Separate motion-detecting mechanisms for first- and second-order patterns revealed by rapid forms of visual motion priming and motion aftereffect

Andrea Pavan   Department of General Psychology, University of Padua, Padua, Italy

Gianluca Campana   Department of General Psychology, University of Padua, Padua, Italy

Michele Guerreschi   Department of General Psychology, University of Padua, Padua, Italy

Mauro Manassi   Department of General Psychology, University of Padua, Padua, Italy

Clara Casco   Department of General Psychology, University of Padua, Padua, Italy

Fast adaptation biases the perceived motion direction of a subsequently presented ambiguous test pattern (R. Kanai & F. A. Verstraten, 2005). Depending on both the duration of the adapting stimulus (ranging from tens to hundreds of milliseconds) and the duration of the adaptation-test blank interval, the perceived direction of an ambiguous test pattern can be biased towards the same or the opposite direction of the adaptation pattern, resulting in rapid forms of motion priming or motion aftereffect respectively. These findings were obtained employing drifting luminance gratings. Many studies have shown that first-order motion (luminance-defined) and second-order motion (contrast-defined) stimuli are processed by separate mechanisms. We assessed whether these effects also exist within the second-order motion domain. Results show that fast adaptation to second-order motion biases the perceived direction of a subsequently presented second-order ambiguous test pattern with similar time courses to that obtained for first-order motion. To assess whether a single mechanism could account for these results, we ran a cross-order adaptation condition. Results showed little or no transfer between the two motion cues and probes, suggesting a degree of separation between the neural substrates subserving fast adaptation of first- and second-order motion.

Introduction

After prolonged exposure (adaptation) to a moving pattern in a certain direction, observation of a stationary pattern evokes an experience of motion in the opposite direction. This perceptual effect is known as motion aftereffect (MAE) (for a review see Mather, Pavan, Campana, & Casco, 2008). Generally, MAE is induced by adapting for tens of seconds; however, electrophysiological studies have described much faster forms of adaptation (i.e., few hundreds of milliseconds). In particular, when the same stimulus is presented twice in rapid succession, the neural response to the latter stimulus

presentation is considerably reduced (Chance, Nelson, & Abbott, 1998; Finlayson & Cynader, 1995; Nelson, 1991; Stratford, Tarczy-Hornuch, Martin, Bannister, & Jack, 1996). This pattern of activity has been described both at low-level (V1) and high-level of motion analysis (e.g., MT) (Lisberger & Movshon, 1999; Priebe, Churchland, & Lisberger, 2002). For example, Priebe et al. (2002) have shown that MT neurons respond with a transient-sustained firing rate to briefly (e.g., 256 ms) presented motion stimuli. They find that the transition from a transient rate to a sustained rate occurs over a temporal window of 20–80 ms and consider it a form of short-term adaptation. On the other hand, it has been shown that very brief stimulations are also able to produce facilitation for

subsequently presented stimuli which leads to an increase of neuronal responsiveness (Castro-Alamancos & Connors, 1996; Hempel, Hartman, Wang, Turrigiano, & Nelson, 2000). Hempel et al. (2000) investigated short-term plasticity in the excitatory synapses in the rat medial prefrontal cortex. When they stimulated layers II/III of the prefrontal cortex they found short-term depression and short-term facilitation. These forms of short-term plasticity were very similar to that reported in other cortical areas. Moreover, they found that synapses in the prefrontal cortex show a longer lasting form of short-term synaptic enhancement. That is, an enhancement of the synaptic transmission which can last for seconds and which can be induced by stimulus trains of brief duration. In addition, the authors found that synapses in layer III in the primary visual cortex (V1) exhibit a similar transmission enhancement, though smaller than that reported for the synapses in the prefrontal cortex. Hempel et al. (2000) argued that such synaptic transmission enhancement could force a neuronal circuit to sustain persistent activity after a transient stimulus.

Thus, these two opposite forms of neural plasticity (facilitation vs. inhibition following adaptation) might serve distinct functional roles in the nervous system and could operate in order to manage different perceptual outcomes as a function of the task employed. Recent psychophysical studies have described some possible relationships between these fast forms of neural plasticity and patterns of psychophysical behavior.

It has been found that for first-order (luminance-defined) motion very brief exposures to directional stimuli can bias the perceived motion direction of a subsequently presented ambiguous test pattern (Kanai & Verstraten, 2005). In particular, depending on both the duration of the adaptation pattern and the duration of the blank inter-stimulus interval (ISI), the perceived direction of an ambiguous test pattern can be biased towards the opposite direction (aftereffect), or towards the same direction (priming) of the adaptation pattern (see also Pinkus & Pantle, 1997). Using brief adaptation durations (80 or 160 ms) and ISIs (40 or 120 ms) Kanai and Verstraten (2005) showed that the perceived direction of an ambiguous test pattern was biased towards the direction of the adaptation pattern, resulting in a rapid form of visual motion priming (rVMP). Alternatively, slightly increasing the adaptation duration to 320 or 640 ms, and using the same ISI produced a perceived bias in the opposite direction to the adaptation pattern (rapid motion aftereffect—rMAE). Thus the findings of Kanai and Verstraten (2005) suggest that these rapid forms of neural plasticity arise at low-levels of motion analysis. In addition, they found that using adaptation durations up to 300 ms, and ISIs longer than 2 sec, the perceived motion direction of the test pattern was biased towards the motion direction of the adaptation pattern. Kanai and Verstraten (2005) called such form of facilitation Perceptual Sensitization (PS). This effect arises gradually over time and probably reflects

facilitation at higher-levels along the motion processing hierarchy, such as MT. In fact, PS is likely to be mediated by the same mechanism that produces motion priming in visual search tasks (Campana, Cowey, Casco, Oudsen, & Walsh, 2007; Campana, Cowey, & Walsh, 2002, 2006; Campana, Pavan, & Casco, 2008; Kristjánsson, 2009).

Many psychophysical studies have pointed out the existence of distinct motion detecting mechanisms for first-order and second-order motion, and each mechanism is able to encode different characteristics of a moving stimulus such as spatial frequency, temporal frequency and spatial position (Bressler & Whitney, 2006; Hutchinson & Ledgeway, 2007; Ledgeway & Hutchinson, 2005; Ledgeway & Smith, 1994, 1997; Pavan & Mather, 2008).

A variety of psychophysical studies have highlighted relevant differences between these two motion mechanisms in terms of their spatial and temporal tuning. Adaptation studies have revealed that the mechanism responsible for detecting first-order motion is band-pass, whereas the mechanism underlying the detection of second-order motion appears to be low-pass in the temporal domain. The findings of Bressler and Whitney (2006) for the motion-induced position shift of first- and second-order moving stimuli confirmed that a first-order motion mechanism is temporally bandpass, but also has narrow spatial frequency tuning. Conversely, they found that the second-order mechanism is temporally lowpass and more broadly tuned for spatial frequency. Hutchinson and Ledgeway (2006) explored the spatiotemporal "window of visibility" for first-order motion and for a variety of second-order motion patterns. The authors measured the direction discrimination thresholds over a five octave range of spatial and temporal frequencies, from 0.5 to 16 c/deg, and from 0.5 to 16 Hz respectively. The results showed that sensitivity functions for first-order patterns were bandpass, whereas for second-order motion patterns functions were predominantly lowpass both in the spatial and temporal domain. These differences support the notion that the mechanisms responsible for encoding first-order and second-order motion are, at least at threshold, independent in the human visual system.

It has been shown that first- and second-order motion cues differ also in terms of their temporal acuity (Derrington, Badcock, & Henning, 1993). Derrington et al. (1993) have shown that a stimulus duration of 200 ms or greater is required to correctly discriminate the motion direction of a second-order drifting stimulus (beat pattern). These findings demonstrate that second-order motion exhibits poorer temporal acuity than first-order motion, and sensitivity to second-order motion declines to a greater extent with increasing the temporal frequency than for first-order motion (Derrington, 1994; Holliday & Anderson, 1994; Smith & Ledgeway, 1998).

In the current study we assessed whether rVMP, rMAE and PS also exist in the second-order motion domain. In addition, we explored the existence of these effects under a cross-order adaptation condition in which we adapted to

first-order and tested with second-order motion, and vice versa. This paradigm selectively taps the response of low-level first- and second-order motion detectors (rVMP and rMAE), as well as the motion detectors present at higher levels of motion processing (PS). In particular, we aimed to investigate: (i) whether second-order rVMP, rMAE and PS exist and if so, do they exhibit the same or different temporal course as those observed for first-order motion, and (ii) using a cross-adaptation condition, whether first-order and second-order signals are integrated or are kept separate both at low- and higher levels of motion analysis.

Since a number of studies have shown a different temporal tuning (Hutchinson & Ledgeway, 2006) for first- and second-order motion signals, we expected different time courses for first- and second-order rVMP, rMAE and PS. Moreover, based on previous results (Campana et al., 2008; Edwards & Badcock, 1995; Ledgeway & Smith, 1994; Pavan & Mather, 2008) we expected no interaction between first- and second-order motion in the cross-adaptation condition.

Methods

Apparatus

Stimuli were displayed on a Sony Trinitron 200PS monitor with a refresh rate of 75 Hz and generated with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1280×1024 pixels. The minimum and maximum luminances of the screen were 0.43 cd/m^2 and 93.57 cd/m^2 respectively. The mean luminance of the stimuli was 15.17 cd/m^2. Luminance was measured using 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.

Subjects

Two authors and six subjects who were unaware of the purpose of the study participated in both Experiments 1 and 2. Two authors and a new sample of ten subjects, naïve respect to the purpose of the experiment, participated in Experiment 3. Subjects sat in a dark room 57 cm from the screen. Viewing was binocular. They were instructed to fixate a point at the center of the screen and were given training at the beginning of each experiment to familiarize with the stimuli and task. All subjects had normal or corrected-to-normal visual acuity.

Stimuli

Stimuli were vertically oriented first- and second-order Gabor patterns. First-order Gabors consisted of sinusoidal luminance modulation of a dynamic noise carrier enveloped by a static Gaussian. The Gabors had a full width of 8 deg at half maximum amplitude. Formally the first-order Gabors used can be defined as:

$$G(x,y,t) = L\text{mean}\left\{0.5 \cdot \left[1 + \frac{m}{2}\sin(2\pi f_x x + 2\pi f_t t + \phi)\right] + C_n R(x,y,t)\right\}e^{-\frac{(x^2+y^2)}{\sigma^2}}, \quad (1)$$

where $G(x, y, t)$ represents the luminance at each point of the stimulus at the instant t, Lmean is the mean luminance of the resultant pattern, m is the modulation depth of the sinusoidal modulation (range 0–1), f_x is the spatial frequency (1 c/deg), f_t is the temporal frequency, ϕ is the phase shift of the sinusoidal modulation, C_n is Michelson contrast of the dynamic noise carrier $R(x, y, t)$. The noise carriers were generated by assigning each screen pixel (1.9 arcmin) a value between -1 and $+1$ with an equal probability. Dynamic noise was created by updating the noise carriers every phase shift of the sinusoidal modulation, subsequently referred to as "frame" for convenience. The Gaussian envelope is expressed by the exponential of Equation 1, where x and y represent the respective horizontal and vertical distances from the Gaussian peak and σ is the spatial constant of the Gaussian (3.2 deg). The Gaussian envelope was always static, whereas the sine wave drifted either leftward or rightward. Second-order Gabors consisted of sinusoidal contrast modulation of a dynamic noise carrier enveloped by a static Gaussian. A second-order Gabor can be defined as:

$$G(x,y,t) = L\text{mean}\{1 + 0.5 \cdot [1 + m\sin(2\pi f_x x + 2\pi f_t t + \phi)] \cdot C_n R(x,y,t)\}e^{-\frac{(x^2+y^2)}{\sigma^2}}, \quad (2)$$

where $G(x, y, t)$, Lmean, m, f_x, f_t, ϕ, C_n, $R(x, y, t)$ and σ had the same parameter values as in Equation 1. Equiluminant first- and second-order stimuli were used in order to ensure that contrast-defined motion did not contain any residual luminance (first-order) artifacts; each subject's equiluminance value was established using the procedures described below.

Procedures

The experiments involved four different steps (see also Pavan & Mather, 2008): (1) determining the contrast threshold; (2) estimating the subjective equiluminance point for second-order Gabors; (3) equating first- and second-order motion cues for salience; (4) the actual experiments involving the judgment of the direction of motion of a test pattern relative to the motion direction of

an adapting pattern. Subjects took part either in Experiment 1 (adapt and test with a first-order stimulus) and Experiment 2 (adapt and test using a second-order stimulus), or in Experiment 3 (adapt with a first-order and test with a second-order stimulus, and vice versa).

Contrast threshold (step 1)

A two-alternative forced-choice (2AFC) procedure was used to estimate the contrast threshold corresponding to 90% correct answers for motion direction, separately for first- and second-order stimuli. Two drifting Gabors were presented in succession at the center of the screen and drifted either rightward or leftward. Each of the Gabors was presented for 480 ms and was separated by a 480 ms inter-stimulus interval (ISI). To aid fixation the central part of the Gabor was replaced by a gray disk (0.7 deg in diameter) with the same mean luminance as the background (15.17 cd/m^2) and a white fixation point (0.16 deg) was present at the center of the gray disk for the entire stimulus duration. Motion direction was determined by shifting the phase of the sine-wave by ±90 deg every 80 ms, thus the Gabors drifted with a constant velocity of 3.12 deg/s. Observers pressed a response button to report whether the two Gabors drifted in the same or different direction.

The contrast of the Gabors, determined by the modulation depth of the sine wave, was varied adaptively using a maximum likelihood procedure (MLP; Green, 1990, 1993), while the contrast of the noise carrier was kept constant at 1.0 (Michelson contrast). We employed this procedure to track the 90%-correct point on the psychometric function. Each participant's measurement of the threshold was calculated at the end of a single block of 32 trials.

The contrast values used in the subsequent steps of the procedure were calculated by multiplying the obtained threshold contrasts by 4 to ensure the stimuli were clearly visible to the observer. The resulting modulation depths were: 0.42 Michelson Contrast (*SEM*: 0.04) and 0.98 Michelson contrast (*SEM*: 0.017) respectively for first- and second-order motion.

Minimum motion technique (step 2)

A minimum motion technique (see Anstis & Cavanagh, 1983; Nishida, Edwards, & Sato, 1997; Seiffert & Cavanagh, 1998) was used to find the subjective equiluminance value for second-order patterns. First- and second-order Gabors were presented at the center of the screen and interleaved in a four-frame sequence with a frame duration of 120 ms. First-order Gabors were presented in odd frames and second-order Gabors were presented in even frames (velocity: 2.08 deg/s). Each Gabor's sinusoidal modulation was shifted by 90 deg from frame to frame. As in the previous step the gray disc and

white fixation point were presented to aid fixation. Whilst the maximum luminance (*L*max) of the noise carrier was fixed at 93.57 cd/m^2 and mapped to +1, we varied the value of the minimum luminance (*L*min) of the noise carrier of the second-order frames. At −1 *L*min was 0.43 cd/m^2. In this way we produced a luminance imbalance in second-order frames between high-contrast and low-contrast strips. This luminance imbalance, paired with the luminance imbalance of the first-order frames, produced a net directional first-order motion in the four-frame sequence. We aimed to estimate for each subject the variation of *L*min of the second-order noise carrier required to null or cancel out any net directional motion. A simple Up-Down staircase (Levitt, 1971) controlled the minimum luminance of the noise carrier. The initial value of *L*min was 3.49 cd/m^2 (corresponding to −0.4 in the range −1 to +1). After the 1st, 3rd, 7th and 15th reversal of apparent direction the step size was halved, and after each halving of the step size the subsequent run was started with a *L*min value that was the average of the peaks and valleys of the preceding step size. On each trial (480 ms), subjects were asked to indicate the perceived motion direction, either leftward or rightward, using a button press, increasing the *L*min of the noise carrier when the observer perceived the pattern to move rightward and decreasing the *L*min for the opposite response. Testing was terminated after a total of 24 runs and the average of peaks and valleys of all the runs was taken as an estimate of the point of subjective equality (PSE; Finney, 1971; McKee, Klein, & Teller, 1985). Therefore PSE corresponded to the *L*min of the noise carrier of the second-order frames that produced a percept of ambiguous motion (mean PSE: 0.49 cd/m^2, *SEM*: 0.01). It should be noted that the variation of *L*min produced not just equiluminant second-order patterns, but also (as a side effect) a variation of the Michelson contrast of the noise carrier and consequently of the whole second-order patterns. However, the low PSEs estimated ensured that the contrast variations introduced in second-order patterns were very weak and substantially below threshold (mean: 0.011 Michelson contrast, *SEM*: 0.0038).

Equating stimuli for salience (step 3)

A possible complication of the stimulus was that although first- and second-order patterns were equated in terms of motion discriminability, they were not equated in terms of subjective pattern salience because first-order patterns appeared more salient. This could give rise to some differences in the judgments of the direction of the test pattern both when first- and second-order are presented separately and when they are tested in the cross-adaptation condition. Therefore, by using a variant of the minimum motion technique (Anstis & Cavanagh, 1983; Bressler & Whitney, 2006; Gurnsey, Fleet, & Potechin, 1998; Ledgeway & Smith, 1994; Pavan &

Mather, [2008]), we matched first-order and second-order Gabors' salience by adjusting the contrast (i.e., the modulation depth of the sine wave) of first-order Gabors to equate their saliency to that of second-order Gabors.

Subjects fixated a point at the center of the screen. First- and second-order Gabors were presented at the center of the screen and alternated in a six-frame sequence (frame duration was set at 80 ms), with first-order Gabors
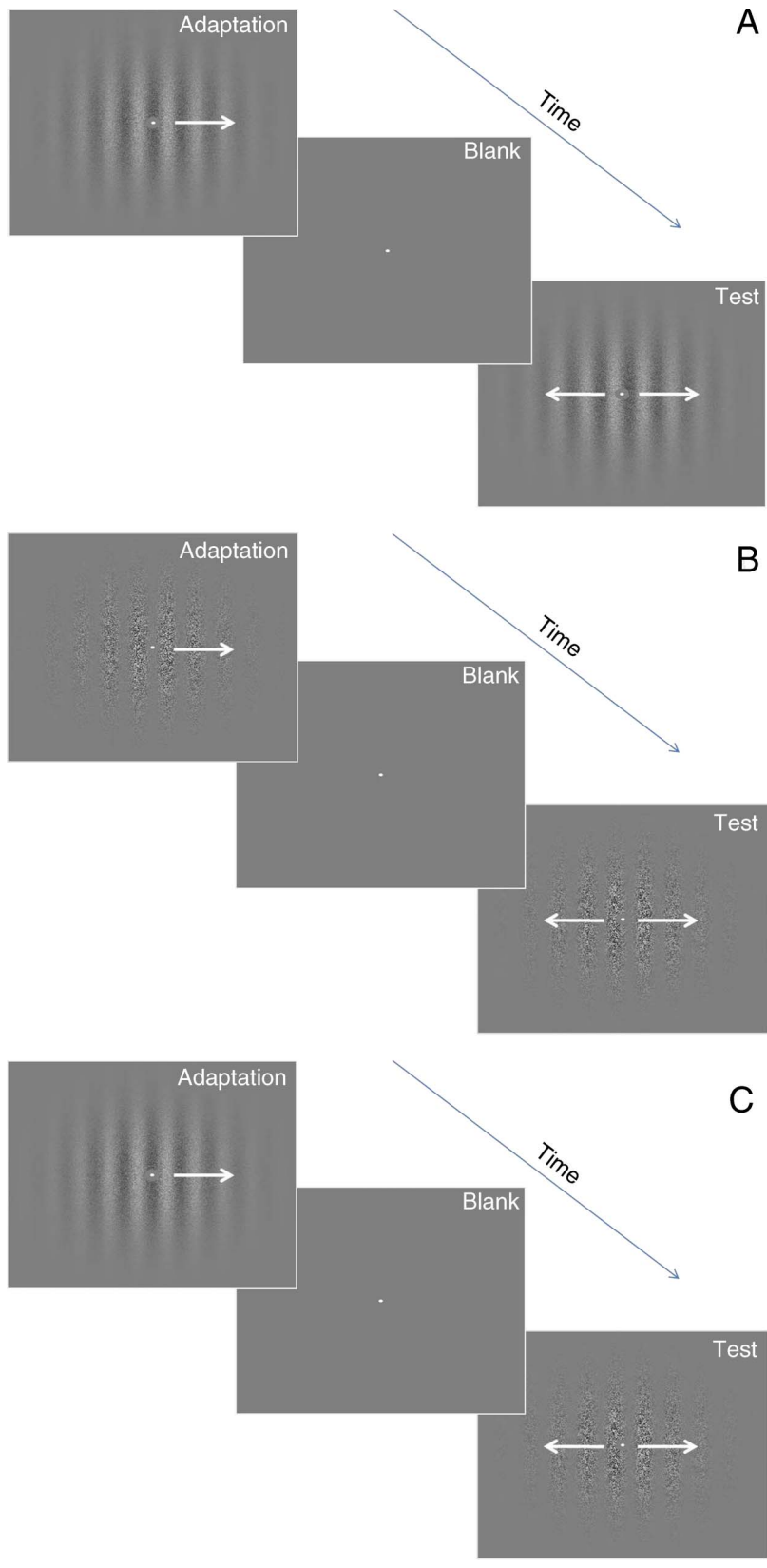
presented in odd frames and second-order Gabors presented in even frames. Each first-order Gabor's sinusoidal modulation was shifted by 90 deg (i.e., quadrature phase) on each appearance, and each second-order Gabor's sinusoidal modulation was shifted by a corresponding amount in the opposite direction on each appearance. We then adjusted the modulation depth of the sine wave in the first-order Gabor. For second-order Gabors, we used the modulation depth estimated in step 1 of the experiment multiplied by four, and the Lmin value of the noise carrier estimated in the step 2. We then varied first-order contrast from trial to trial according to a simple Up-Down staircase (Levitt, 1971). When the contrast of the first-order sine wave is set very low or zero, the perceived motion direction of the six-frame sequence follows that of the second-order sinusoidal modulation. We measured the adjusted contrast of the first-order sine wave required to null the unidirectional motion of the second-order stimulus, assuming that this contrast equated the salience between first-order and second-order stimuli (mean modulation depth for first-order stimuli: 0.55 Michelson contrast, *SEM*: 0.07).

Measuring directional biases (step 4)

In the step 4 of the experiment we assessed the temporal dynamics of the visual motion priming (VMP), motion aftereffect (MAE) and perceptual sensitization (PS) employing different adaptation periods and inter-stimulus intervals (ISI) (Kanai & Verstraten, 2005). To aid fixation we used the same configuration that was used in the previous steps of the experiment. Both directional and ambiguous stimuli were created by shifting the phase of the sinusoidal modulation. A horizontal directional stimulus was created by shifting the phase left or right (±90 deg). This phase shift was chosen because Pinkus and Pantle (1997) showed that the visual motion priming is maximum at a 90 deg phase shift. Ambiguous test patterns were created by shifting the phase 180 deg every 80 ms.

Figure 1. Trial sequence for (A) first-order stimuli, (B) second-order stimuli and (C) cross-order stimuli (the picture shows only the case in which adaptation is a first-order drifting Gabor patch and test is a second-order drifting Gabor patch. However, in the experiment we used also the reciprocal condition). For all the experiments the adaptation stimulus was always directional apparent motion obtained by shifting the phase of the sinusoidal modulation by ±90 deg. After a variable adaptation period of 80, 160, 320 or 640 ms, a blank screen was presented for 40, 120, 480, 1000, 2000 or 5000 ms, during which the fixation point was always present. After the blank interval an ambiguous test pattern was displayed. Ambiguous motion was obtained by shifting the phase of the sinusoidal modulation by 180 deg. The duration of the test stimulus was always constant (80 ms × 4 frames = 320 ms). For illustrative purposes the Gabors patches reported here have sinusoidal modulations with exaggerated contrast.

Velocity of the test stimuli was equal to that of the adaptation stimulus (6.25 deg/s). In step 1 of the experiment we used a drift velocity of 3.12 deg/s to facilitate the task at low contrast levels.

Derrington and Goddard (1989) found that at low contrast, direction discrimination is highly accurate when the stimulus has a long duration (e.g., 108 ms) and a low temporal frequency (e.g., 2 Hz). Accuracy is also high for a brief duration (e.g., 27 ms) with a high temporal frequency (e.g., 8 Hz). Thus, the temporal frequency (that, being the spatial frequency of our stimuli 1 c/deg, corresponds to the velocity) and the stimulus duration that we used in step 1 are sufficient for reliable contrast threshold estimation. Also in step 2 and 3 of the experiment we used a lower temporal frequency (3.12 and 2.08 Hz respectively) to that employed in step 4. Our pilot observations indicated that when first- and second-order frames were quickly interleaved at 6.25 Hz, the motion sequences looked jerky and the observers found it difficult to make a direction discrimination task. Indeed, employing a similar technique, also Ledgeway and Smith (1994) used a low velocity (4.2 deg/s), although higher than ours. However, the phase shift of the sinusoidal modulations was equal across all the experimental steps (±90 deg), except the phase shift of the test pattern in step 4. The motion direction of the adaptation stimulus was balanced and randomized across trials. Four adaptation durations were used: 80, 160, 320, and 640 ms. After a variable ISI (40, 120, 480, 1000, 2000 and 5000 ms) during which the display was blank (except the fixation point, that was present also during the ISI), an ambiguous test pattern was presented for 320 ms (Figure 1). Subjects judged whether the test stimulus was moving in the same direction or opposite to the adaptation pattern. For first- and second-order stimuli presented separately there was a total of 24 conditions; 4 (adaptation durations) × 6 (ISIs), whereas for cross-order motion there were 48 conditions; 2 (adapting to first-order and test with second-order motion, adapting to second-order and test with first-order motion) × 4 (adaptation durations) × 6 (ISIs). Twenty trials were performed for each condition, and the order of conditions was randomized across trials.

Results

A repeated measures ANOVA did not show a main effect of the motion order [$F(1,7) = 0.510$, $p > 0.05$], nor any significant interaction involving the motion order. This means that the time courses of the directional biases found for first- and second-order moving stimuli (Figures 2 and 3) are very similar. However, in order to investigate in detail the characteristics of rapid adaptation with each of the two types of motion, we performed separate analyses on the results obtained for first- and second-order motion
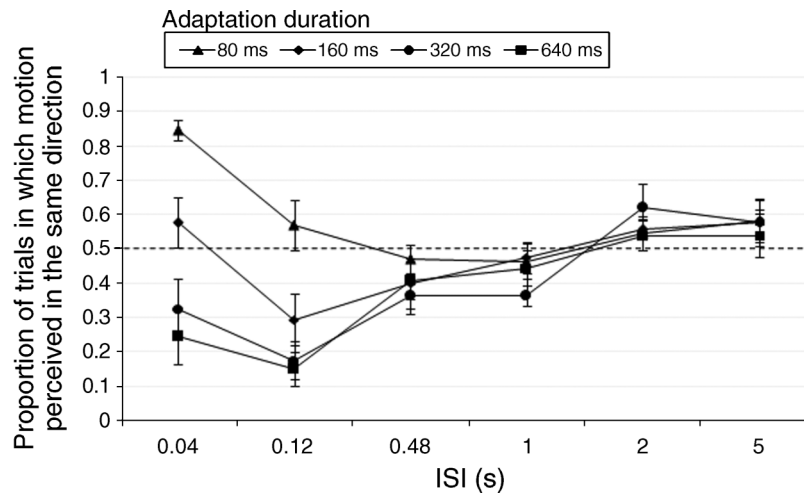
Figure 2. Results from Experiment 1 (first-order moving patterns; *N* = 8). For each adaptation duration the proportion of trials in which observers judged the test stimulus as drifting in the same direction as the adaptation stimulus is shown as a function of the inter-stimulus interval duration (ISI). The results are shown for four adaptation durations; 80 ms (solid triangle), 160 ms (solid diamond), 320 ms (solid circle), and 640 ms (solid square). See text for details about the results. Error bars ±1 *SE*.

cues. We used a repeated measures ANOVA in order to test the significance of main effects and interactions (Bonferroni-corrected *t*-tests were used for pairwise comparisons). We also performed a series of one-sample *t*-tests to assess if each condition was significantly different from chance level. Multiple one-sample *t*-tests were corrected using the False Discovery Rate procedure (Benjamini & Hochberg, 1995; Benjamini & Yekutieli, 2001).

First-order motion

Figure 2 shows the results for first-order motion. We plotted the proportion of trials in which the ambiguous

test pattern was perceived to drift in the same direction to that of the adaptation pattern, as a function of the duration of the ISI. A repeated measures ANOVA showed a significant main effect of the adaptation duration [$F(3,7) = 20.05$, $p < 0.01$], a significant main effect of the ISI [$F(5,7) = 6.92$, $p < 0.01$], and a significant interaction between adaptation and ISI [$F(15,7) = 5.82$, $p < 0.01$]. Pairwise comparisons revealed a significant difference between adaptation at 80 ms with respect to the other adaptation periods ($p < 0.05$) for ISIs of 40 and 120 ms, whereas we did not find any significant difference between adaptation at 80 ms and the other adaptation durations over the other ISIs. No significant differences were found between the longer adaptation durations (160, 320, and 640 ms) across all the ISIs tested.
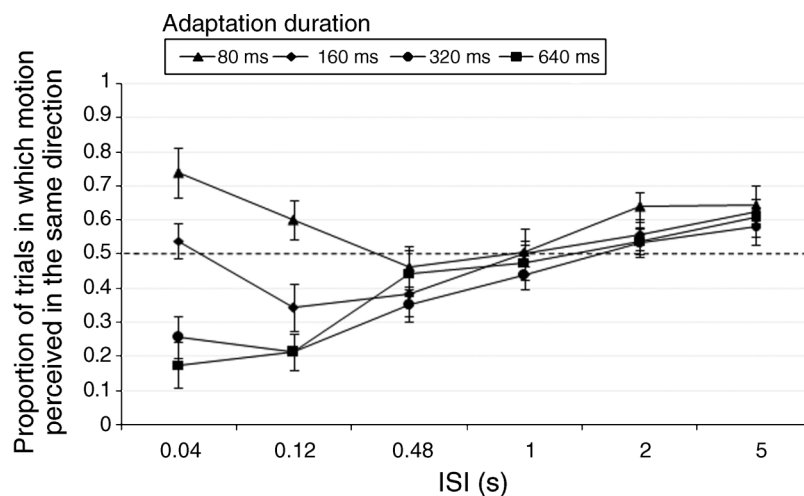

Figure 3. Results from Experiment 2 (second-order moving patterns; *N* = 8). For each adaptation duration, the proportion of trials in which observers judged the test stimulus as drifting in the same direction as the adaptation stimulus is shown as a function of the ISI duration. The results are shown for four adaptation durations; 80 ms (solid triangle), 160 ms (solid diamond), 320 ms (solid circle), and 640 ms (solid square). See text for details about the results. Error bars ±1 *SE*.

To further distinguish whether a particular combination of adaptation and ISI induced priming (facilitation) or motion aftereffect (suppression) we performed a series of one-sample *t*-tests for each combination of adaptation duration and ISI.

We found that using an adaptation period of 80 ms with an ISI of 40 ms the perceived direction of the ambiguous test pattern was significantly biased towards the direction of the adaptation stimulus (84% of response in the same direction) $[t(7) = 11.26, p < 0.01]$, resulting in a rVMP. In the first-order condition we did not find any other priming effect, though there was a weak tendency towards facilitation for longer ISIs of 2 or 5 s (Perceptual Sensitization), but only for adaptation duration of 320 ms.

Upon increasing adaptation duration we found that the perceived direction of the ambiguous test pattern was biased towards the opposite direction to that of the adapting stimulus (rMAE). In particular, adapting for 320 ms produced a significant bias opposite the motion direction of the adaptation stimulus after 120 ms (17% of response in the same direction) $[t(7) = -5.99, p = 0.001]$ and 1 second (36% of response in the same direction) of ISI $[t(7) = -4.66, p = 0.002]$. Adapting for 640 ms also produced a bias towards the opposite direction of the adapting stimulus after 120 ms of ISI (15%) $[t(7) = -7.13, p < 0.001]$.

Second-order motion

Figure 3 shows the results obtained for the second-order condition. We found a pattern of results very similar to that found with first-order stimuli: a repeated measures ANOVA showed a significant main effect of the adaptation $[F(3,7) = 15.48, p < 0.01]$, a significant main effect of the ISI $[F(5,7) = 8.56, p < 0.01]$, and a significant interaction between adaptation and ISI $[F(15,7) = 5.08, p < 0.01]$. Pairwise comparisons revealed no significant differences between adaptation at 80 ms and 160 ms ($p > 0.05$) for ISI of 40 ms, whereas we found significant differences between the adaptation at 80 ms and the adaptation at 320 ($p = 0.007$), and between adaptation at 80 ms and 640 ms ($p < 0.05$), both for ISIs of 40 ms. In addition, we found a significant difference between the adaptation at 160 ms and the adaptation at 640 ms for ISIs of 40 ms. We also found significant differences between the adaptation at 80 ms and the other adaptation durations for the 120 ms ISI ($p < 0.05$), but no other significant differences between the other adaptation durations for the same ISI, nor for ISIs longer than 120 ms. Also for second-order stimuli we conducted one-sample *t*-tests in order to assess if a particular combination of adaptation and ISI gives a significant bias either towards the same or different direction with respect to the adaptation pattern. Adapting for 80 ms to a second-order stimulus and presenting an ambiguous second-order test pattern after an ISI of 40 ms produced a significant bias towards the

direction of the adaptation pattern $[t(7) = 3.28, p < 0.05]$ (73% of responses in the same direction) (rVMP). Moreover, we obtained a significant bias towards the adapting direction at 80 ms with an ISI of 2 seconds $[t(7) = 3.27, p < 0.05]$ even though the percentage of responses in the same direction is quite low (63% of same responses) (PS). Similarly, adapting for 160 ms biases the perceived direction of the test pattern towards the direction of the adapting stimulus, but only with an ISI of 5 s $[t(7) = 3.31, p < 0.05]$, even if the magnitude of the effect was quite small (63% of same responses) (PS). Longer adaptation durations biased the perceived direction of ambiguous second-order patterns to the opposite direction of the adapting stimulus resulting in rMAE. In particular, adapting for 320 ms biased the perceived position in the opposite direction across the shorter ISI durations; that is, 40 ms (25% of same responses) $[t(7) = -3.96, p = 0.005]$, 120 ms (21% of same responses) $[t(7) = -5.49, p = 0.01]$ and 480 ms (35% of same responses) $[t(7) = -3.24, p < 0.05]$. Similar results were obtained adapting at 640 ms. Indeed, we found significant biases opposite the direction of the adapting pattern only for the shorter ISIs: 40 ms (17% of same responses) $[t(7) = -4.77, p = 0.002]$ and 120 ms (21% of same responses) $[t(7) = -5.40, p = 0.001]$. These multiple one-sample *t*-tests pointed out slightly different time courses about rVMP, rMAE and PS for first- and second-order motion. However, it should be noticed that we did not obtain a significant effect of the motion order (either as a main effect or as interaction), suggesting that the differences obtained between first- and second-order motion are indeed very small.

To summarize, for first- and second-order stimuli presented separately, a brief adaptation period of 80 ms biased the perceived direction of a subsequent ambiguous test pattern to the same direction of the adapting stimulus resulting in a rapid form of motion priming (rVMP), whereas longer adaptation periods (320 and 640 ms) biased the perceived direction of the ambiguous test pattern away from the direction of the adaptation pattern, resulting in rMAE. These directional biases arose and decayed rapidly within half a second.

Moreover, we found perceptual sensitization (PS) effects using second-order motion, whereas no significant effects for first-order motion stimuli, though the presence of a weak tendency.

Cross-order motion

Since the results for first- and second-order motion were similar, in the cross-order condition we tested whether a single mechanism or two distinct mechanisms could account for the effects obtained presenting the two motion cues separately. The results for the cross-adaptation condition are shown in Figure 4. A repeated measures ANOVA did not reveal a significant effect of the motion order used for adaptation $[F(1,11) = 3.99, p > 0.05]$. We then analyzed
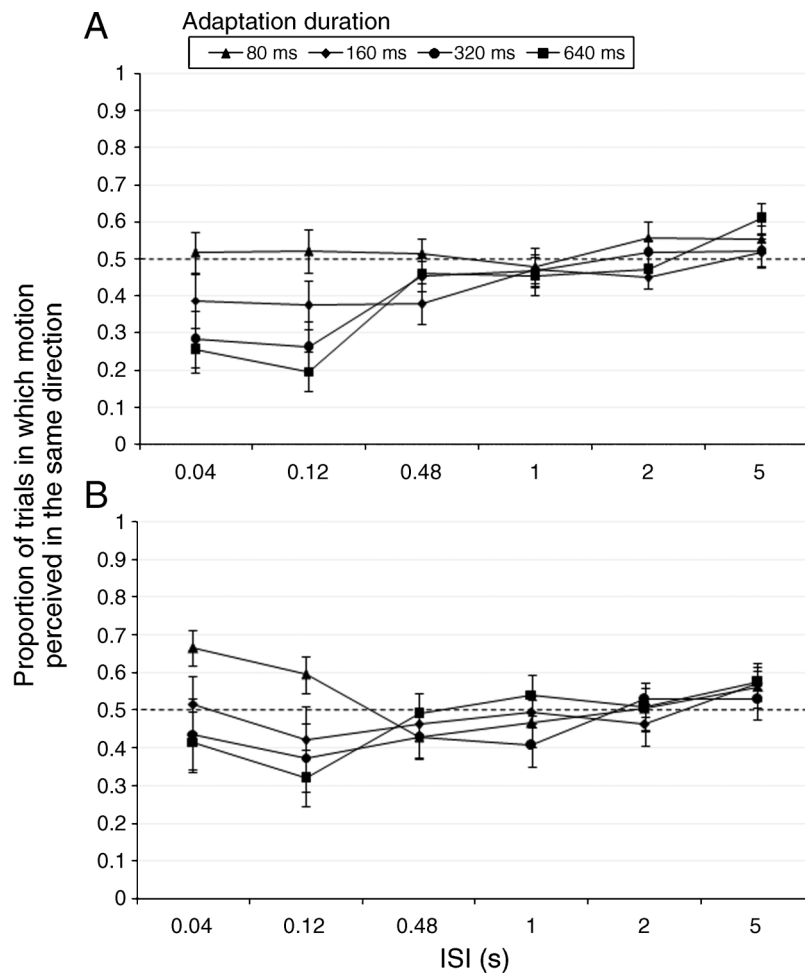
Figure 4. Results from Experiment 3 (cross-order adaptation; N = 12). As in Experiments 1 and 2, for each adaptation duration, the proportion of trials in which observers judged the test stimulus as drifting in the same direction as the adaptation stimulus is shown as a function of ISI. The results are shown for four adaptation durations: 80 ms (solid triangle), 160 ms (solid diamond), 320 ms (solid circle), and 640 ms (solid square). (A) Results from the condition in which adaptation was a first-order drifting Gabor and test was a flickering second-order Gabor. (B) Results from the condition in which adaptation was a second-order drifting Gabor and test was a flickering first-order Gabor. See text for details about results. Error bars ±1 SE.

separately the results obtained adapting to first-order and testing with second-order and the results obtained adapting to second-order and testing with first-order.

Adapting to first-order and testing with second-order (Figure 4A) we found a main effect of adaptation [$F(3,11)$ = 11.45, $p < 0.01$], a significant effect of the ISI [$F(5,11)$ = 5.39, $p < 0.01$] and a significant interaction between adaptation duration and ISI [$F(15,11)$ = 4.99, $p < 0.01$]. Pairwise comparisons showed a significant difference between adaptation at 80 ms and other adaptation durations for the shorter ISI (40 ms) ($p < 0.05$). For the second level of ISI (120 ms) we found a significant difference between the adaptation at 80 ms and the other adaptation periods ($p < 0.05$). We did not find any other significant difference between adaptation periods for the other ISIs used. We also conducted one-sample t-tests to ascertain whether the obtained bias were significantly different from chance level.

Adapting to first-order and testing with second-order motion we only found rapid forms of motion aftereffects (rMAE) (rather than rVMP), in particular when: (i) adapting at 320 ms and at ISIs equal to 120 ms [$t(11)$ = −3.42, $p < 0.001$] (26% of same responses), (ii) adapting at 640 ms and with an ISI of 40 ms [$t(11)$ = −4.11, $p < 0.01$] (25% of same responses) and (iii) adapting at 640 ms and with an ISI of 120 ms [$t(11)$ = −5.68, $p < 0.001$] (19% of same responses).

The same statistical analyses were conducted for the condition in which we adapted to second-order and tested with first-order (Figure 4B). Here we only obtained a significant interaction between adaptation time and ISI [$F(15,11)$ = 3.58, $p < 0.01$]. Pairwise comparisons highlighted a significant difference between adaptation at 80 ms and adaptations at 320 and 640 ms, but only for the ISI at 120 ms. On the other hand, one sample t-tests did not show any significant effect. In summary the

cross-adaptation condition it reveals that, when using rapid forms of adaptation and short ISI, first-order motion can influence the processing of second-order motion, giving rise to rapid forms of MAE, whereas second-order motion appears not to influence the processing of first-order motion.

Discussion and conclusions

The results obtained with first- and second-order motion presented separately are very similar and are in general agreement with the findings obtained by Kanai and Verstraten (2005). We showed for both first- and second-order motion the presence of three different effects: (i) rapid form of visual motion priming (rVMP), (ii) rapid motion aftereffect (rMAE) and (iii) perceptual sensitization effects (PS) (i.e., facilitations obtained with ISIs ≥ 2 seconds). In particular, we found that adaptation of 80 ms biased the perceived motion direction of the ambiguous test pattern towards the same direction to that of the adaptation pattern, but only with a very short ISI (i.e., 40 ms), resulting in a rapid form of motion priming in concurrence with Pinkus and Pantle (1997).

However, using slightly longer adaptation duration (320 and 640 ms) and short ISIs (less than 120 ms), the perceived direction of the test pattern was biased to the opposite direction of the adaptation pattern. Thus, rVMP and rMAE occurred with the same stimulus configuration, producing two opposite effects due to a slight change in adaptation duration. An interesting finding was that short adaptations worked as prime, whereas a longer adaptation had an opposite effect. We found that these effects arise and decline within half-a-second of the inter-stimulus interval. In addition, Kanai and Verstraten (2005) found that using longer ISIs the perceived direction of the test was biased again towards the direction of the adaptation pattern, resulting in facilitation that took time to arise (PS). In our experiment we also used longer ISI durations, obtaining only a weak tendency in such direction with first-order motion, and a significant PS for the shorter adaptation durations (80 and 160 ms) and for the longer ISIs (2 and 5 seconds) with second-order motion, though these effects were very weak in comparison to those obtained by Kanai and Verstraten (2005). We argue that the randomization that we employed might have weakened or masked the PS effect. Kanai and Verstraten (2005) used only one adaptation duration to investigate the time course of PS. It is possible that subjects learned to respond to the test pattern as drifting in the same direction to that of the adaptation pattern in correspondence of the longer ISIs, because of the similarity of the percept evoked across trials. Indeed the PS effect could be sensitive to attentional influences and strategies, since it probably involves high level areas. The data of Kanai and

Verstraten (2005) in Experiment 3, Figure 3A, show that from 3 to 5 seconds the PS effect reaches a plateau of about 70% of "same answer". Moreover it should be noted that this is valid for both ambiguous and directional adaptation conditions. We argue that using four different adaptation durations within the same block makes it harder for observers to employ response strategies, since the four adaptation durations produce very different perceptual outcomes when combined with the shorter ISIs. Nonetheless, we obtained slightly weaker PS effects in both first- and second-order motion conditions. The results for the rapid effects and PS were very consistent across observers.

At which neural locus/loci do these effects take place? Kanai and Verstraten (2005) also found that both rVMP and rMAE are absent after adaptation to a counterphase flickering pattern (i.e., to energy-balanced motion). The authors distinguished two stages: (i) an early stage in which motion units detect local motion energy of the stimulus and, (ii) a later stage which is related to perceptual decision-making based on the integration of the local motion signals. They suggested that a counterphase grating should activate motion detectors for opposite directions simultaneously at the early stage. However, observers usually perceive only one of the two directions. They argued that this perceived direction is determined at the later stage. Indeed, Williams, Elfar, Eskandar, Toth, and Assad (2003) found that the responses of many direction-selective neurons present in parietal cortex were predictive of the monkey's perceived direction of perceptually ambiguous motion. They found a high percent of these neurons within LIP, less in area MST, and none in area MT. Williams et al. (2003) argued that the relationship between parietal activity and the perceived direction could reflect attentional modulation. Thus, the reasoning behind using ambiguous motion during adaptation (Kanai & Verstraten, 2005) was to bypass the directional biases induced by adaptation in the early stage motion detectors. Since the local motion energy of ambiguous motion is balanced between the two opponent directions, exposure to ambiguous motion should not cause a directional bias at the early stage. If rVMP and rMAE occur at late stages, these effects should be observed even when the adaptation does not contain net directional motion. Otherwise, if these effects depend on the early stage of motion analysis no rVMP and rMAE should be observed. The results showed no rVMP and rMAE adapting to energy-balanced motion, suggesting that these two effects reflect facilitation (potentiation) and suppression (inhibition) at an early stage of motion processing.

The rapid forms of motion priming and motion aftereffect found in this study are induced by very brief adaptation duration. Since these effects arose and decayed in less than 1 second, they appear to involve different neural substrates with distinct rapid plasticity with respect to the classic MAE, which is generally obtained after adapting for several seconds (see Mather, Verstraten, &

Anstis, 1998 for a review), and classical motion priming (Campana et al., 2002, 2006, 2008; Kristjánsson, 2009). These rapid forms of neural plasticity might take place in the early motion processing stage responsible for motion energy detection.

Since we obtained similar results for second-order motion, we assume the presence of similar mechanisms for this kind of motion perception. In particular, brief exposure to a second-order, contrast-modulated moving pattern might reflect adaptation in second-order motion detectors present at low-level of motion processing. A number of electrophysiological studies in cats and monkeys indicate visual areas V2 and V3 as the first stage in which there is a high percentage of neurons that respond to second-order motion, showing a directional and orientation selectivity (Barraclough, Tinsley, Webb, Vincent, & Derrington, 2006; Leventhal, Wang, Schmolensky, & Zhou, 1998).

Thus, both first- and second-order rVMP and rMAE might reflect fast adaptation at the early stages of motion analysis in V1, V2 and V3. In addition, some electro-physiological studies suggest that for first-order motion the rapid suppression responsible for the rMAE and the rapid form of facilitation responsible for the rVMP take place even at the synapses from LGN to V1 (Carandini, Heeger, & Senn, 2002; Chance et al., 1998; Chung, Li, & Nelson, 2002).

What is the functional role and the underlying mechanism to brief adaptation? A study by Greenlee, Georgeson, Magnussen, and Harris (1991) investigated the time required for recovery from contrast adaptation. They adapted observers to first-order gratings flickering at 5 Hz, with durations ranging from 1 second to 1000 seconds at various contrast values. They found that time to recovery depended on adaptation duration and not on the contrast of the adaptation stimulus. In particular, increasing the adapting contrast increased the initial threshold elevation but did not significantly increase the time required to recover from adaptation. From these results the authors argued that contrast adaptation is a *short-term memory store* where the effects of adaptation persist for a length of time proportional to the adapting time. Greenlee et al. (1991) argued that these contrast adaptation effects could be mediated by a contrast gain control mechanism. Indeed, there is neurophysiological evidence from cats (Ohzawa, Sclar, & Freeman, 1985) and monkeys (Sclar, Lennie, & DePriest, 1989) that cortical cells adjust their gain to the prevailing contrast level. In a previous study Greenlee and Heitger (1988) showed that, after adaptation to a high contrast grating, contrast discrimination improved for gratings of high contrast. The authors account for such an improvement in terms of a contrast response function that shifts its operating range, increasing the slope, and thus the sensitivity of the function in the other range. This suggests the presence of a mechanism that responds quickly to the fast changes in contrast.

Moreover, such fast changes are evident for short adaptation times (Greenlee et al., 1991).

Greenlee et al. (1991) suggested that another possible functional role of contrast gain control in visual channels might be the "*self-calibration*" of the visual system. That is, if a visual feature is coded by a certain number of channels, the activity of these channels might vary due to the presence of errors in the visual system. In this case, the gain of individual channels could be adjusted to minimize these errors. When we adapt a specific dimension of a visual stimulus such as motion direction, the initial rise in the activity and the persistence of the enhanced activity of a certain channel leads to a reduction in its gain and thus to subsequent aftereffects, or to an enhancement in its gain if the adaptation duration is very brief, generating facilitation. This idea implies that each visual channel carries a trace of its past activity averaged across time. Therefore, according to Greenlee et al. (1991) there could be two functional roles for adaptation to spatial contrast: (i) the short-term change in gain which shifts the operating range of the channel into the prevailing range of contrasts to maximize contrast resolution; (ii) a long-term mechanism which compensates for the effects of constant errors, or drifts, in the performance of visual channels. Such short- and long-term mechanisms could be responsible for the rMAEs and the facilitation effects that arise for long ISIs (PS).

These mechanisms, could operate together to originate and maintain a "record" of past activity in channels that influence the perception of the ambiguous test pattern. Such a contrast gain control mechanism varies not only as a function of the adaptation duration, but also as a function of the ISI duration.

For rVMP, Pinkus and Pantle (1997) proposed a model based on motion energy detectors (Adelson & Bergen, 1985; Pantle & Turano, 1992; Strout, Pantle, & Mills, 1994). The first stage of the model consisted of direction-ally selective detectors. Once the opponent energy has been calculated as the difference between the outputs of the rightward and leftward motion energy units, in a second stage the directional imbalance is delayed by a low-pass temporal filter. Such a temporal filter is necessary otherwise any directional imbalance would disappear before the ambiguous sequence occurs. Indeed, as we and other have found, rVMP drops within 500 ms (Anstis & Ramachandran, 1987; Ramachandran & Anstis, 1983). Without the temporal filter stage, the directional stimulus could not bias the direction of a subsequent ambiguous stimulus, especially if the ambiguous stimulus is delayed for a period longer than the temporal impulse response of the motion energy units. Thus, any directional imbalance in the first stage is extended in the second stage filter, making the directional signal available for integration with a balance signal produced by an ambiguous stimulus. Such integrated opponent energy causes the ambiguous motion stimulus to be seen in the same

direction as the unambiguous motion. However, according to findings of Derrington and Goddard (1989) a static saturating nonlinearity should be added to the model. They found that, at low temporal frequencies (2 Hz) and short durations (27 ms), direction discrimination improves when increasing the contrast of a sine wave grating but only when the contrast was low. On the contrary, at higher contrasts direction discrimination declines with increasing contrast. However, the authors also showed that using higher temporal frequencies (8 Hz) or longer durations (108 ms) of the stimulus, the decline of the direction discrimination at high contrasts was absent. They explained these findings by proposing a model in which two direction-selective filters tuned to opposite directions pass through a saturating nonlinearity. These outputs are then subtracted to obtain opponent motion. The authors proposed that the output of the first-stage of the model can be simply obtained by integrating the product of the temporal frequency spectrum of the stimulus and the temporal tuning characteristics of the direction-selective filters. Note that a brief stimulus of 27 ms, for example, has a very broad temporal frequency spectrum. Moreover, if this stimulus moves only at 2 Hz, its spectrum will spread 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 contrast 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. In this case the saturation removes the inequality between the outputs of the detectors at the first-stage. Hence, at the first stage, detectors tuned to opposite direction would respond almost equally to the stimulus. This decrement in simple motion direction discrimination could affect, as a consequence, more complex effects such as rVMP or rMAE. Indeed, Pinkus and Pantle (1997) found that increasing the contrast of the directional stimulus, rVMP reached a plateau. However, if the stimulus has high temporal frequency or long durations for example, the response of the first stage of motion detectors will be unequal and very different and direction discrimination will be unaffected at high contrast. This is because the difference in response between the first-stage filters is too large to be cancelled by saturation, though saturation is still present. Indeed, the relatively long stimulus durations (>80 ms) and/or the relatively high temporal frequency (6.25 Hz) should have prevented any decrement of performance due to the high contrast and the resulting saturation.

Kanai and Verstraten (2005) argued that a later stage of motion analysis appears to be involved in PS. We found only a tendency for first-order motion, and weak perceptual sensitization effects using second-order motion (i.e., adapting at 80 and 160 ms, after ISIs of 2 and 5 seconds respectively). It seems that such an effect involves a later stage of motion analysis such as MT. Indeed this effect is

characterized by a gradual development of potentiation, and no decay at least up to 5 seconds. This facilitation could be considered as a motion priming effect that arises after long ISIs. This hypothesis is supported by recent findings of Campana et al. (2002, 2006, 2008) and Huang, Holcombe, and Pashler (2004). In particular, Huang et al. (2004) argued that priming can occur at a later stage in the perceptual process, reflecting an episodic memory representation of the preceding trial. It is possible that adaptation helps build an episodic memory representation of the motion direction of the pattern.

Such a representation is built over time and can influence the perceived motion direction of the ambiguous test pattern presented after several seconds. Such episodic memory trace might be maintained through long adaptation-test blank intervals by a long-term compensation mechanism, which adjusts the gain of the channels stabilizing the percept of the ambiguous test stimulus as described by Greenlee et al. (1991). Alternatively, shorter ISIs could block or interfere with the building of such episodic representation. Using TMS Campana et al. (2002, 2006) found that motion priming with ISIs greater than 2 seconds depends on the functional integrity of area MT. This suggests that progressively increasing the period between prime (i.e., in this case the adaptation) and probe (i.e., the ambiguous test stimulus) the locus of representation of priming could shift at intermediate or very high levels of elaboration. This is also supported by a recent study of Campana et al. (2008), who found that motion priming exists and is dependent upon the spatial position with both first- and second-order motion. However, with cross-order motion priming the effect was much smaller and not bound to the spatial position. This suggests (i) a partial independence of the mechanisms subserving motion priming with first- and second-order-motion, and (ii) a shift of the neural locus mediating this effect, depending on the stimuli used, from low-levels retinotopically organized, to higher levels where the retinotopical organization is lost or at least very coarse.

However, it is not clear why we found perceptual sensitization only for the briefer adaptation durations employed in second-order motion, and no effects within the first-order domain. Perhaps, as outlined above, the procedure employed in this experiment is non-optimal to isolate such a slow effect.

Since we obtained similar results for first- and second-order motion, we ran a cross-adaptation condition in order to assess how the visual motion system combined and integrated these two motion cues, and if a single mechanism was responsible for the effects obtained using first- and second-order motion presented separately.

Overall, we found that cross-order adaptation produced a much weaker and asymmetric transfer for rVMP and rMAE further suggesting some degree of separation between first- and second-order motion mechanisms. In particular, first-order motion seemed to influence the processing of second-order motion. Indeed, when we

adapted to first-order and tested with second-order, we found rMAEs (but not rVMP or PS), although this effect was much weaker than that obtained in the within-order conditions. On the contrary, second-order motion did not influence the processing of first-order motion. Schofield, Ledgeway, and Hutchinson (2007) found similar interactions using dynamic MAE and employing longer adaptation durations. They tested the transfer of the dynamic MAE using counterphasing flickering test patterns between first-order motion stimuli and second-order motion stimuli. They found strong dynamic MAEs (tuned for spatial frequency) when the adaptation and test patterns were of the same type. There was also a partial transfer of the dynamic MAE when the adaptation pattern was first-order and the test pattern was second-order, though such transferred effect did lose its spatial frequency tuning, yet there was little or no transfer from second-order to first-order patterns.

Since we matched our first- and second-order motion stimuli for saliency, our results cannot be due to an imbalance of salience between the two types of stimuli. Moreover, we used dynamic test patterns which are considered to be more sensitive measure of MAE than static test patterns to. Indeed, Kanai and Verstraten (2005) showed that static test patterns did not induce rVMP and rMAE.

The asymmetric transfer between first-order and second-order motion found in this experiment could be due to the hierarchical organization between first-order and second-order motion systems. The first-order motion system operates at both low- and high-levels of motion analysis, and appears to influence the perception of second-order motion, whereas the second-order motion system seems to operate mostly at intermediate- and high-levels of motion processing and does not influence the processing of first-order motion. It should be noted, however, that first-order motion influences second-order motion only for adaptation durations equal or higher than 320 ms, defining a temporal constraint within which first-order motion signals can influence second-order motion signals. Taken together these results suggest some degree of separation between first-order and second-order motion. The mechanisms that process first- and second-order motion signals appear to be separated from the earlier stage of motion processing (V1, V2/V3) up to and including the level at which global motion is extracted (i.e., MT). Using a global motion stimulus, Edwards & Badcock (1995; see also Badcock & Khuu, 2001) assessed whether first- and second-order signals are integrated at the level of area MT (Baker, Hess, & Zihl, 1991). On each trial a small proportion of dots moved coherently in the same direction while the others moved randomly. The percentage of coherently moving dots was varied to determine threshold. The observers' task was to judge the motion direction of the coherently moving dots. The result showed that, whereas adding first-order dots impaired the ability to extract second-order global-motion,

adding second-order dots did not impair the ability to extract first-order global motion.

This asymmetry was due to the fact that first-order dots also had a contrast envelope which represents a second-order signal. Thus, while both motion systems detect the movement of the luminance-increment dots, only the second-order motion system would detect the movement of second-order dots. Indeed, the additional second-order dots increased the threshold for the second-order system but not for the first-order system and, consequently, the threshold level for first-order dots was unchanged.

This result suggests that the first- and second-order systems are still separate at level in which global motion is extracted (MT).

The task and the stimulus configuration that we employed investigated low-levels (V1, V2/V3) and intermediate levels (MT) of motion processing. Despite the presence of some weak 'cross-talk' along the motion processing pathway, it seems that first- and second-order motion are not well integrated or combined. However it is still possible that integration occurs at higher neural substrates.

Acknowledgments

Corresponding author: Andrea Pavan.
Email: andrea.pavan.1@unipd.it.
Address: Department of General Psychology, University of Padua, Via Venezia 15, 35131, Padua, Italy.

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