A motion aftereffect seen more strongly by the non-adapted eye: evidence of multistage adaptation in visual motion processing

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Abstract

We found that the motion aftereffect measured using a directionally ambiguous counterphase grating (flicker MAE) can be stronger when it is measured for the non-adapted eye than when measured for the adapted eye. The monocularly viewed adaptation stimulus was the movement of a missing-fundamental grating (2f + 3f motion), for which the movement of the higher-order spatial structure was dominantly perceived, while the first-order structure was physically moving in the opposite direction. For observers who perceived the MAE consistently in the direction opposite to the movement of the higher-order structures, the MAE was larger for the non-adapted eye than for the adapted eye. This finding of ‘over-100% transfer’ invalidates the standard view that the IOT is a direct measure of the binocularity of the adapted neurones. In addition, the finding provides convincing support for the hypothesis that the flicker MAE reflects adaptation at multiple processing stages © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

1.1. Interocular transfer

Visual aftereffects occur even when the adaptation and test stimuli are presented to different eyes, and psychophysical assessments of the ocularity of the mechanisms underlying this interocular transfer (IOT) have provided insights into where in the visual stream these aftereffects are produced. The magnitude of an IOT, defined as the aftereffect strength measured for the non-adapted eye relative to that measured for the adapted eye, has been reported to range from 0% (no transfer) to 100% (perfect transfer) (Mitchell et al., 1975; Moulden, 1980; Raymond, 1993), a range consistent with the fact that neurone ocularity ranges from purely monocular to perfectly binocular. Such a direct relationship between the IOT and neurone ocularity, however, may collapse when the aftereffect reflects adaptations of multiple mechanisms that inspect different aspects of the stimulus. The results of the recent studies on the motion aftereffect (MAE), reviewed below, suggested to us that the MAE produced by a specific combination of adaptation and test stimuli would be stronger for the non-adapted eye than the adapted eye. Here, we report that this effect, which can be called ‘over-100% IOT’ if we follow the standard definition of IOT, is indeed observed.

1.2. Motion aftereffects

The MAEs measured using stationary tests (static MAE) differ in a number of respects from those measured using counterphase gratings (flicker MAE) (Ashida & Osaka, 1994, 1995; Nishida, Ashida, & Sato, 1994; Nishida & Sato, 1995; see also, Culham et al., 1998 for a review). One difference is the way they respond to higher-order motion stimuli.
Motion stimuli can be classified according to the order of moving structure of the stimulus (Cavanagh & Mather, 1989; Chubb & Sperling, 1988). First-order motion is the movement of first-order spatial structures (features defined by a single point, e.g. luminance), while second-order motion is the movement of second-order structures (features defined at two points, e.g. contrast modulation). We can also perceive the movements of some higher-than-second-order features (e.g. Victor & Conte, 1990).

After adaptation to second-order or higher-order motion, flicker MAE occurs, but static MAE does not (Ledgeway, 1994; McCarthy, 1993; Nishida & Sato, 1995). This is not simply because second-order adaptation generates weak MAEs that can be measured only by sensitive dynamic tests. The two kinds of MAEs are qualitatively different. The critical finding is that after adaptation to the same motion stimulus in which the first-order motion component and the higher-order motion component oppose each other, static MAE is induced in the direction opposite the first-order component, and flicker MAE is induced in the direction opposite the second-order component (Nishida & Sato, 1995).

IOT also indicates that the two kinds of MAE differ qualitatively. For observers having normal binocular vision, the IOT of static MAE is always partial (see Wade, Swanston, & de Weert, 1993, for a review), implying that the static MAE occurs at a relatively early site in the brain where the neurones have clear ocular dominance. The IOT of flicker MAE, in contrast, can be complete (Nishida et al., 1994).

We considered the implication of these results in relation to a model of visual motion system (Nishida, Ledgeway, & Edwards, 1997; Nishida & Sato, 1995), whose basic architecture has much in common with the models proposed by other researchers (e.g. Cavanagh & Mather, 1989; Chubb & Sperling, 1988; Clifford & Vaina, 1999; Lu & Sperling, 1995; Simoncelli & Heeger, 1998; Wilson, Ferrera, & Yo, 1992; Zhou & Baker, 1993). First-order motion signals are processed by a pathway that contains multiple-scale motion sensors, each tuned to a narrow range of spatial frequency. Second-order motion signals are processed by another pathway that consists of a non-linear demodulation process followed by motion sensing at multiple spatial scales. At the next stage, the motion signals are integrated across spatial scales and between the two pathways. There might also be a third motion pathway for feature tracking, and its output would also be fed to the integration mechanism. The first-order and second-order pathways are primarily monocular (see also Lu & Sperling, 1995), while the feature tracking pathway and the high-level integrator are completely binocular in the sense that they respond equally to input from either eye\(^1\). The ways in which the two types of MAE differ with regard to the effects of higher-order motions and the magnitude of IOT led us to conjecture that the static MAE reflects adaptation of first-order motion sensors, while the flicker MAE reflects adaptation of a high-level mechanism that integrates first- and second-order motion signals (Nishida & Sato, 1995).

More recently, however, we have revised this conjecture on the basis of new results concerning the IOT of flicker MAEs (Nishida & Ashida, 2000). We found that the transfer was complete when the duration of MAE in the central visual field was measured while observers were paying attention to the adaptation stimulus, but that the transfer was partial when the MAE nulling strength was measured, when the duration of MAE in the peripheral visual field was measured, or when the observers’ attention was distracted by a secondary task. These results indicate that flicker MAE has two components, a low-level component reflecting adaptation of partly monocular motion-detection stages, and a high-level component reflecting adaptation of a completely binocular motion-integration stage. IOT is complete when the contribution of the low-level component is negligible, but IOT is partial when the contribution of that component is significant. The effect of measurement method can be accounted for if the high-level component persists as long as, or longer than, the low-level component. Then, for the MAE duration, the low-level component is concealed by the high-level component, while for the nulling MAE strength, it is effective because this strength is measured immediately after the adaptation. The effect of eccentricity can be accounted for if the high-level mechanism primarily operates in the central visual field, whereas the low-level mechanism operates effectively over a wide area of the visual field. The effect of the secondary task can be accounted for if the attentional modulation is much stronger for the high-level mechanism than for the monocular mechanisms. Then, the attention-distracting task would reduce the binocular component of flicker MAE significantly, while affecting the monocular component only slightly, thereby changing complete transfer to partial transfer.

### 1.3. \(2f + 3f\) motion

In light of this revised view of the flicker MAE, we reconsidered the mechanisms responsible for the same adaptation stimulus being able to produce the static and flicker MAEs in opposite directions (Nishida & Sato, 1995).

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\(^1\) To account for complete IOT, these high-level mechanisms must be OR-type binocular systems rather than AND-type systems that respond only to simultaneous inputs from the two eyes (cf. van Kruysbergen & de Weert, 1994).
One of the adaptation stimuli that have such an effect is a $2f + 3f$ motion (Fig. 1a and b). It consists of two sinusoidal components that correspond to the second ($2f$) and third ($3f$) harmonics of the pattern fundamental frequency ($1f$) at which there is actually no component. This pattern is shifted by one-fourth of the cycle of the missing $1f$ component. Given that first-order motion detection is quasi-linear, the contribution of each Fourier component to the total first-order motion energy is almost independent (Adelson & Bergen, 1985; van Santen & Sperling, 1985). The $3f$ component jumps three-fourths of the cycle in the shift direction, which is equivalent to one-fourth of the cycle in the anti-shift direction, thus having a stronger motion energy in the anti-shift direction. The $2f$ component that jumps half a cycle just adds the same motion energy to both directions. It is thus expected that the first-order motion energy of the $2f + 3f$ motion is stronger in the anti-shift direction than in the shift direction. However, the contrast envelope and the other higher-order features have a spatial frequency of $1f$, and they move in the shift direction. As a result, the first-order spatial structures (luminance) and higher-order structures (contrast modulation or other salient features) are expected to move in opposite directions\(^2\). In effect, the perceived direction of this stimulus depends on the temporal condition. For short inter-jump intervals, the stimulus moves predominantly in the first-order (anti-shift) direction, while for long intervals, it moves in the second-order (shift) direction (Nishida & Sato, 1995). This cannot be a result of the change in the predominant direction of first-order motion, since the static MAE is always generated in the direction opposite to the first-order component even when the adaptation stimulus is perceived to move in the second-order direction (Nishida & Sato, 1992). See Nishida and Sato (1992, 1995) and Fleet and Langley (1994) for further discussion of this stimulus.

In general, when the observer is adapted to $2f + 3f$ motion stimuli and tested with a $3f$ counterphase grating

\(^2\) It has been suggested that the low-level second-order sensors may not detect second-order motion stimuli effectively (Ashida & Osaka, 1998; Derrington & Ukkonen, 1999; Seiffert & Cavanagh, 1998). Note that it is not critical for our argument whether the movement of the $1f$ beat pattern is detected by the second-order sensors (Nishida & Sato, 1995), by the feature tracking mechanism (e.g. Seiffert & Cavanagh, 1998), or by both, as long as the movement is detected in the final integration stage.
Fig. 2. (a) Responses of various stages of the motion processing system to an adaptation stimulus ($2f + 3f$ motion) presented to the left eye. In each block, the direction and the strength of the response to the adapting $2f + 3f$ motion are indicated by an arrow. Black arrows indicate the first-order direction, and white arrows indicate the second-order direction. (b, c) Processing stages activated by a test stimulus (counterphase grating) presented to the (b) adapted or (c) non-adapted eye. Arrows indicate the direction and strength of the MAE signals. See text for details.

(Fig. 1c and d), the direction of the flicker MAE is opposite the perceived direction of the adaptation stimulus (Nishida & Sato, 1995). For instance, the $2f + 3f$ stimulus with a 90 ms inter-jump interval was perceived to move in the second-order (shift) direction, and the MAE direction was opposite that second-order direction for the majority of observers (five of eight). This result is consistent with the notion that the flicker MAE reflects adaptation of a high-level integration mechanism (Nishida & Sato, 1995).

As described above, however, we have noticed that the flicker MAE also reflects the adaptation of low-level motion sensors (Nishida & Ashida, 2000). Adaptation of first-order sensors to the $2f + 3f$ stimulus should lead to a low-level aftereffect whose direction is opposite to that of the almost invisible first-order motion. This low-level aftereffect thus counteracts the high-level aftereffect. The finding that the direction of flicker MAE is opposite the second-order direction implies that the high-level aftereffect is stronger than the low-level aftereffect. When the low-level aftereffect overrides the high-level aftereffect, an MAE in the direction opposite the first-order component is expected, even with a flicker test. In fact, the results obtained from the three of the eight observers in the study of Nishida and Sato (1995) showed this pattern.

1.4. ‘Over-100% transfer’

If this reasoning is correct, the flicker MAE will be stronger for the non-adapted eye when subjects adapt to a $2f + 3f$ motion stimulus with a long inter-jump interval and are tested with a $3f$ counterphase grating. Fig. 2a illustrates how the $2f + 3f$ motion presented to the left eye activates each stage of motion processing. The first-order sensors, especially those tuned to the spatial frequency of $3f$, detect motion in the anti-shift direction, whereas both the second-order sensors tuned to $1f$ and the feature tracking mechanism detect motion in the shift direction. The later integration stage also detects the motion in the shift direction, as indicated by the empirical fact that the second-order direction is predominantly perceived when inter-jump intervals are long. This figure also illustrates that the low-level motion sensors are partly monocular, so these mechanisms are activated differently by the monocular input in ways that depend on their ocular preference. The feature tracking and motion integration mechanisms, in contrast, are completely binocular.

Consider next how the $3f$ counterphase test activates each stage of motion processing and gives rise to an aftereffect (Fig. 2b and c). At the partly monocular level, the luminance-modulated test stimulus effectively activates the first-order sensors, giving rise to an MAE.
in the direction opposite to the anti-shift (first-order) direction. Because the sensors are spatial-frequency-selective, the $3f$ test is the optimal stimulus revealing this adaptation effect. However, it is unlikely that the $3f$ luminance grating effectively stimulates the second-order sensors that had been adapted by the $1f$ second-order motion component, since direction-selective threshold elevation for second-order motion is selective to both stimulus order and spatial frequency (Nishida et al., 1997). In the binocular level, the test stimulus effectively activates both the feature tracking and integration mechanisms, resulting in MAE in the direction opposite to the shift (second-order) direction. Thus, the low-level monocular aftereffect and high-level binocular aftereffect oppose each other. When the test stimulus is presented to the adapted eye (monocular condition, Fig. 2b), there is a substantial low-level aftereffect that opposes the high-level aftereffect and reduces the total MAE. However, when the test stimulus is presented to the non-adapted eye (interocular condition, Fig. 2c), the low-level aftereffect is weaker, and the perceived MAE consists almost exclusively of the high-level component.

As a result, the MAE seen by the adapted eye is expected to be smaller than that seen by the non-adapted eye. The following experiments supported this prediction.

2. Method

2.1. Observers

The two authors (S.N. and H.A.) and six naïve subjects participated in the experiment. All of them had normal or corrected-to-normal vision.

2.2. Stimulus

The adaptation stimulus was a monocularly viewed $2f + 3f$ compound grating, consisting of 1.0 and 1.5 c/deg sinusoidal gratings with 30% contrast (Fig. 1a and b). The pattern was shifted by 0.5 deg every 90 ms. The test stimulus was a 1.5 c/deg sinusoidal grating with 30% contrast and was counterphase-flickering at 2.0 Hz (Fig. 1c and d). The adaptation and test stimuli subtended 3.2 deg in height and 7.5 deg in width. A red fixation cross was presented at the centre. A reference patch of a compound grating, consisting of 1.0 and 1.5 c/deg sinusoidal gratings, was presented side by side on a monitor (Chouomusen CD-B2120 or NANAO FlexScan 56TS). The monitor had a refresh rate of 100 Hz, and a spatial resolution of 32 pixel/deg. In a dimly lit room, the observer viewed the monitor with a chin rest through a mirror haploscope.

2.3. Apparatus

Two stimulus patterns for the left and right eyes were presented side by side on a monitor (Chouomusen CD-B2120 or NANAO FlexScan 56TS). The monitor was driven by a VSG 2/3 (Cambridge Research Systems) that provided 14-bit luminance resolution. The monitor had a refresh rate of 100 Hz, and a spatial resolution of 32 pixel/deg. In a dimly lit room, the observer viewed the monitor with a chin rest through a mirror haploscope.

2.4. Procedure

In each trial, the adaptation stimulus was presented for 30 s, and the test stimulus was then presented for 30 s. All observers reported verbally that the $2f + 3f$ stimulus moved in the shift (second-order) direction during the adaptation period, while some occasionally reported a brief direction reversal. We asked the six observers to report the perceived direction by pressing one of two buttons throughout the adaptation period, as in our earlier study (Nishida & Sato, 1995), and found that the probability of seeing the shift direction was, on average, 91% (S.N.: 100%; H.A.: 99.6%; K.T.: 98.9%; N.T.: 96.9%; T.T.: 77.6%; K.S.: 76.2%).

Without motion adaptation, the percept of the counterphase grating that was physically made of two oppositely drifting gratings was ambiguous, jumping leftwards, jumping rightwards, or just counterphasing without moving coherently in a direction. After motion adaptation, the probability of seeing jumps in one direction increased for a while. To measure the direction and magnitude of this flicker MAE, we asked the subjects to report the perceived direction of motion by pressing one of two buttons throughout the test period (Nishida et al., 1994). Neither button was pressed when the subject could not decide on the motion direction. As far as we know, the two directions of jumping motion were never seen transparently. It was occasionally noticed, however, that the test grating as a whole was moving very slowly in a direction that was not the same as the jumping direction of the grating. We inferred from its appearance that this slow movement was a variant of the static MAE, which is known to be dissociated from the flicker MAE after adaptation to the $2f + 3f$ motion (Nishida & Sato, 1995). We told the observers to judge the direction of grating jump without taking into account the direction of this slow movement.
In each block, eight trials were conducted in a random order: two monocular conditions (left and right eyes) and two interocular transfer conditions (left to right, and right to left) × two directions of adaptation. The inter-trial interval was at least 1 min. At least two blocks were conducted for each stimulus condition.

3. Results

Fig. 3 shows the time course of the button-press probability for the first-order and second-order directions during the 30 s test period. The first-order and second-order directions are, respectively, the directions opposite the anti-shift (first-order) and the shift (second-order) directions of the adaptation stimulus. A data point indicates the probability of button press for each direction at a certain time. Solid lines: monocular condition. Dashed lines: interocular condition.
(first-order) direction of the adaptation stimulus, and the second-order direction is the direction opposite to the shift (second-order) direction of the adaptation stimulus. A value of 1.0 indicates that at that moment of the test, the button for that direction was pressed in all the trials. The time course averaged over observers indicates that the response probability for the second-order direction increased immediately after the adaptation, then decayed in about 20 s. After that, the response probability for the second-order direction was nearly the same as that for the first-order direction. The response probability for the first-order direction was nearly constant throughout the test period except for a slight increase during the first few seconds of the monocular condition. When the button-press probability was compared between the two ocular conditions, the second-order response was much stronger for the interocular condition, and the first-order response was slightly stronger for the monocular condition. These tendencies are evident in most of the individual results.

The button press was not direction-selective during the latter half of the test period, and this can be ascribed to the inherent direction ambiguity of the counterphase grating. For some observers, the counterphase grating never stood still, but fluctuated between one direction of motion and the other. The individual results indicate that observers T.T., I.M., and K.S. had this type of percept.

To eliminate the effects of direction ambiguity of the test stimulus on the estimated strength of the MAE, we subtracted the total duration of response for the first-order direction from the total duration of the response for the second-order direction. As in our previous studies, we defined this difference as the MAE duration of each trial (Nishida & Sato, 1995).

Fig. 4 shows the results. For all observers, the MAE duration defined above was larger for the interocular condition than for the monocular condition. A paired t-test showed that the difference was statistically significant \[ t(7) = 6.55, \ p < 0.01 \]. All the observers except one (K.S.) perceived the MAE in the second-order direction under both the monocular and interocular conditions. For these seven observers, the MAE duration was longer for the interocular condition than for the monocular condition ('over-100% IOT'). Observer K.S. perceived the MAE in the first-order direction under the monocular condition [as Nishida and Sato (1995) found for a few observers under a binocular viewing condition] but in the second-order direction under the interocular condition. This direction change resulted in a negative value for IOT. This ‘reversed IOT’ provides further support of our hypothesis (see Section 4).

For three observers, we also measured the MAE magnitude by using a nulling method. The MAE seen in a counterphase grating was nulled by increasing the contrast of the drifting component whose direction was opposite to that of the MAE and decreasing the contrast of the other drifting component (Ledgeway, 1994; Nishida & Ashida, 2000). Each session consisted of a 30 s initial adaptation followed by repetitive presentations of a 1 s test and a 10 s top-up adaptation. In each test, the observer was required to judge the direction of the test stimulus. According to the response, a staircase program adaptively changed the contrast ratio of the test stimulus while keeping the total contrast 30%. The final step size was \( \times 1.04 \), and the nulling MAE strength was estimated by computing the geometric mean of the last four of the six reversal points. Two staircases, one for the monocular condition, and the other for the interocular condition, were randomly mixed within each session.

Fig. 5 shows the results of the nulling experiment. For all observers, the MAE (in the second-order direction opposite the shift direction of the adaptation stimulus) was stronger for the interocular condition than for the monocular condition. For S.N., who showed a

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**Fig. 4**. (Top) MAE duration (the button press duration for the second-order direction minus that for the first-order direction) obtained under monocular (filled circles) and interocular (open square) conditions for eight observers. Each data point was the average of eight to 24 measurements. The average for the results of all observers is shown on the right. The error bars show \( \pm 1 \) standard error across trials. (Bottom) Interocular transfer calculated from the ratio in the MAE duration.
significant monocular MAE, the IOT was over 100%. The other two observers did not show any measurable monocular MAE. These results confirm the tendency found with the MAE duration.

4. Discussion

The IOT has been regarded as a direct reflection of the (averaged) binocularity of the adapted neurones (e.g. Moulden, 1980). For instance, IOTs of 0 and 100% are respectively interpreted as indicating that the adapted neurones are completely monocular and completely binocular. The present finding of 'over-100% IOT', however, cannot be interpreted in the same way, because it is quite unlikely that the same neurones that respond more strongly to the left-eye input during the adaptation phase then respond more strongly to the right-eye input during the test phase.

There are two basic assumptions behind our interpretation of the 'over-100% IOT'. One is that the flicker MAE reflects adaptation of multiple levels of motion processing, and the other is that the 2f + 3f motion should be smaller for the 1f test stimulus than for the 3f test stimulus. Since the CM stimulus is primarily detected by the second-order sensors and/or the feature tracking mechanism, the influence of the aftereffects of first-order sensors should be limited in this test. The results for three observers indicated that the averaged IOT was 125.0% for the 1f stimulus and 99.7% for the CM stimulus (Fig. 6), while the IOT for the same three observers was 232.4% for the 3f test stimulus. This corroborates our interpretation that the 'over-100% IOT' resulted from incompatible first-order MAE signals.

5. Conclusion

The present results provide strong support for the idea that the flicker MAE reflects adaptation of both partly monocular motion sensors and completely binocular high-level mechanisms (Nishida & Ashida, 2000). The classical MAE seen in static stimuli, in contrast, primarily reflects adaptation of the monocular first-order motion sensors (Derrington & Badcock, 1985; Nishida & Sato, 1992).

In addition, the present results indicate that, for the flicker MAE and, presumably, for other aftereffects in which multiple processing levels take part, the IOT may not reveal either the extent of the binocularity of the

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Footnote:

3 The effects of the low-level and high-level MAEs are integrated when the observer perceives the MAE. The strength of each component can be inferred but is hard to measure directly.
adapted neurones or the ratio of monocular and binocular neurones. We do not, however, think that this is a limitation of using the IOT as a psychophysical analysing tool. We demonstrated that the IOT could reveal interactions between the monocular and binocular neurones when the adaptation stimulus activated low-level mechanism and high-level mechanisms differently. Processing streams in the visual system generally comprise early monocular stages and late binocular stages. The present findings therefore imply that the IOT can serve as a powerful tool for the analysis of the hierarchical structures of the visual system.

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