cortical level, longer adaptation duration could be necessary to overcome the initial facilitatory phase.

Lack of phase-shift selectivity

The results of our third experiment did not point out any significant effect of the phase shift, though we obtained slightly stronger DrMAE with a phase shift of 90° relative to 45° (i.e., 86% [*SEM*: 2.78] responses opposite to the direction of the adapting pattern) when adapting for 733.3 ms and with an ISI of 41.7 ms (Figure 5, Panel B). On one hand, the lack of phase shift selectivity appears to be somewhat at odds with the predictions of some current models of motion sensing. Baker et al. (1989) reported that optimal displacement for SMAE was slightly less than one fourth of the spatial period of a grating (see also Turano & Pantle, 1985). Nakayama and Silverman (1985) measured contrast sensitivity for direction discrimination as a function of spatial displacement, and found an optimal spatial displacement equal to one fourth of the spatial period (i.e., quadrature phase). The results of these studies are compatible with models of motion sensing with receptive fields in spatial and temporal quadrature (Adelson & Bergen, 1985; van Santen & Sperling, 1984, 1985; Watson & Ahumada, 1983, 1985; Watson et al., 1986). Based on such results, one would expect stronger DrMAE with a phase shift of 90° (i.e., one fourth of the spatial period) rather than 45° (one eighth of the spatial period).

On the other hand, there is psychophysical evidence that the optimal displacement for the detection of motion is likely to be less than one fourth of the spatial period (Baker et al., 1989; Boulton & Hess, 1990; Watson, 1990). Boulton and Hess (1990) investigated the optimal spatial displacement using a motion direction discrimination task with spatially narrow-band gratings. The optimal spatial displacement found was equivalent to one sixth of the spatial period of the stimulus for low contrast stimuli and one fifth of the spatial period for higher contrast stimuli. These results seem to be in conflict with models of motion sensing that use spatial and temporal filters in quadrature phase. Baker et al. (1989) suggest that if each spatial filter has an associated temporal phase shift greater than quadrature, then the discrepancy from quadrature in the spatial phase offset could be compensated for, and this would result in a net quadrature relation after filtering. Moreover, there is evidence that the minimum displacement for the detection of motion is improved at low contrasts (Boulton, 1987; Boulton & Hess, 1990; Derrington & Goddard, 1988, 1989). We therefore

speculate that the high contrast we used for adapting and test patterns ($10 \times$ contrast threshold) in Experiment 3 may have slightly increased the relative optimal displacement towards one fourth of the spatial period. While this offers a potential explanation of our results, it is difficult to infer the optimal displacement for DrMAE from our data since we did not systematically vary the spatial displacement of the adapting patterns. Further studies are also necessary to better understand the relationship between spatial displacement and stimulus contrast in rapid adaptations.

Role of adapter direction discrimination

The shortest adaptations of 66.7 ms with a phase shift of 90° (Experiments 1, 2B, and 3) did not bias the perception of dynamic test patterns in either direction (i.e., DrMAE or rapid visual motion priming [rVMP]). This might be due to decreased direction discrimination of the adapting stimulus, which prevents the subsequent establishment of a perceptual directional bias.

Watson (1990) argued that quadrature models generally predict an optimal displacement of one fourth of spatial period for two-frame displays. In line with this prediction, previous studies (Kanai & Verstraten, 2005, 2006; Pavan et al., 2009) have reported that a single motion step of directional motion (stimulus duration 80 ms, 90° phase shift) was sufficient to induce a rapid form of visual motion priming when testing with counterphase flickering patterns. However, in those reports the motion step was discriminated above chance (e.g., $\sim 75\%$ in Pavan et al., 2009), whereas in the present study the direction of a motion step of 66.7 ms with a 90° phase shift was not discriminated.

The fact that in our study observers were not able to discriminate the motion direction of stimuli presented for 66.7 ms and with a phase shift of 90° is seemingly in contradiction with earlier results reported by Derrington and Goddard (1989). The authors found that at low temporal frequencies (2 Hz) with very short stimulus durations (27 ms), the direction discrimination of a high-contrast 1 c/deg grating declined with increasing contrast. However, they also showed that using a temporal frequency of 8 Hz, the decline of the direction discrimination at high contrasts was absent. A brief stimulus of 27 ms and 2 Hz has a very broad temporal frequency spectrum spreading on both sides of the origin of the temporal frequency axis, so a stimulus moving leftward will also excite detectors tuned to rightward motion, and vice versa. Thus, the failure of direction discrimination at high contrasts could occur because a substantial fraction of the temporal frequency spectrum of the stimulus represents motion in the opposite direction with respect to the direction in which the stimulus is moving. However, increasing the temporal frequency of the stimulus shifts its temporal frequency spectrum to higher frequencies, as a conse-

quence of which the proportion of the spectrum that represents motion in the direction opposite to that of the stimulus diminishes.

Derrington and Goddard (1989) proposed a model in which two direction-selective filters tuned to opposite directions pass through a saturating nonlinearity, which removes the difference between the outputs of the detectors at the first stage. Thus, at the first stage detectors tuned to the opposite direction would respond to the stimulus almost equally strongly. In our study the motion direction of a high-contrast 66.7 ms (and 100 ms) grating drifting at 7.5 Hz (phase shift 90°) was not discriminated. This could be due to the phase shift we employed, since it has been demonstrated that it plays a relevant role in direction discrimination. Green and Blake (1981), for example, showed the presence of a spatial phase range for direction discrimination. Using a single motion step consisting of a two-frame sequence (5 ms per frame) made up by low spatial frequency gratings, the authors found that when the phase shift was 90° in the dichoptic condition, observers were not able to discriminate the motion direction across a range of ISIs between the two frames and contrast levels. Their results suggest the presence of a “short range” motion system that detects sequentially presented stimuli separated by 10'–15', and operates best when stimuli are viewed monoptically. However, in our case, a 90° phase shift of 1 c/deg gratings evoked a translation of ~26'.

Thus, the “short range” system may actually operate over a fixed phase range rather than a fixed retinal distance (Bell & Lappin, 1973; Green & Blake, 1981). Therefore, it is possible that a phase shift of 90° in association with the brief stimulus presentation(s), the relatively low spatial frequency and the dichoptic presentation of our stimuli may have prevented adequate direction discrimination and hence the establishment of rMAE (or rVMP) effects.

Temporal frequency tuning

The results of Experiment 4 pointed out the presence of a temporal frequency tuning of the DrMAE. In particular, we showed that when adapting at low/intermediate temporal frequencies (i.e., 3.75 and 7.5 Hz) the peak effect is obtained when testing with the same temporal frequencies. On the other hand, when adapting to 15 and 30 Hz we measured quite strong DrMAEs across all the test temporal frequencies employed, suggesting the presence of a band-pass mechanism. These results are consistent with previous studies that, using contrast-masking paradigms, investigated the number and the spatiotemporal characteristics of the visual channels. These studies reported the presence of at least two (Cass & Alais, 2006) or three (Hess & Snowden, 1992; Kulikowski & Tolhurst, 1973; Mandler & Makous, 1984) channels; one low-pass,

sensitive to low temporal frequencies (up to about 4 Hz), and one or two band-pass channels tuned to intermediate and high temporal frequencies (Hess & Snowden, 1992; Mandler & Makous, 1984). Hess and Snowden (1992) showed that temporal sensitivity is most likely based on no more than three broadband mechanisms. Specifically, they found a low pass mechanism and a band pass one, centered at 8 Hz. The first one exhibited a band pass spatial dependence (peaking at 3 c/deg), whereas the second one was tuned to low spatial frequency, confirming covariation between temporal and spatial frequency sensitivity. The existence of a third band pass mechanism, centered on low spatial frequency and at a temporal frequency of 20 Hz was equivocal. Cass and Alais (2006), indeed, only revealed the presence of two channels, one low-pass (sustained) and one band pass (transient channel) peaking at 8 Hz. However, it should be noted that they only manipulated temporal frequency, where both target and masking gratings had a constant spatial frequency of 4 c/deg. The temporal frequency tuning we observed is compatible with the properties of the two (or three) temporal channels described previously; however, we cannot provide a full and detailed account of their properties since we did not assess their spatial frequency selectivity.

In addition, a recent rTMS study by Campana, Pavan, Maniglia, and Casco (2011) reported that the storing of the DrMAE relies on the functional integrity of the early visual areas (i.e., V1/V2) as well as the extrastriate area V5/MT, suggesting that DrMAE could share the same spatiotemporal properties as the classic DMAE: relying on the same neural substrates and tapping both slow and fast motion sensors (Alais et al., 2005; van der Smagt, Verstraten, & van de Grind, 1999; Verstraten et al., 1998, 1999). Shioiri and Matsumiya (2009), adapting to two superimposed sinusoidal gratings with different spatial frequencies and testing with stationary and dynamic counterphase flickering test patterns, found evidence for slow and fast motion sensors. In particular, the results showed that the SMAE was the aftereffect of the motion system selective for high spatial and low temporal frequency tuning (i.e., slow motion sensors) and the DMAE was the aftereffect of the motion system with a low spatial and high temporal frequency tuning (i.e., fast motion sensors). These two channels also differed from one another in their orientation tuning and sensitivity to relative motion. In addition, the difference in temporal frequency tuning was not influenced by the presence or absence of attention, nor did it depend on the speed of the adapting or test stimuli. These results suggest that the two types of motion sensors operate at a low/intermediate stage of motion analysis (e.g., V1/V2, complex V3, and V5/MT) that takes place prior to the attention-based motion analysis.

The slow mechanism pointed out by Shioiri and Matsumiya (2009) could be responsible also for the DrMAE we observed when adapting and testing with low temporal frequencies, and when adapting to high and testing with low temporal frequency. Indeed, Bex et al. (1996) showed similar low-pass tuning for motion detectors, irrespective of adaptation temporal frequencies. Our results suggest that both motion sensors have sensitivity at relatively low temporal frequencies and that there is a relatively large overlap between the two mechanisms in terms of temporal frequency tuning (Shioiri & Matsumiya, 2009). Even though further psychophysical and neuroimaging experiments are necessary to clarify the spatiotemporal properties of the channels and the cortical areas involved in rapid forms of both SMAE and DMAE, the data available suggest that DMAEs and DrMAEs might involve at least partially overlapping temporal mechanisms/channels, which do not tap a single population of cells, but multiple populations present at different stages of motion analysis depending on the spatiotemporal properties of both adapting and test stimuli (Bex & Baker, 1999; Cavanagh & Favreau, 1980; Kanai & Verstraten, 2005; Maruya, Watanabe, & Watanabe, 2008; Pavan et al., 2009; Pavan et al., 2010; Shioiri & Matsumiya, 2009; Smith et al., 2000).

Conclusion

Despite a growing number of physiological and psychophysical investigations on the effects of rapid adaptations, still little is known about their spatiotemporal characteristics and functional role (Hu, Wang, & Wang, 2011; Kohn, 2007; Nordström et al., 2011). It is now well established that, physiologically, adaptation takes place on the same timescale as the detection of motion itself (Nordström et al., 2011). Neural adaptation mechanisms are therefore an intrinsic component of rapid motion perception and as such must contribute substantially to the perceptual outcome of the processing of the motion signal. For some behaviors the visual system has to quickly recalibrate its stimulus sensitivity in response to fast stimulus changes over short periods of time (Clifford et al., 2007; Fairhall, Lewen, Bialek, & de Ruyter Van Steveninck, 2001; Gutnisky & Dragoi, 2008; Kohn, 2007; Kregelberg, van Wezel, & Albright, 2006; Müller, Metha, Krauskopf, & Lennie, 1999; Priebe & Lisberger, 2002). Thus the contribution to the response from previous changes has to be suppressed so that the visual system can continuously update itself to new incoming stimuli (Nordström et al., 2011). Measurements of ocular pursuits have shown that they are matched to the substantial variation in acceleration and speed of stimuli present in local scenes, which

suggests that local adaptation needs to build up and decay rapidly within the time scale of a single fixation (Frazor & Geisler, 2006; Nordström et al., 2011; Priebe & Lisberger, 2002). This is just one of the possible roles that rapid neural adaptation could play in optimizing motion perception. A full characterization of the implications these rapid mechanisms might have for motion perception or visually guided performance, however, is still far from complete as psychophysical evidence of perceptual benefits of motion adaptation remains limited (Kohn, 2007). Our study provides some evidence for the involvement of the same temporal mechanisms/channels mediating classic DMAE and DrMAE. It thus bridges a part of the gap between physiological and psychophysical evidence of rapid forms of adaptation and is therefore a valuable step towards understanding the contribution of rapid neural mechanisms to motion perception and the benefits it may have for visual performance. However, a better characterization of the spatial and temporal properties of the visual channels is necessary, and the employment of long adaptation as well as masking/brief adaptation durations provides a useful tool to further improve our understanding of the human visual motion processing.

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